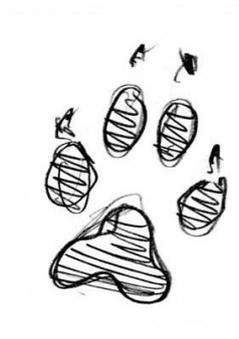


Diet composition of wolves (*Canis lupus*) on the Scandinavian peninsula determined by scat analysis



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 the 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 the 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). Both studies describe a higher importance of roe deer than it was observed in previous studies. 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 about 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 the method to identify prey items consumed. In contrast to carcass search we were able to cover a larger study area as well as a larger study period and it was possible to identify prey species that are usually consumed completely and therefore not detectable with carcass search. Since we were also interested in the 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 the differences between the methods and to look for criterions 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*), sometimes intermixed with deciduous trees like 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.

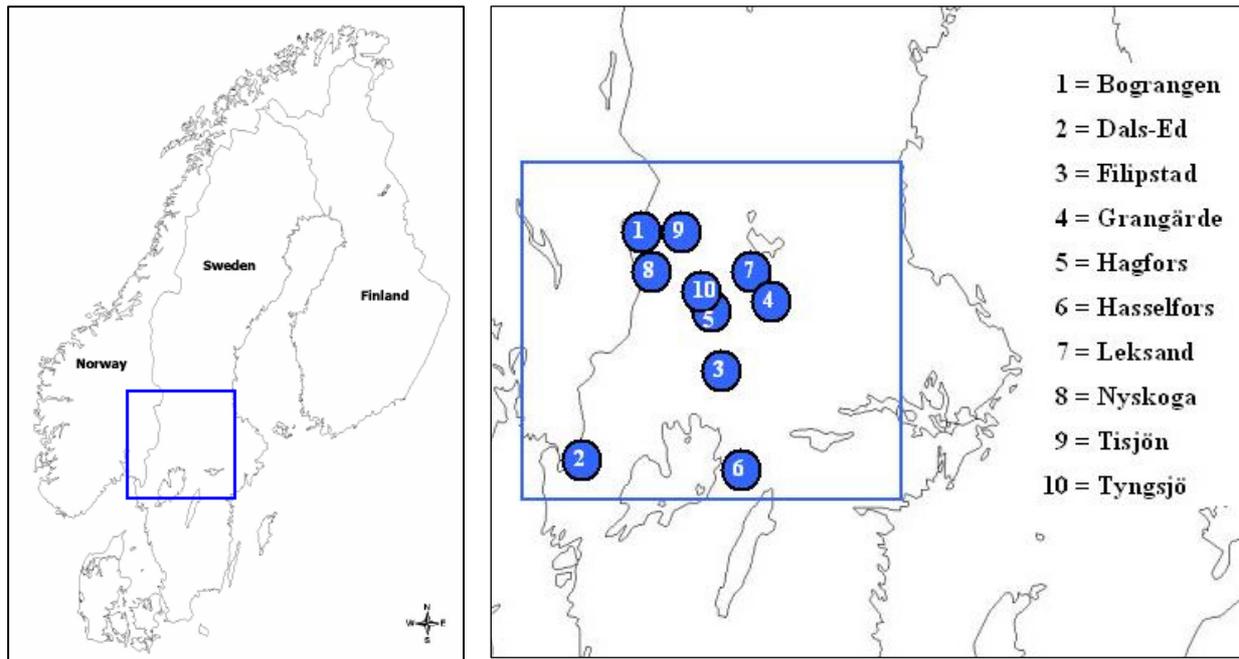


Figure 1: Map of the study area with the locations of the 10 territories that were analysed in detail.

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 the 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 with 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 the summer months about 2.1 million free-grazing sheep can be 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 the 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 criteria 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 the 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).

Prior to the analyses the observers were trained in identifying scat contents by practicing with reference material and reference scats. As recommended by CIUCCI et al. (1996), MECH & BOITANI (2003) and MATTIOLI et al. (2004) a blind test was performed with 30 scat samples to assess the accuracy of identification by the laboratory personal. The errors were below the threshold of 5% (MATTIOLI et al. 2004).

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 (represents 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 because 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 looking at the 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, GOSZCYNKI 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):

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

$$y = \text{estimated biomass consumed per scat}$$

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 Equivalents	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 Equivalents	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 (nach 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] $D / \Sigma D$

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 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).

