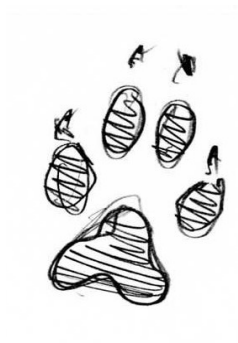


Diet composition of wolves (*Canis lupus*) on the Scandinavian Peninsula determined by scat analysis



Sabrina Müller
Sweden, July 2006



If you talk to the animals they will talk with you and you will know each other.

If you do not talk to them you will not know them,

and what you do not know you will fear.

What one fears one destroys.

Chief Dan George (1899-1981)

Preface

This paper is the English summarization of the thesis '**Saisonale Variation im Nahrungsspektrum des Wolfes in Skandinavien. Oder: Was ist wirklich drin im Wolfskot?**' (30 ECTS) submitted to the School of Forest Science and Resource Management, Technical University of Munich (Germany) in partial fulfilment of the requirements for the diploma degree in Forest Science.

Due to the collaborative nature of this work, in particular the scat collection and scat analysis, I have used the term 'we' instead of 'I' in this paper. I did all of the data analysis and writing and take full responsibility for any errors contained in this paper.

Abstract

Seasonal diet composition of wolves (*Canis lupus*) was studied on the Scandinavian Peninsula by analysing 2063 wolf scats. The scats were collected during summer and winter of the years 1992 to 2005. A reduced data set ($n = 1594$) was used to describe the seasonal feeding pattern of 10 Scandinavian wolf territories in detail.

Although the diverse diet confirmed the wolves' nature as opportunistic predators, moose was the most common item in percent frequency of occurrence in summer (53.7%) and winter (68.5%), representing 88.9% and 95.7% of the mammalian biomass consumed in summer and winter, respectively. Other prey species like roe deer, beaver, badger, hare, small rodents and birds were regularly used during the year, with emphasis on the summer months. Within the studied period domestic animals only contributed marginally to the diet of wolves. Nevertheless, domestic animals were more frequently identified in summer than in winter with 1.3% and 0.1%, respectively.

Moose was the preferred prey in summer (Manly's Alpha = 0.68) and winter (Manly's Alpha = 0.54). Food niche breadth was broader in summer ($B_A = 0.11$) than in winter ($B_A = 0.04$). This may be explained by the higher availability of smaller prey species like beaver, hare, small rodents and birds during the summer period.

The diet pattern described for the sub sample of 10 Scandinavian territories did not differ from the pattern shown by the remaining sample. The interterritorial comparison showed a high similarity among the seasons as well. Only two territories located in areas with comparably high roe deer densities differed from the others with respect to moose : roe deer ratio determined by the analysis of summer and winter scats.

In comparison to previous studies on the foraging ecology of wolves in Scandinavia, moose appeared to be even more frequently consumed, also in areas with high roe deer densities.

1 Introduction

The conflict between humans and wolves has always been grounded on the wolf's role as predator on wild game and domestic animals. Therefore a detailed knowledge on the seasonal diet composition is fundamental for a better understanding of wolves as predators and for the management of prey as well as predator populations. Since the pioneering work of Murie in the 1940s on foraging behaviour of wolves in Denali National Park (MECH & BOITANI 2003), innumerable studies have been carried out world-wide to investigate predation ecology.

Although the diet of wolves appears to be diverse and opportunistic (SALVADOR & ABAD 1987, CUESTA et al. 1991), it is evident that wild ungulates constitute the main prey type (i.a. BALLARD et al. 1987, KOHIRA & REXSTAD 1997, JĘDRZEJEWSKI et al. 2000). Depending on the local availability, wolves mainly prey on middle-sized wild ungulates such as white-tailed deer (*Odocoileus virginianus*), red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) (i.a. SCOTT & SHACKLETON 1980, BALLARD et al. 1987, POTVIN et al. 1988, SIDOROVICH et al. 2003, NOWAK et al. 2005). In boreal conifer forest landscapes moose (*Alces alces*) is an important prey species for wolves as well (i.a. THEBERGE & COTTRELL 1977, PETERSON et al. 1984, KOJOLA et al. 2004).

In areas where wolves live in close neighbourhood to humans, anthropogenic food sources such as garbage or domestic animals are also used by the large carnivores (FRITTS & MECH 1981, SALVADOR & ABAD 1987, SIDOROVICH et al. 2003, THEUERKAUF 2003, CHAVEZ & GESE 2005, GAZZOLA et al. 2005, NOWAK et al. 2005). Predation on domestic animals causes the biggest problems with humans. This is also evident on the Scandinavian Peninsula where 400 to 600 sheep are killed by wolves annually. (SWEDISH WILDLIFE DAMAGE CENTRE 2004). However, GAZZOLA et al. (2005) and ANSORGE et al. (2006) argue that wolves prefer wild ungulates to domestic ungulates if wild prey is available in adequate numbers.

On the Scandinavian Peninsula numerous studies have been carried out on predation ecology of wolves (PALM 2001, WIKENROS 2001, JOHANSSON 2004, PEDERSEN et al. 2005, SAND et al. 2005, SAND et al. 2006, SAND et al. in press), whereas most of the studies have been performed during the winter months. With the help of carcass search it was possible to describe that moose is the predominant prey for wolves in Scandinavia, followed by roe deer.

The only studies on wolf diet in Scandinavia based on scat analyses have been performed by OLSSON et al. (1997) and ØSTRENG (2000). The data published by ØSTRENG (2000) was also collected within a SKANDULV research project. Therefore the dataset was included into our study to provide more detailed information on the diet of wolves in Norwegian territories.

The aim of this study was to describe the diet composition of wolves in Scandinavia in summer and winter on an area-wide scale. We chose scat analysis as a method to identify prey items consumed.

In contrast to carcass search we were able to cover both a larger study area and a larger study period. It was possible to identify prey species that are usually consumed completely and therefore not detectable by carcass search. Since we were also interested in seasonal utilization of plant material and small rodents, scat analysis was a suitable research method. To describe the seasonal foraging pattern of wolves on the Scandinavian Peninsula we were interested into the following questions:

- Is there a difference in diet composition between summer and winter?
- What is the preferred prey for wolves?
- How important is alternative and smaller prey such as beaver, badger, hare, birds and small rodents in both seasons?
- Is there a difference in Food Niche Breadth in summer and winter and is the Food Niche Breadth influenced by prey densities?

We also compared the conventional methods to calculate biomass consumed to show differences between the methods and to look for criteria how to choose an adequate method for a given study.

2 Study area

The study area is located in the south-central part of the Scandinavian Peninsula (Sweden and Norway) between lat 59°N and 61°N, long 11°W and 16°W (Figure 1). The area is mostly covered with boreal forest dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), intermixed with deciduous trees such as birch (*Betula verrucosa*, *B. pubescens*), aspen (*Populus tremula*), and alder (*Alnus incana*, *A. glutinosa*). Agricultural land prevails in the southern part of the study area. Forestry practices on the Scandinavian Peninsula result in small scale mosaics of forests of different densities and age classes as well as clearings with pioneer vegetation including birch (*Betula spec.*) and dwarf shrubs such as blueberry (*Vaccinium spec.*) and heather (*Calluna vulgaris*).

The area is hilly with altitude ranging from 50m to 1000m a.s.l.. The climate is characterized as continental with mean temperature of 15°C in July and -7°C in January. Normally the ground is covered with snow from December till March, and mean snow depth is between 20cm and 50cm.

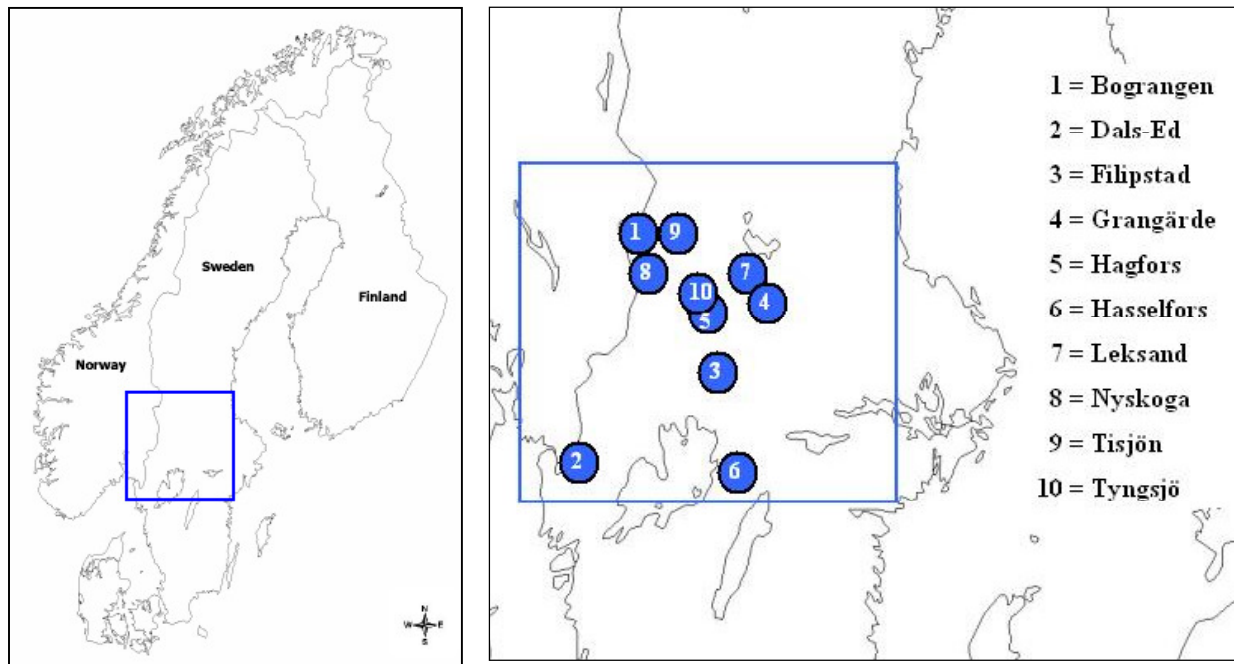


Figure 1: Map of the study area with the locations of the 10 territories that were analysed in detail.