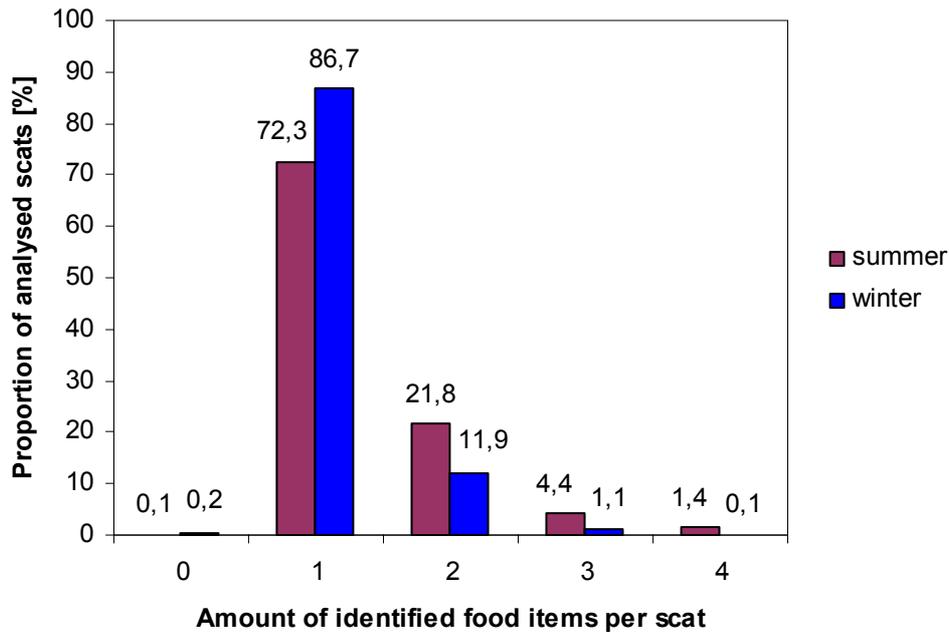


Figure 2: Amount of food items per scat in summer and winter.

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, fox, 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
Aves (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	

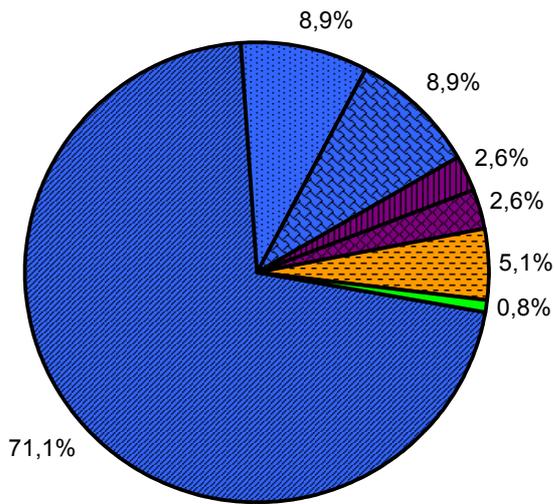
The %WSE index for big and medium-sized mammals confirmed the results received from the %FO/I calculation (Table 3). However the WSEs showed that smaller prey items such as small rodents, birds, insects, berries and grams were less important than supposed by interpreting the %FO/I index. Those items 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.

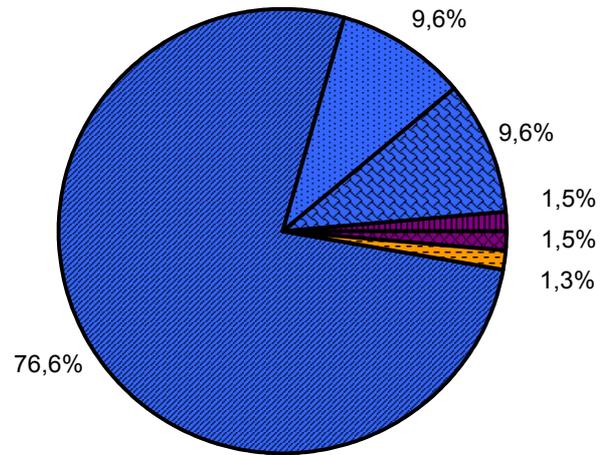
Prey item	WSE					
	Summer		Winter		All seasons combined	
	n	%WSE	n	%WSE	n	%WSE
<i>Alces alces</i> (moose)	494,8	62,3	907,8	73,3	1421,7	68,9
<i>Capreolus capreolus</i> (roe deer)	70,3	8,9	92,4	7,5	164,4	8,0
<i>Cervidae</i> (undetermined)	72,6	9,1	122,8	9,9	202,1	9,8
<i>Meles meles</i> (badger)	16,9	2,1	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 the mammalian biomass consumed than in summer with 95,7%Bio and 88,8%Bio, respectively. Hence smaller prey was of higher importance in summer with 5,1%Bio than in winter with 1,3%Bio. The 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 the moose biomass consumed.

Summer:



Winter:



- Moose (calf)
- Moose (yearling)
- Moose (adult)
- Moose (yearling)
- Roe deer (adult + yearling)
- Roe deer (fawn)
- Domestic animals
- 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 the 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.

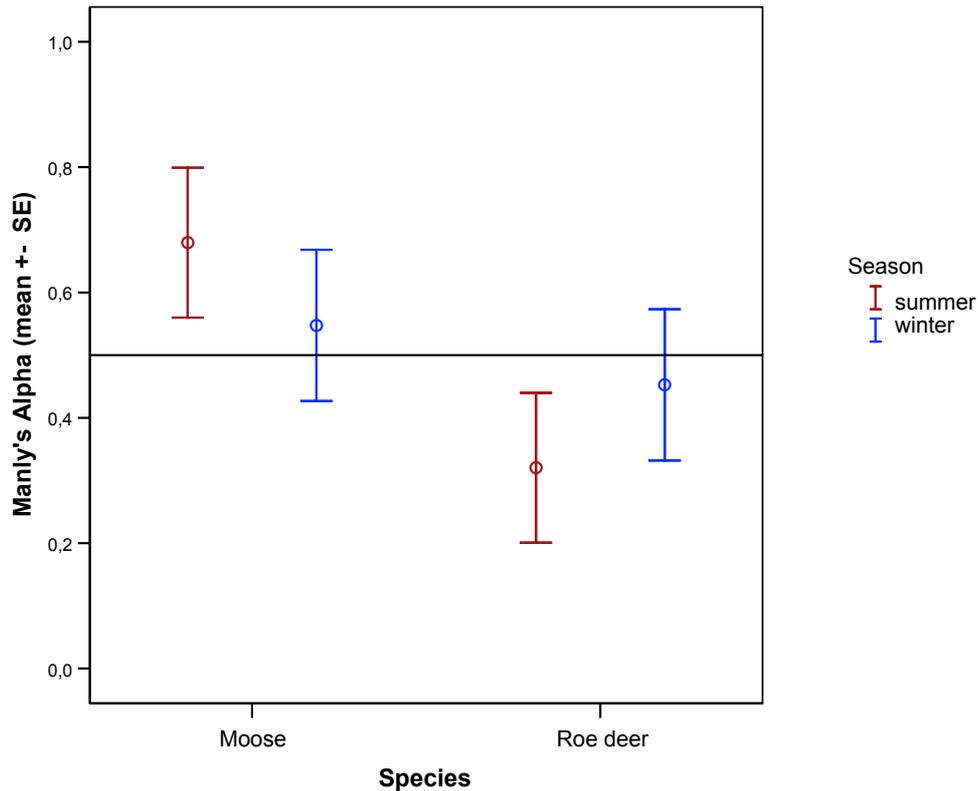
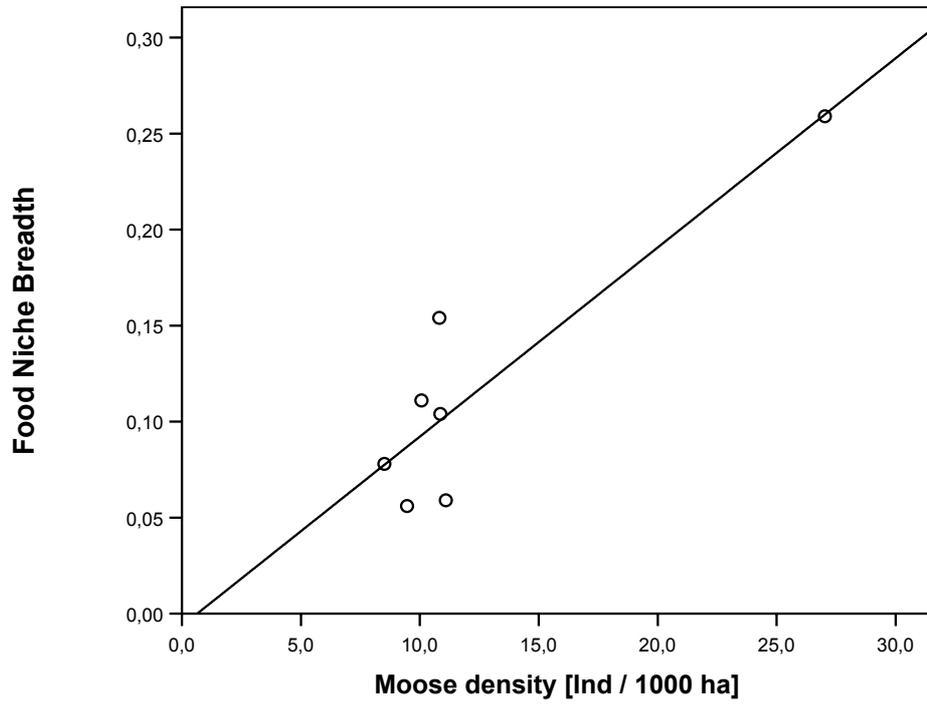


Figure 4: Manly's Alpha preference index (mean \pm SE) calculated for moose and roe deer consumption in summer and winter. Values above and below the line indicate preference and avoidance of the two species, respectively.