Population density on the Scandinavian Peninsula varies a lot, whereas the average density within the study area is less than 1 person/km² (WABAKKEN et al. 2001).

Potential prey species for wolves on the Scandinavian Peninsula include moose (*Alces alces*), roe deer (*Capreolus capreolus*), beaver (*Castor fiber*), badger (*Meles meles*), hare (*Lepus europaeus*, *L. timidus*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*) as well as small rodents (*Apodemus spec.*, *Microtus spec.*, *Sciurus spec.* etc.) (OLSSON et al. 1997, JOHANSSON 2004). In Norway the diet can be supplemented regionally with red deer (*Cervus elaphus*) and wild reindeer (*Rangifer tarandus*) (WABAKKEN et al. 2001). The main prey for wolves in Scandinavia is moose and roe deer (SAND et al. in press). The population densities of the two cervid species have been estimated by pellet group counts in most of the wolf territories and resulted in an average of 0,6 - 2,5 moose/km² and 0,1 - 3,5 roe deer/km² (SAND 2005). Moose is available on the entire Scandinavian Peninsula. Their number is estimated with more than 300.000 individuals. Roe deer numbers more than 1 million individuals and is also abundant in Norway and Sweden, except for the northern part of both countries (LIBERG 2006).

Approximately 400.000 domestic reindeer occur in the reindeer husbandry area, which makes up the northern third of the Scandinavian Peninsula. During summer months about 2.1 million free-grazing sheep are found over large parts of Norway (KJØRSTAD 2005). In Sweden sheep mostly graze on fenced pastures.

In addition to wolves, other carnivores in the study area include lynx (*Lynx lynx*), brown bear (*Ursus arctos*), and red fox (*Vulpes vulpes*).

3 Material and Methods

Scats were randomly collected on travel routes, carcass sites, den sites, and rendezvous sites from 1991 to 2006. The scats were stored in labelled plastic bags indicating location and date, and were frozen until further analyses at Grimsö Research Station. Prior to the analyses the scats were dried for 48h at 90°C ($\pm 5^\circ\text{C}$). After the drying process, dry weight of the scats was taken (0,01g precision).

Altogether 2799 scats were collected, whereof 2063 scats were chosen for the diet analysis. For seasonal comparisons among territories at least 15-20 scats per territory and season were required (SAND unpublished data, ELMHAGEN et al. 2002). As soon as these criterions were fulfilled, the scats were chosen randomly. The total sample was subdivided into 2 sub samples: 1 summer (May 01–September 30; n = 794) and 1 winter sample (October 01 – April 30; n = 1238). 31 blank dated scats needed to be excluded from the seasonal comparison, but were integrated into the total representation. The procedure to analyse the scat contents followed SPAULDING et al. (1997). Each scat was broken apart by hand and the single prey items were sorted. If there was more than one prey item found in the scat, we assumed that the macro and micro components originated from the found items in the same proportion (CIUCCI et al. 1996). We identified the macro components in the scats (e.g. bird remains, hairs, hooves, teeth) with the help of reference manuals (MOORE et al. 1974, DEBROT et al. 1982, TEERINK 1991) and a reference collection developed at Grimsö Research Station. The hairs were first examined visually concerning colour pattern, length, thickness, and thereafter identified microscopically by medullary pattern and cuticular scale (TEERINK 1991). With the help of a reference grid we visually estimated the relative volumetric proportion for each prey item identified in a scat (REYNOLDS & AEBISCHER 1991).

The prey items identified in the scats were pooled into the following categories:

moose	beaver	domestic animals
roe deer	hare	insects
badger	small rodents	berries
fox	forest birds	plant material
wolf	birds	others

The category ‘others’ represents non food items like stones, leather, and plastic. If it was not possible to identify a prey item correctly, we rather grouped those items into the following categories than identifying them wrong: undetermined cervids (represent moose and roe deer), undetermined carnivores, undetermined mammals (REYNOLDS & AEBISCHER 1991).

The distinction into juvenile and adult cervids was carried out due to the characteristic hair pattern of young animals. We were not able to distinguish consistently between juvenile and adult animals since the typical juvenile hair pattern is only visible from birth to the first autumn molt in August / September. Because of that it is not possible to distinguish between juveniles and adults during the

winter season by examining hairs (JAMES 1983, PETERSON et al. 1984, POTVIN et al. 1988, CIUCCI et al. 1996). To make a reasonable differentiation into juveniles and adults we applied the age class distribution for consumed cervids described by JOHANSSON (2004), PEDERSEN et al. (2005), SAND (unpublished data) for the present diet analysis:

moose	=>	calves : yearlings : adults	=>	80:10:10
roe deer	=>	fawns : adults	=>	50:50

Following CIUCCI et al. (1996) and ANSORGE et al. (2006) non food items such as conifer needles, leaves, twigs, and non-organic material (e.g. pebble stones) were not included into the diet analysis. As recommended by DALERUM & ANGERBJÖRN (2000) graminoides that made up less than 5% of the dry volume of the scat were excluded from further analyses as well. We assumed that in these small proportions, the grasses were consumed accidentally and did not contribute to the wolves' diet (MECH 1966, CHESEMORE 1968, GOSZCZYNSKI 1974, GARROTT et al. 1983, ELMHAGEN et al. 2000).

Single wolf hairs were found year round, occurring in 14,4% of the scat sample. Those hairs were not integrated into the analyses, because we regarded them as accidentally ingested as a result of grooming behaviour (JAMES 1983).

As recommended by ZABALA & ZUBEROGOITIA (2003) and CIUCCI et al. (1996) we combined frequency based and volumetric methods when analysing the diet composition. The frequency based methods show how often an item was eaten, whereas the volumetric methods demonstrate the importance of an item in the diet and therefore are supposed to be biologically more meaningful. Percent frequency of occurrence/scats (%FO/S) was calculated for comparison with published literature. However, further statistical analyses were performed with percent frequency of occurrence/item (%FO/I). %FO/S is the frequency by which a food item occurs in the scat sample, whereas %FO/I is known as the item's frequency among all identified food items. We also calculated the Whole Scat Equivalent (WSE), which summarizes the relative dry volume for a given food item within the scat sample (ANGERBJÖRN et al. 1999). For instance if there is 80% moose and 20% beaver in one scat, and 20% moose and 80% beaver in a second scat, this was regarded as one scat unit with 100% moose and another scat unit with 100% beaver. The total number of scats stays the same. Additionally the biomass of prey consumed was calculated using the Weaver equation (WEAVER 1993):

$$y = 0,439 + 0,008x \quad \text{where } x = \text{assumed live weight of prey species} \quad (1)$$

y = estimated biomass consumed per scat

We calculated the mean prey weight for moose and roe deer in both seasons by considering the above mentioned age class distribution for consumed cervids, and using live weights derived from JOHANSSON (2004) and SAND (unpublished data). The average weight for the remaining mammals was obtained from JOHANSSON (2004) and OLSSON et al. (1997). Table 1 describes the calculation of biomass consumed using the Weaver equation as well as the calculation of the mean prey weight. The biomass equations have been developed for mammalian prey which means that non-mammalian prey had to be excluded from biomass estimations.

Table 1: Estimate of biomass consumed in kg and percent calculated using the Weaver equation (WEAVER 1993).

Summer:

mammalian prey	assumed average live weight of prey species (kg)	Whole Scat Equivalentents	biomass consumed per scat (kg)	biomass consumed (kg)	biomass consumed (%)
	[A]	[B]	[C]	[D]	[E]
Moose	116,7	494,8	1,4	679,2	88,8
Roe deer	17,1	70,3	0,6	40,5	5,3
Badger	10,5	16,9	0,5	8,8	1,2
Fox	6,5	0,0	0,5	0,0	0,0
Wolf	44,0	2,2	0,8	1,8	0,2
Beaver	18,0	30,5	0,6	17,8	2,3
Hare	3,5	10,5	0,5	4,9	0,6
Small rodents	0,025	12,5	0,4	5,5	0,7
Domestic animals	25,0	9,7	0,6	6,2	0,8

Winter:

mammalian prey	assumed average live weight of prey species (kg)	Whole Scat Equivalentents	biomass consumed per scat (kg)	biomass consumed (kg)	biomass consumed (%)
	[A]	[B]	[C]	[D]	[E]
Moose	192,0	907,8	2,0	1792,9	95,7
Roe deer	20,0	92,4	0,6	55,3	3,0
Badger	10,5	3,3	0,5	1,7	0,1
Fox	6,5	0,0	0,5	0,0	0,0
Wolf	44,0	1,5	0,8	1,2	0,1
Beaver	18,0	19,9	0,6	11,6	0,6
Hare	3,5	10,8	0,5	5,0	0,3
Small rodents	0,025	9,7	0,4	4,3	0,2
Domestic animals	25,0	1,0	0,6	0,6	0,0

Table 1: (continued) Estimate of biomass consumed in kg and percent calculated using the Weaver equation (WEAVER 1993).

- [A] Moose** (summer): average weight calculated as follows: $(0,8*78,4 \text{ kg})+(0,1*220 \text{ kg})+(0,1*320 \text{ kg})$
Moose (winter): average weight calculated as follows: $(0,8*160 \text{ kg})+(0,1*290 \text{ kg})+(0,1*350 \text{ kg})$
 resulting from calf:yearling:adult = 80:10:10 (derived from SAND unpubl. data, PEDERSEN et al. 2005);
 average weights for certain age groups derived from JOHANSSON (2004) and SAND (unpubl. Data);
- Roe deer** (summer): $(0,5*9,3 \text{ kg})+(0,5*25 \text{ kg})$
 resulting from Juvenile:Adult = 1:1 (JOHANSSON 2004);
 average weights for certain age groups derived from JOHANSSON (2004) and SAND (unpubl. Data);
Roe deer (winter): 20 kg; average weight for all age groups (SAND unpubl. data)
- Badger, Beaver, Hare** (JOHANSSON 2004)
Wolf (SAND 2005)
Small rodents (OLSSON et al. 1997)
Domestic animals (derived from OLSSON et al. 1997)
- [B]** WSE
[C] calculated using the Weaver equation (WEAVER 1993): $y = 0,439 + 0,008x$
 x = assumed live weight of prey species (see [A]);
 y = estimated biomass consumed per scat (kg);
[D] B * C
[E] D / Σ D

To compare the conventional methods for biomass calculations, we also applied the equations developed by FLOYD et al. (1978) (2) and RÜHE (unpublished, derived from table 1 in RÜHE et al. 2003) (3):

$$y = 0,383 + 0,02 \quad \text{(Floyd equation)} \quad (2)$$

$$y = 0,0731 + 0,00406 \quad \text{(Rühe equation)} \quad (3)$$

To investigate if wolves in Scandinavia prefer one of the two cervid species, Manly's Alpha preference index was calculated:

$$\alpha_i = \frac{r_i}{n_i} \frac{1}{\sum (r_j / n_j)} \quad \text{where} \quad \alpha_i = \text{Manly's Alpha (preference index) for prey type } i \quad (4)$$

$r_i, r_j =$ Proportion of prey type i or j in the diet
 $n_i, n_j =$ Proportion of prey type i or j in the environment

Selective feeding does not occur, if $\alpha_i = 1/m$ (m = total number of prey types). Prey species i is preferred if α_i is greater than $1/m$, whereas negative selection is found if α_i is less than $1/m$.

Levin's Food Niche Breadth (FNB) was used to measure specialization quantitatively for the diet composition of wolves on the Scandinavian Peninsula:

$$B = \frac{1}{\sum p_j^2} \quad \text{where } B = \text{Levin's Food Niche Breadth} \quad (5)$$

$p_j =$ Proportion of fractions of items in the diet that are
of food category j

Levin's Food Niche Breadth can be standardized and expressed in a scale from 0 to 1 with the help of equation (6), where 0 represents high specialisation and 1 stands for equal use of all prey items.

$$B_A = \frac{B-1}{n-1} \quad \text{where } B_A = \text{Levin's standardized Food Niche Breadth} \quad (6)$$

$B =$ Levin's Food Niche Breadth
 $n =$ Number of possible resource states

Statistical analyses

The data was analysed using SPSS version 13.0 and 14.0 as well as StatView. We compared diet composition among the two seasons based on absolute frequency of occurrence with which individual prey items occurred in the sample. The analyses were conducted by using 2x2 contingency table analysis at a significance level of $p = 0.05$. We used linear regression analysis to investigate the relationship between population densities and FNB. Pellet group counts to quantify population densities were carried out in springtime, hence we assumed that the densities were on an equal level in summer and winter. To compare FNB between summer and winter, data pairs consisting of different territories were analysed using Wilcoxon signed ranks test.

4 Results

Diet composition of wolves on the Scandinavian Peninsula

A total of 2063 wolf scats was analysed, whereas 794 scats were collected in summer and 1238 in winter. The amount of food items identified in the scats ranged between 0 and 4 during both seasons (Figure 2).

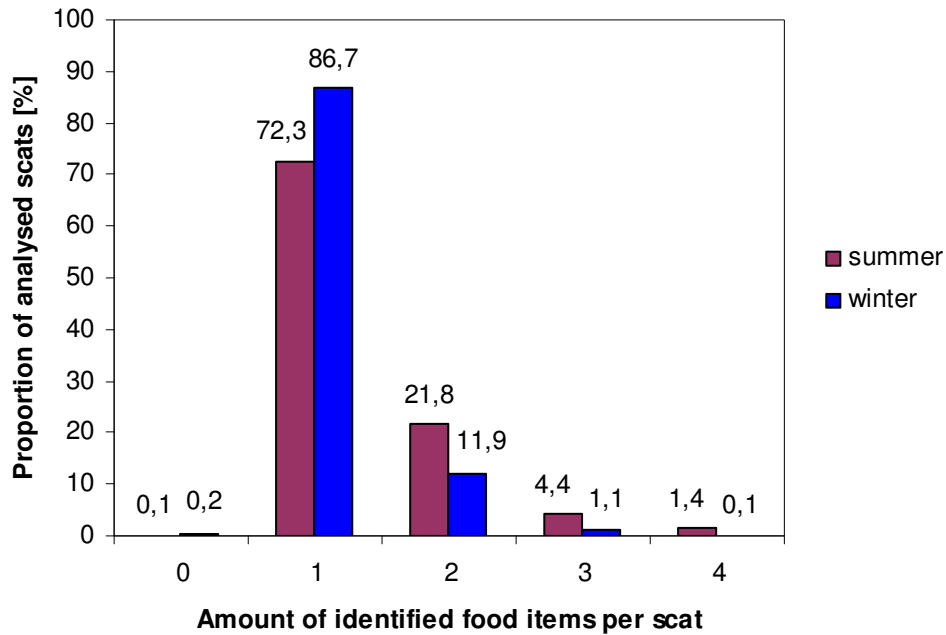


Figure 2: Amount of food items per scat in summer and winter.

Moose was the predominant prey species for wolves in Scandinavia in summer and winter making up 53,7% FO/I and 65,5% FO/I, respectively (Table 2). Moose consumption appeared to be significantly higher in winter than in summer ($\chi^2 = 77,182$; $p < 0,0001$). Consequently alternative prey items, in particular smaller prey species, made up a larger proportion of the summer diet. In general smaller prey species such as badger, beaver, hare, small rodents and birds only contributed marginally to the diet of wolves. The second important cervid species in Scandinavia, roe deer, only constituted 7,8% FO/I in summer and 7,1% FO/I in winter. Remains of domestic animals were only detected in 15 scats, with a higher proportion in summer than in winter.

Table 2: Seasonal occurrence of food items detected in 2063 wolf scats collected in Scandinavia during summer and winter. Results are also presented for the whole year.

Prey item	Summer (May - September)			Winter (October - April)			All seasons combined		
	n	% FO/S	% FO/I	n	% FO/S	% FO/I	n	% FO/S	% FO/I
<i>Alces alces</i> (moose)	574	72,3	53,7	968	78,2	68,5	1562	75,7	62,0
<i>Capreolus capreolus</i> (roe deer)	83	10,5	7,8	100	8,1	7,1	185	9,0	7,3
<i>Cervidae</i> (undetermined)	94	11,8	8,8	143	11,6	10,1	244	11,8	9,7
<i>Meles meles</i> (badger)	28	3,5	2,6	5	0,4	0,4	33	1,6	1,3
<i>Vulpes vulpes</i> (fox)	0	0,0	0,0	0	0,0	0,0	1	0,0	0,0
<i>Canis lupus</i> (wolf)	4	0,5	0,4	2	0,2	0,1	6	0,3	0,2
<i>Carnivora</i> (undetermined)	6	0,8	0,6	8	0,6	0,6	14	0,7	0,6
<i>Castor fiber</i> (beaver)	40	5,0	3,7	27	2,2	1,9	70	3,4	2,8
<i>Lepus spec.</i> (hare)	19	2,4	1,8	19	1,5	1,3	39	1,9	1,5
<i>Rodentia, Insectivora</i>	36	4,5	3,4	31	2,5	2,2	67	3,2	2,7
<i>Mammalia</i> (undetermined)	1	0,1	0,1	2	0,2	0,1	3	0,1	0,1
Forest birds	9	1,1	0,8	17	1,4	1,2	26	1,3	1,0
<i>Aves</i> (birds)	29	3,7	2,7	29	2,3	2,1	58	2,8	2,3
Domestic animals	14	1,8	1,3	1	0,1	0,1	15	0,7	0,6
Insects	39	4,9	3,6	6	0,5	0,4	45	2,2	1,8
Berries	31	3,9	2,9	17	1,4	1,2	48	2,3	1,9
Plant material (grams)	62	7,8	5,8	38	3,1	2,7	104	5,0	4,1
Total (n, %)	1069	135	100	1413	114	100	2520	122	100
Total number of scats		794			1238			2063	

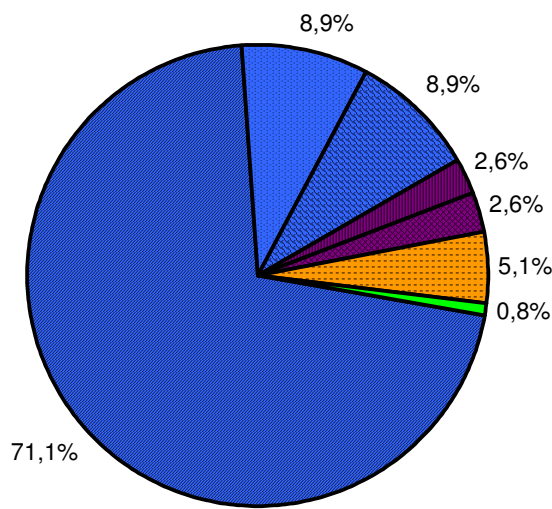
The %WSE index for big and medium-sized mammals confirmed the results obtained from %FO/I calculations (Table 3). However the WSEs showed that smaller prey items such as small rodents, birds, insects, berries and grams were less important than supposed by interpreting the %FO/I index. Those items may occur in many scats but contribute only marginally to the wolves' diet.

Table 3: The seasonal diet of wolves in Scandinavia shown both as whole scat equivalents (WSE) and %WSE. The category 'Non Food Items' includes stones, branches, leaves and single wolf hairs that cannot be regarded as consumed food.

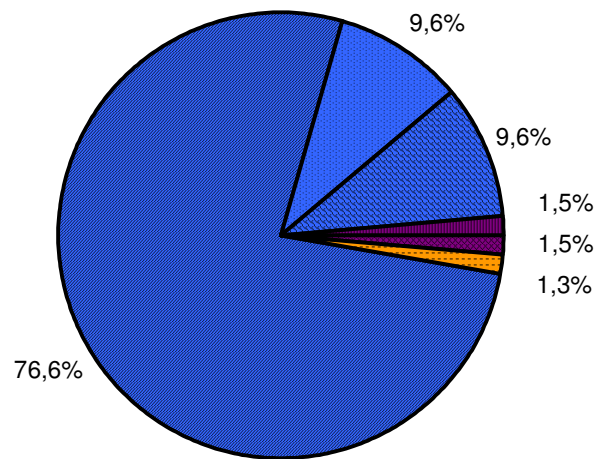
Prey item	WSE		WSE		WSE	
	Summer	Summer	Winter	Winter	All seasons combined	All seasons combined
	n	%WSE	n	%WSE	n	%WSE
<i>Alces alces</i> (moose)	494,8	62,3	907,8	73,3	1421,7	68,9
<i>Capreolus capreolus</i> (roe deer)	70,3	8,9	92,4	7,5	164,4	8,0
<i>Cervidae</i> (undetermined)	72,6	9,1	122,8	9,9	202,1	9,8
<i>Meles meles</i> (badger)	16,9	2,1	3,3	0,3	20,2	1,0
<i>Vulpes vulpes</i> (fox)	0,0	0,0	0,0	0,0	0,0	0,0
<i>Canis lupus</i> (wolf)	2,2	0,3	1,5	0,1	3,7	0,2
<i>Carnivora</i> (undetermined)	4,9	0,6	4,5	0,4	9,4	0,5
<i>Castor fiber</i> (beaver)	30,5	3,8	19,9	1,6	53,0	2,6
<i>Lepus spec.</i> (hare)	10,5	1,3	10,8	0,9	21,3	1,0
<i>Rodentia, Insectivora</i>	12,5	1,6	9,7	0,8	22,2	1,1
<i>Mammalia</i> (undetermined)	0,5	0,1	0,8	0,1	1,3	0,1
Forest birds	2,2	0,3	6,6	0,5	8,8	0,4
<i>Aves</i> (birds)	4,1	0,5	2,7	0,2	6,7	0,3
Domestic animals	9,7	1,2	1,0	0,1	10,7	0,5
Insects	1,3	0,2	0,1	0,0	1,3	0,1
Berries	4,4	0,6	2,3	0,2	6,7	0,3
Plant material (grams)	21,4	2,7	17,2	1,4	39,4	1,9
Non Food Items	35,4	4,5	34,7	2,8	70,1	3,4
Total (n, %)	794	100	1238	100	2063	100

Biomass estimates proofed the dominance of moose as prey (Figure 3). In winter moose made up a higher proportion of mammalian biomass consumed than in summer with 95,7%Bio and 88,8%Bio, respectively. Consequently smaller prey was of higher importance in summer with 5,1%Bio than in winter with 1,3%Bio. Consumption of roe deer played a minor part in both seasons (summer = 5,2%Bio ; winter = 3,0%), whereas the proportion even declined in winter in favour of moose biomass consumed.

Summer:



Winter:



- Moose (calf)
- Moose (adult)
- Roe deer (adult + yearling)
- Domestic animals
- Moose (yearling)
- Roe deer (fawn)
- smaller prey

Figure 3: Percent biomass consumed in summer and winter calculated using the Weaver equation (WEAVER 1993).

All three biomass calculations showed the same trend with moose making up the largest proportion of whole biomass consumed, followed by roe deer and beaver in both seasons (Table 4). Only the Weaver equation showed a slight deviation from the results given by the Ruhe and Floyd equations. Particularly the proportion of moose biomass consumed was smaller when using the Weaver equation. Smaller prey species such as beaver, badger, hare and small rodents were of slightly higher importance in comparison to the results of the Ruhe and Floyd calculations. However, the values for biomass consumed derived from the Ruhe and Floyd equations resembled strongly.

Table 4: Biomass consumed (kg, %) in summer and winter calculated using 3 different equations.

Summer:

mammalian prey	assumed live weight of prey species [kg]	Floyd equation		Weaver equation		Rühe equation	
		biomass consumed [kg] ^a	biomass consumed [%]	biomass consumed [kg] ^b	biomass consumed [%]	biomass consumed [kg] ^c	biomass consumed [%]
Moose	116,7	1344,4	92,8	679,2	88,8	270,6	93,0
Roe deer	17,1	51,0	3,5	40,5	5,3	10,0	3,4
Badger	10,5	10,0	0,7	8,8	1,2	2,0	0,7
Fox	6,5	0,0	0,0	0,0	0,0	0,0	0,0
Wolf	44,0	2,8	0,2	1,8	0,2	0,6	0,2
Beaver	18,0	22,7	1,6	17,8	2,3	4,5	1,5
Hare	3,5	4,7	0,3	4,9	0,6	0,9	0,3
Small rodents	0,025	4,8	0,3	5,5	0,7	0,9	0,3
Domestic animals	25,0	8,5	0,6	6,2	0,8	1,7	0,6

Winter:

mammalian prey	assumed live weight of prey species [kg]	Floyd equation		Weaver equation		Rühe equation	
		biomass consumed [kg] ^a	biomass consumed [%]	biomass consumed [kg] ^b	biomass consumed [%]	biomass consumed [kg] ^c	biomass consumed [%]
Moose	192,0	3833,6	97,4	1792,9	95,7	774,0	97,5
Roe deer	20,0	72,3	1,8	55,3	3,0	14,2	1,8
Badger	10,5	2,0	0,0	1,7	0,1	0,4	0,0
Fox	6,5	0,0	0,0	0,0	0,0	0,0	0,0
Wolf	44,0	1,9	0,0	1,2	0,1	0,4	0,0
Beaver	18,0	14,8	0,4	11,6	0,6	2,9	0,4
Hare	3,5	4,9	0,1	5,0	0,3	0,9	0,1
Small rodents	0,025	3,7	0,1	4,3	0,2	0,7	0,1
Domestic animals	25,0	0,9	0,0	0,6	0,0	0,2	0,0

The calculation of Manly's Alpha preference index showed that moose was selected positively in summer and winter (Figure 4). Consequently roe deer was avoided as prey in both seasons although the trend appeared to be stronger in summer than in winter.

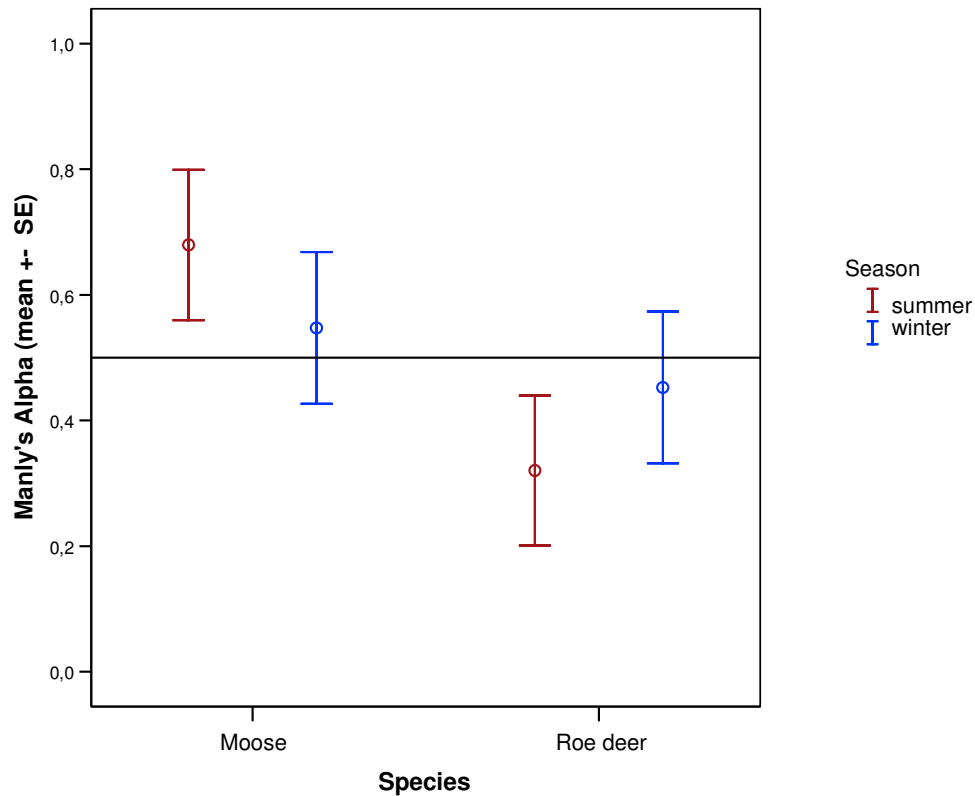
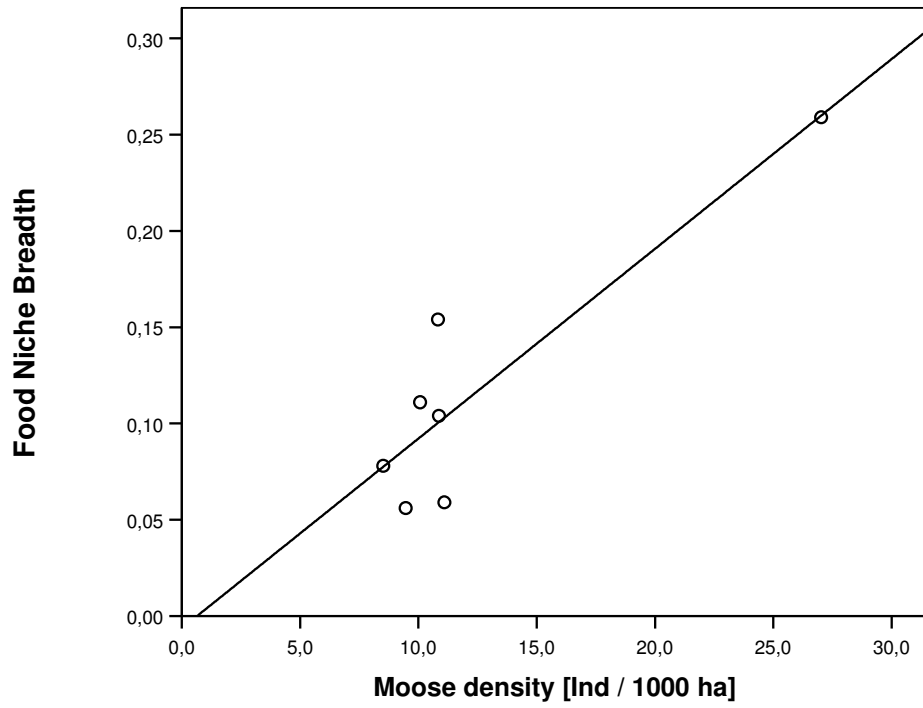


Figure 4: Manly's Alpha preference index (mean \pm SE) calculated for moose and roe deer consumption in summer and winter. Values above and below the line indicate preference and avoidance of the two species, respectively.

Using linear regression analysis we showed that the number of moose available affected the wolves' prey selection (Figure 5). In summer FNB was broader the higher the moose density was. This relationship was tested significant ($R^2 = 0,799$; $p = 0,007$). In winter a reverse trend could be observed, although this trend was not significant ($R^2 = -0,525$; $p = 0,065$). The outlier in both figures was made up by the Bograngen territory. Because of being aware of the fact that the slope of the regression line was influenced by the Bograngen values, we proofed and recalculated the values repeatedly. The regression analysis was also carried out with roe deer densities and FNB, but didn't show any trend (summer: $R^2 = -0,178$; $p = 0,297$; winter: $R^2 = 0,135$; $p = 0,371$).

Summer:



Winter:

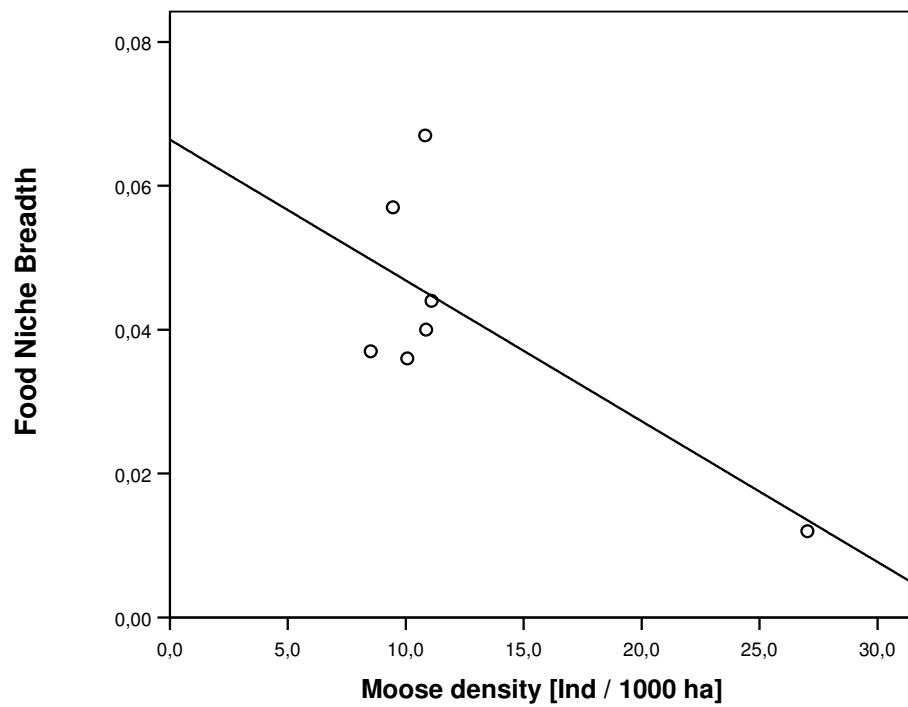
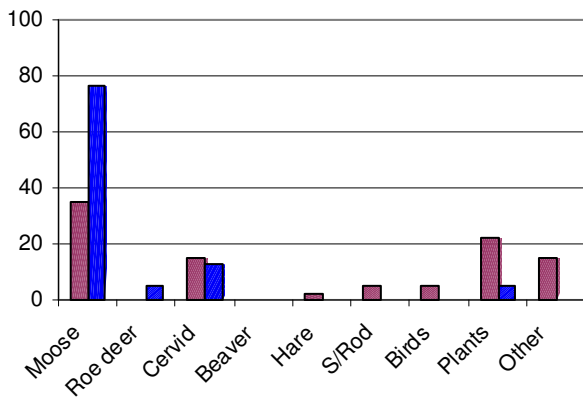
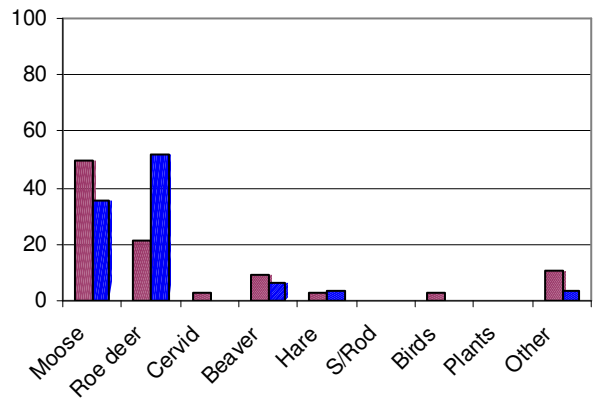


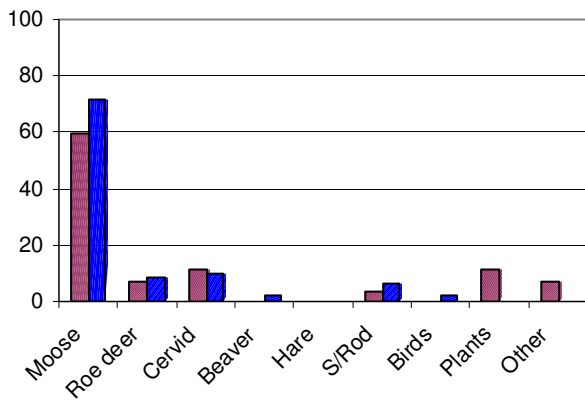
Figure 5: Correlation between moose density [Ind/1000 ha] and Levin's standardized food niche breadth in summer and winter.



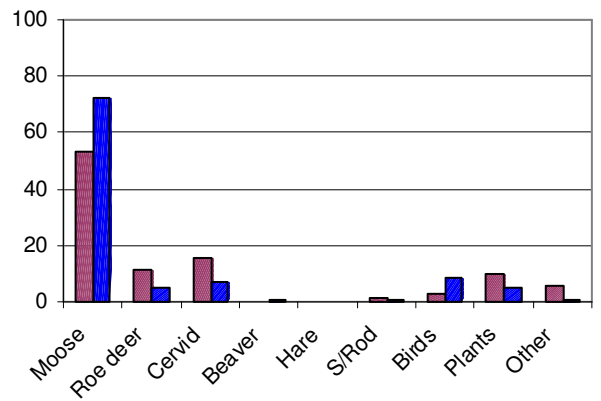
Bograngen



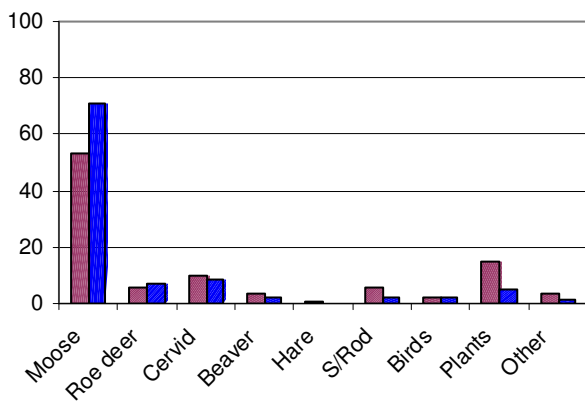
Dals-Ed



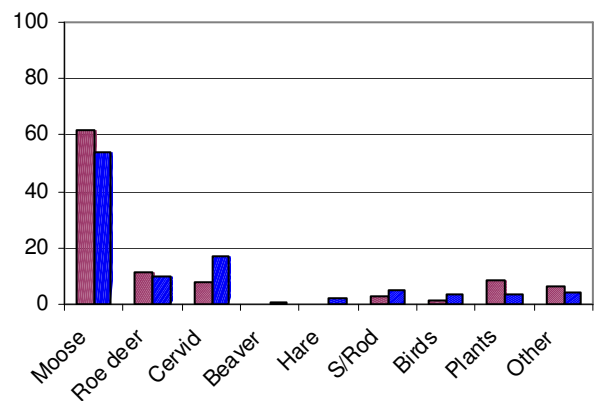
Filipstad



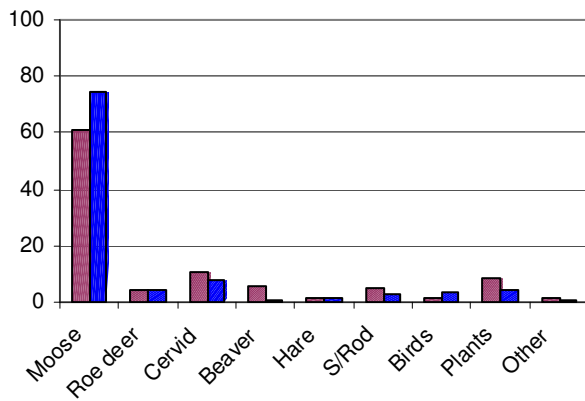
Grangärde



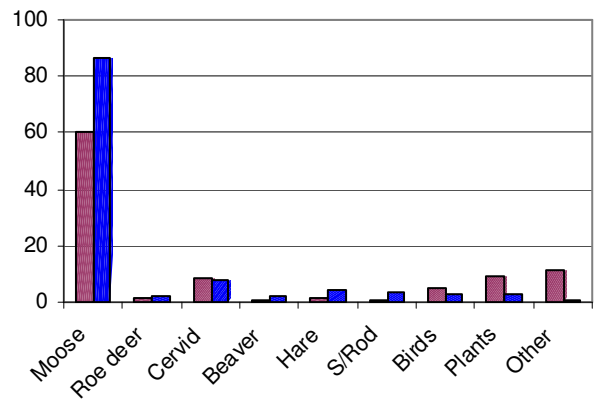
Hagfors



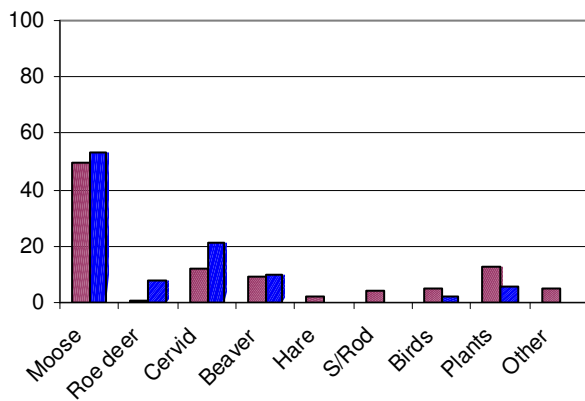
Hasselfors



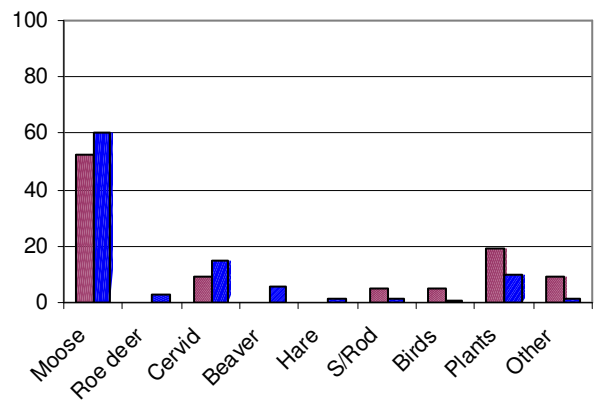
Leksand



Nyskoga



Tisjön



Tyngsjö

Figure 6: Seasonal %FO / I in 10 Scandinavian wolf territories during summer (red) and winter (blue). ‘Plants’ include berries and grasses. ‘Other’ includes wolf, badger, undetermined carnivores, undetermined mammals, insects and domestic animals. The category ‘Cervid’ contains moose and roe deer that could not be determined to the species level.

Diet composition in 10 Scandinavian territories

Moose was the predominant prey in 9 out of 10 Scandinavian wolf territories in both seasons (Figure 6). The solitary exceptional case was Dals-Ed during winter when roe deer made up 51,6%FO/I. A statistically significant difference between summer and winter diet composition could be observed in 5 territories (Table 5). In all territories except for Dals-Ed and Hasselfors, moose was more frequently consumed in summer than in winter. The consumption of non-cervid food items varied a lot among the analysed territories and ranged from no utilization in Bograngen (summer) to use of all secondary prey items during both seasons in the territories of Leksand and Nyskoga.

Table 5: Statistical analysis (2x2 Contingency table analysis) to show the difference in moose consumption in summer and winter.

	χ^2 - values	p-values	Significance
Bograngen	15,888	< 0,001	*
Dals-Ed	2,203	0,138	
Filipstad	1,374	0,241	
Grangärde	4,566	0,033	*
Hagfors	7,030	0,008	*
Hasselfors	0,111	0,740	
Leksand	6,749	0,009	*
Nyskoga	8,210	0,004	*
Tisjön	1,470	0,225	
Tyngsjö	1,345	0,246	

To analyse the selection of prey items in the above mentioned territories it was important to consider the densities of the main prey species (moose and roe deer). As can be seen in Table 6, cervid densities differed among territories. Hasselfors showed the highest roe deer density with 3,5 individuals / km², whereas the highest moose density was found in Bograngen (2,7 individuals / km²). Density surveys were not carried out area-wide in Scandinavia, wherefore density numbers were only available for 7 out of 10 territories.

Table 6: Mean densities for moose and roe deer in 7 Scandinavian wolf territories, estimated from pellet counts (SAND et al. unpublished data).

	Moose density Ind / km ²	Roe deer density Ind / km ²
Bograngen	2,7	0,0
Grangärde	1,1	0,2
Hagfors	1,0	0,0
Hasselfors	0,9	3,5
Leksand	0,9	0,1
Nyskoga	1,1	0,1
Tyngsjö	1,1	0,1

The cluster analysis presented that the territories show a strong similarity concerning diet composition (Figure 7). The consistency varied from 68,3% to 93%. Additionally 6 territories could be pooled into a summer and a winter cluster in each case. Diet composition in Hasselfors was that similar in both seasons (86,8%) that summer and winter appeared in the same cluster. Dals-Ed showed the strongest discrepancy between the two seasons.

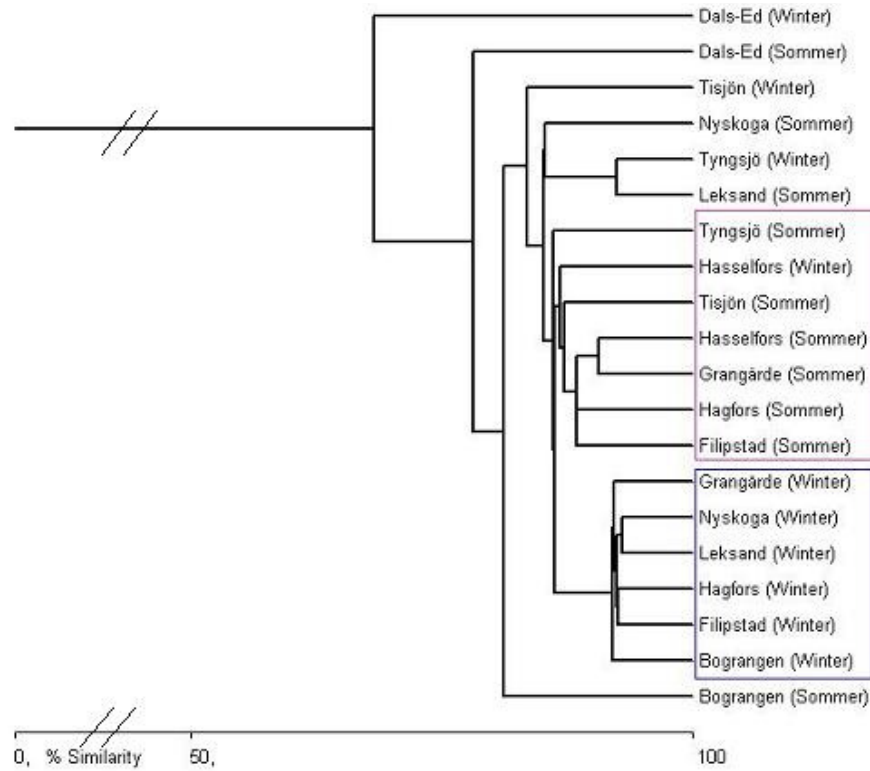


Figure 7: Clustering tree of wolf diet in 10 Scandinavian territories in summer and winter.

In 9 territories Levin's standardized food niche breadth was broader in summer than in winter (Figure 8). The exception was made up by Hasselfors, where FNB was almost equal in both seasons. It was apparent that the difference among summer and winter values varied among the territories, whereas Bograngen showed the largest variation with $\Lambda = 0,25$.

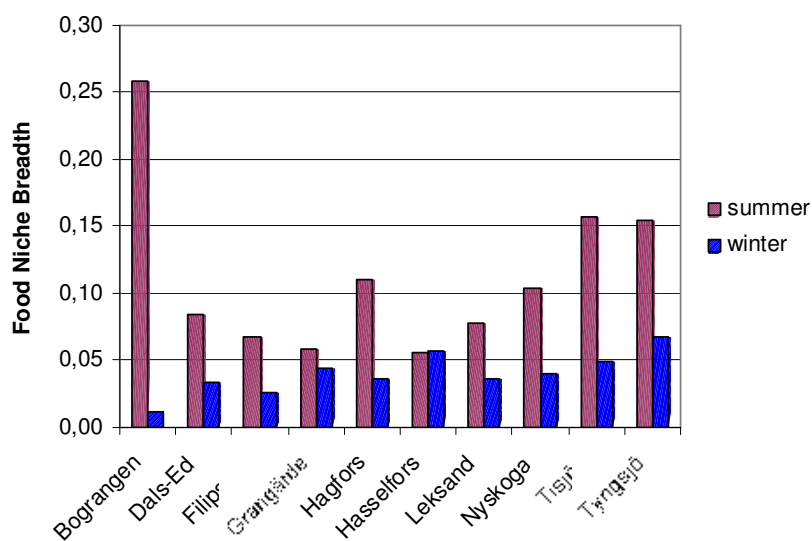


Figure 8: Levin's standardized food niche breadth calculated for 10 territories in summer (red) and winter (blue).

5 Discussion

Seasonal diet composition in Scandinavia

In the course of this study we could verify that moose is by far the most important prey species for wolves in Scandinavia, both by frequency of occurrence and biomass consumed. Numerous studies on wolf diet affirm that wild ungulates and in particular large ungulates make up the main part of diet composition (FRENZEL 1974, VOIGT et al. 1976, MATTIOLI et al. 1995, MERRIGI et al. 1996, GADE-JØRGENSEN & STAGEGAARD 2000, JEDRZEJEWSKI et al. 2000, CAPITANI et al. 2004, SMETANA 2005, ANSORGE et al. 2006). Nevertheless secondary and smaller prey items such as beaver, hare, small rodents and berries can be of seasonal importance (FRENZEL 1974, MECH & BOITANI 2003). The significant difference between diet composition among summer and winter in our study area is mainly based on the increased use of secondary prey items during the summer months. This trend might be explained by the abundance and higher activity of smaller prey species in summer (JOHANSSON 2004). Accordingly the importance of moose even increased during winter months, what might be explained by the effort to earn maximum benefit with minimum costs. LEŚNIEWICZ & PERZANOWSKI (1989) describe that wolves tend to concentrate on large ungulates during winter time to maximize the gained food biomass per successful hunt and therefore prefer larger prey species.

In contrast to a previous study on foraging behaviour of wolves in Scandinavia based on scat analysis carried out by OLSSON et al. (1997), roe deer only contributes marginally to the wolves' diet with a slightly higher importance in summer than in winter. OLSSON et al. (1997) describe that the Scandinavian wolves prey on roe deer with 51 %FO/S in summer and 47 %FO/S in winter, whereas in the current study roe deer constitutes 10,5 %FO/S in summer and 8,1 %FO/S in winter. There are many explanations for the evident differences between our study and the results described by OLSSON et al. (1997). OLSSON et al. (1997) conducted their study in the Nyskoga territory from 1988 to 1992, whereas our data was collected in almost all Scandinavian territories from 1992 to 2005. Additionally the size of the dataset differs strongly (OLSSON et al. 1997: $n = 684$; current study: $n = 2063$). Another explanation for the different results and the high utilization of roe deer from 1988 to 1992 might be the increase in roe deer numbers that was reported in the early 90s, followed by a decrease in population density in subsequent years (SVENSKA JÄGAREFÖRBUNDET 2005).

Although roe deer appears frequently in the diet of wolves within its range in Europe (SALVADOR & ABAD 1987, MATTIOLI et al. 1995, JEDRZEJEWSKI et al. 2000, SIDOROVICH et al. 2003, MATTIOLI et al. 2004, GAZZOLA et al. 2005, NOWAK et al. 2005, ANSORGE et al. 2006), it rarely constitutes the main food source (VALDMANN et al. 1998, GAZZOLA et al. 2005, ANSORGE et al. 2006). AANES et al. (1998) describe this trend with the small amount of biomass offered by roe deer in comparison to red deer or moose. Therefore roe deer appears to be of comparatively inferior quality with regard to effective foraging. Particularly in agricultural and non-forested areas the importance of roe deer as

prey increases due to higher population densities and due to the fact that roe deer is easier to prey on under those circumstances (LINNELL & ANDERSEN 1995, MATTIOLI et al. 2004, ANSORGE et al. 2006).

We observed a relatively high occurrence of plant material, in particular grams, in the analysed scats both in summer and winter. The consumption of grams is supposed to be effective as a purgative and to wipe the intestine from parasites and hairs (MECH & BOITANI 2003). Both grams and berries were consumed more frequently in summer than in winter due to the higher availability during the summer months. Although we assume that grams are partly consumed by chance in consequence of the feeding behaviour of wolves and the habit to lick blood from the ground, grams that appear in well-ordered bundles and with more than 5% of the dry volume of the scat need to be regarded as voluntarily consumed.

Even though the annual number of wolf-killed domestic animals in Sweden is quoted with about 200 individuals, this potential prey only contributed marginally to the diet of wolves within our study. 95% of domestic animals killed in Sweden are sheep (SWEDISH WILDLIFE DAMAGE CENTRE 2004). Detailed numbers for Norway are not known, but it is assumed that 200-400 sheep are killed per year. We identified hairs of sheep (n = 12), pigs (n = 2) and dogs (n = 1) in 14 summer scats and 1 winter scat (Table 2). The only winter scat that contained remains of a domestic animal was collected in Nyskoga and included sheep hairs. The other domestic animal items were observed in summer scats collected in Norwegian territories (Rømskog: n = 2; Våler: n = 10), Dals-Ed that is located in the Norwegian-Swedish border country (n = 1) and Grangärde (n = 1) in Sweden. The seasonal variation in consumption of domestic animals can be explained by the fact that sheep are only found free-grazing or on pastures during the summer months (LIBERG 2006).

The remains of domestic animals only occurred in a few scats. Nevertheless it is obvious that the predation on e.g. sheep is a bigger problem in Norway than in Sweden. Apparently this results from the way of sheep farming in Norway: about 2.1 million sheep range free on large parts of the country and provide an easy meal for predators.

In northern and central Europe, domestic animals do not make up an important part of the wolves' diet (OLSSON et al. 1997, GADE-JØRGENSEN & STAGEGAARD 2000, ANSORGE et al. 2006), whereas wolves in southern and eastern Europe prey on domestic animals to a much higher extend. There the remains of domestic animals are detected from 2,3%FO/I to 95,5%FO/I (derived from BIBIKOV et al. 1985 in OKARMA 1995, SALVADOR & ABAD 1987, MATTIOLI et al. 1995, VOS 2000, CAPITANI et al. 2004, GAZZOLA et al. 2005, NOWAK et al. 2005). The consumption of domestic animals appears to be highest in areas where wild ungulates are rare (MERRIGI & LOVARI 1996, VOS 2000). In areas, where wild and domestic ungulates coexist, wild ungulates constitute the preferred prey (GAZZOLA et al. 2005, ANSORGE et al. 2006).

Prey selection

Our study showed that moose is the preferred cervid species on the Scandinavian Peninsula, both in summer and winter. This result contrasts with the statement by MECH (1970), POTVIN et al. (1988), SPAULDING et al. (1998) und TREMBLAY et al. (2001) that wolves prefer the species that is smaller or easier to catch if there are 2 or more cervid species available. On an intra specific level this statement applies to the Scandinavian wolf population, since 80% of all moose killed are calves (PEDERSEN et al. 2005, SAND unpublished data). Concerning the selection of moose and roe deer we apparently face a different situation in Scandinavia. KUNKEL et al. (2004) argue that the selection of prey takes place on two levels. Wolves select prey that is easiest to locate and that provides the largest amount of biomass per successful attack. Both criterions fit for moose in Scandinavia due to the comparatively high population density (0,6 – 2,5 individuals / km², SAND 2005) and the high biomass per individual (78kg – 350kg, JOHANSSON 2004, SAND unpublished data). Anyhow large prey species and in particular moose are dangerous to attack and a wolf might get injured or even killed when attacking a moose (WEAVER et al. 1992). Nevertheless moose seem to be an easy prey for wolves in Scandinavia. SAND et al. (2006) state that moose in Scandinavia are currently naive to wolves due to the missing and low predation pressure when wolves were extinct on the Scandinavian Peninsula in the 1960s and slowly expanded again in the 1980s. The long period of separation of moose and wolves in Scandinavia apparently caused a loss of an effective anti-predator behaviour, which needs to be regained now. Due to their inexperience with large carnivores moose on the Scandinavian Peninsula are more vulnerable to wolf attacks than moose in North America (SAND et al.2006).

Food Niche Breadth

Standardized Food Niche Breadth was relatively low in both seasons (summer: $B_A = 0,11$; winter: $B_A = 0,04$) what indicates a specialisation on one prey category. In our study the diet of wolves was dominated by cervids. Moreover Food Niche Breadth in summer was significantly broader than in winter. This trend was caused by a higher availability and utilization of alternative prey species such as beaver, hare, small rodents and birds.

MERRIGI et al. (1996) stated in their study that Food Niche Breadth is influenced by large ungulate densities. They described that wolves specialise on large ungulates if those prey species are available in high numbers. Therefore the density of main prey species has an influence on Food Niche Breadth. Our results follow this trend in both seasons. In accordance to MERRIGI et al. (1996) the standardized Food Niche Breadth in winter decreases with increasing moose density. That means that in winter wolves in Scandinavia concentrate even more on moose if their population density is high. Consequently during winter time the wolves seem to prefer the prey category with the highest availability (HAYES et al. 2000). In contrast to the results in winter, a reverse trend could be documented in summer. The standardized Food Niche Breadth increases with raising moose numbers. An explanation for this trend could be that the wolves adapt their foraging behaviour in summer to the

given prey diversity. Apparently wolves supplement their summer diet with alternative prey, although the preferred prey is available in high numbers (THEBERGE & COTTRELL 1977, THEBERGE et al. 1978, FORBES & THEBERGE 1996, TREMBLAY et al. 2001).

Diet composition in 10 Scandinavian territories

In general the diet composition in Scandinavian wolf territories appears to be very similar (Figure 7). Differences among territories within the same season can be explained by varying availability and vulnerability of prey species as well as varying factors (e.g. snow depth, landscape management, clear cutting, road density). Additionally we described that always 6 territories can be pooled in summer clusters and in winter clusters. Therefore we assume that the similarities among the territories are mainly caused by the seasonal availability of given food resources.

Bogragen and Dals-Ed show the highest deviations between summer and winter diet. In Dals-Ed the deviation mainly seems to be caused by the comparatively high roe deer consumption during winter. However, this result needs to be handled carefully, since the seasonal differences may also be caused by the varying sample size (summer: $n = 57$; winter: $n = 29$). The same applies to Bogragen. The evident difference between summer and winter diet seems to be caused by the concentration on cervids and in particular on moose as prey during winter. It is possible that wolves indeed do not resort to secondary prey items because of high availability of moose in winter. Bogragen shows the highest moose density among the studied territories and is known as a winter stand for moose (SAND unpublished data). Nevertheless we cannot exclude that the deviations also might result from a small sample size (summer: $n = 23$; winter: $n = 36$). Therefore it is necessary to carry out further studies including a larger sample size as well as more extensive information about prey densities, to make detailed predictions about the differences in seasonal diet composition.

We also showed that Dals-Ed and Hasselfors are the only territories among the studied ones that show higher moose consumption in summer than in winter. The remaining territories describe the already discussed trend with a high concentration on moose as prey in winter and more extensive use of alternative prey in summer. Both Dals-Ed and Hasselfors are situated in areas with high roe deer densities, however exact numbers are only available for Hasselfors. In our case it is possible that due to the high availability of a second cervid species the wolves do not have to specialise on moose in winter as they apparently do in the remaining territories. This trend is also reflected in the standardized Food Niche Breadth in both seasons. MERRIGI et al. (2004) also argue that roe deer becomes more attractive as prey in areas where it appears in high densities.

As a result we can assume that preferences and utilization of different prey items in the studied territories were influenced by prey densities as well as by seasonal availability of food items. Additionally the selection of certain prey is supposed to be a result of pack size and possible reproductions in the territories (SPAULDING et al. 1998, CAPITANI et al. 2004).

Calculation of biomass consumed

Within this study we compared 3 well-established methods used to calculate biomass consumed. The differences between the 3 calculation methods are evident, but it is difficult to evaluate them statistically. These deviations, in particular concerning large prey, result from the fact that FLOYD et al. (1978), WEAVER (1993) and RÜHE (unpublished, derived from table 1 in RÜHE et al. 2003) took different prey species into account when establishing their equations. The largest prey species that FLOYD et al. (1978) and RÜHE (unpublished, derived from table 1 in RÜHE et al. 2003) integrated into their studies were white-tailed deer and red deer, respectively. Whereas WEAVER (1993) considered elk and moose as well as the data from FLOYD et al. (1978) and TRAVES (1983). Therefore the Weaver equation covers a higher variety of prey species and prey sizes than the other two methods. The comparison between the 3 methods showed the importance of a sound and a crucial selection of the 'right' method when calculating biomass consumed for a given study area. Although RÜHE (unpublished, derived from table 1 in RÜHE et al. 2003) calculated his equation for potential prey species in European ecosystems, it was more reasonable to choose the Weaver equation in our study, because moose appeared to be the main prey for wolves in Scandinavia. And moose is only integrated into the Weaver equation. By choosing the Weaver equation we did not overestimate moose biomass consumed as it would have been the case when choosing the Floyd or Rühle equations.

Table 4 shows that biomass consumed in kg also differs between the 3 methods. The values raise from Rühle to Weaver to Floyd by factor 2. Those deviations result from the different methods Floyd, Weaver and Rühle used when calculating the biomass equations: the amount of scats collected differed as well as the number of wolves. Due to strong variation of biomass consumed in kg we cannot recommend this kind of data presentation. Moreover, the biomass consumed in kg correlates with the number of scats collected and never describes biomass consumed for the whole wolf population.

Conclusions

Although we had an extensive dataset with 2063 scats, it appeared that the sample was not sufficient for seasonal comparisons among territories. Only few territories provided enough scat samples per season to integrate them into the data evaluation. For future studies we therefore recommend a concentration of data collection on only few territories with a sample size of at least 94 scats per season (TRITES & JOY 2005). Additionally the data collection should cover a reasonable period, at least 12 months. Considering these criteria, it is possible to make detailed comparisons among territories, seasons and years. Furthermore the availability of density data for the main prey species should be crucial for the study area selection. In our study several territories could not be assessed and compared in detail due to absent or deficient prey density data. Depending on the research question the study focuses on, it appears to be practical to collect data in areas where density surveys were or will be carried out.

It seems to be meaningful to concentrate on only a few territories and to provide all the necessary biotic as well as a biotic additional information (e.g. prey density, snow depth, road density) depending on the given research question.

Despite the above mentioned foibles, we were able to provide extensive and almost area-wide information about the seasonal diet composition of wolves in Scandinavia. Since previous studies were mainly carried out during winter (PALM 2001, WIKENROS 2001, SAND et al. 2005, BERNELIND 2006, SAND et al. in press), our study represents a good completion to the given dataset, in particular concerning summer diet.

Generally a combination of scat analysis and carcass search provides a broader database, than both methods individually: scat analysis gives overall information about the diet composition and detects prey species that are not or hardly found by doing carcass search. Carcass search on the other hand shows absolute numbers of animals killed and gives information about the carcass site. Therefore scat analysis is not a replacement for carcass search, but rather a supplementary method to get more detailed information.

Résumé

- Moose was the dominant and preferred prey both in summer and winter.
- Secondary prey items such as beaver, hare and small rodents were more frequently used in summer.
- Seasonal differences in the diet composition were given and mainly influenced by the utilization of moose and smaller prey species.
- Food Niche Breadth was relatively narrow in both seasons which is explained by the high concentration on cervids as prey. The even higher utilization of moose during winter resulted into a lower Food Niche Breadth in winter than in summer.
- The moose density in the Scandinavian territories had an influence on the selection of moose as prey and therefore also on the Food Niche Breadth.
- The comparison of the 3 biomass calculation methods showed that it is important to chose the method carefully in coordination with potential prey species in the study area. For future studies it would be desirable to improve the biomass equations and to include a higher number of prey species as well as non-mammalian prey into the calculation.

Acknowledgments

My sincere thanks to:

My Swedish supervisor Håkan Sand, who gave me the opportunity to write my diploma thesis about Scandinavian wolves. Many thanks for all the great and inspirational discussions that enriched my work and for not becoming tired of answering all my questions!

Jens Karlsson, Jean-Michel Roberge, J-O Helldin for helping me out with all kind of problems from identifying scat contents to statistical analysis and mathematics. Thanks for being my friends!

Per Grängsted and J-O for guiding me through the scat analysis and for being there with good advice when some kind of strange things appeared in the scats.

Olle Liberg, Petter Kjellander, Johan Månsson, Jonas Nordström for helping me to identify roe deer remains in the scats and for answering thousands of questions concerning my thesis.

Henrik Andrén for the support in statistics.

Vemund Jaren, Morten Kjørstad and Peter Jaxgård for supplying me with the latest information about wolf management and wolf policy in Sweden and Norway.

Åke Aronson for sharing all the facts about wolves in Scandinavia with me, for answering all my questions about tracking carnivores and for drawing the wolf track pic!

Special thanks to all the people who collected the scats over the years and who put the foundations for my work. Thanks to Per Ahlqvist, Åke Aronson, Örjan Johansson, Johan Månsson (Länsstyrelsen), Håkan Sand, Kent Skjöld, Linn Svensson, Anita Svensson, Sven-Olof Svensson, Camilla Wikenros and all the other people out in the field!

Thanks to all the people at the Grimsö Wildlife Research Station, who were always ready to answer my questions and who were of great help and company during my time in Sweden.

Thanks to my sister Anja for being a good friend and for her support.

A special thanks to my parents for always helping out when needed, for supplying me with food and chocolate when dropping by in Grimsö and for sharing my love for the outdoors and the critters. Many thanks for always supporting and encouraging me to believe in my dreams and to go my way.

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