Using a linear regression analysis we could show that the number of moose available affected the wolves' prey selection (Figure 5). In summer the 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 Bograngen values strongly influenced the slope of the regression line, 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:

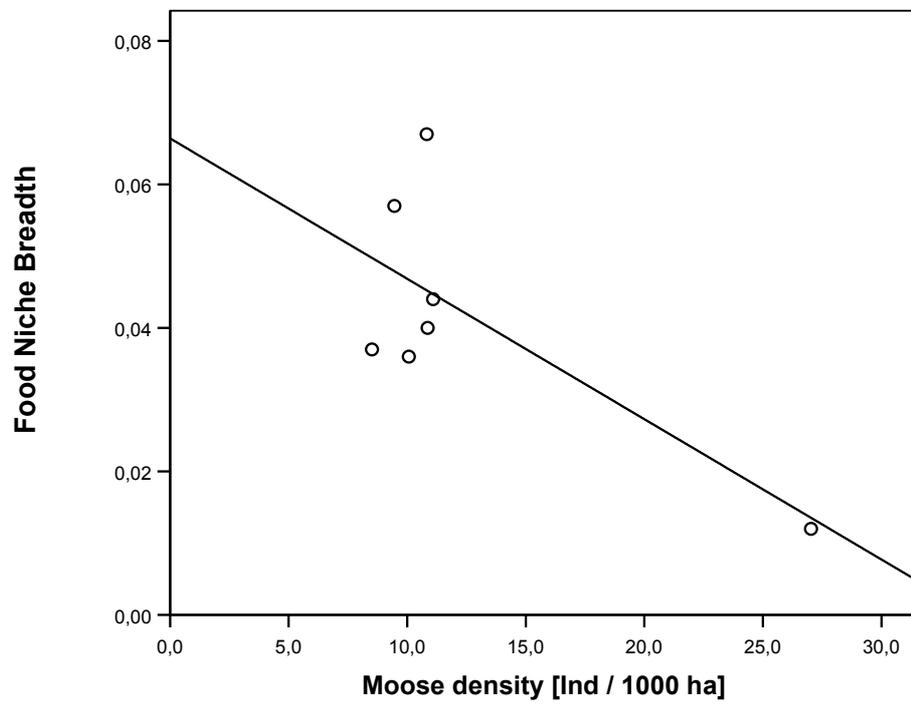
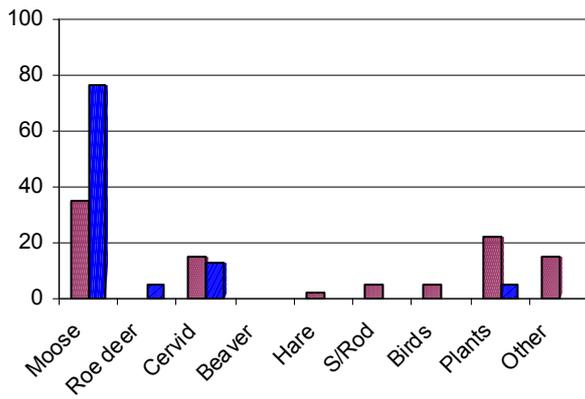
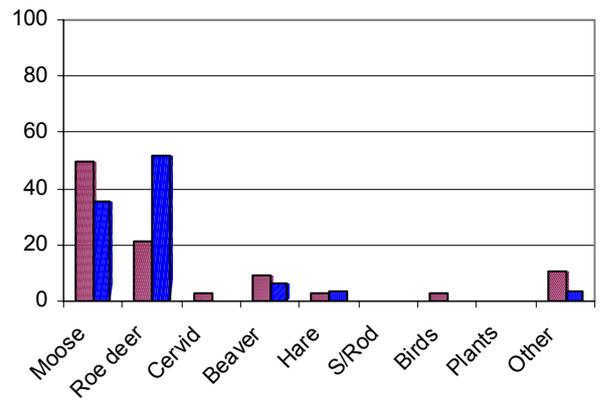


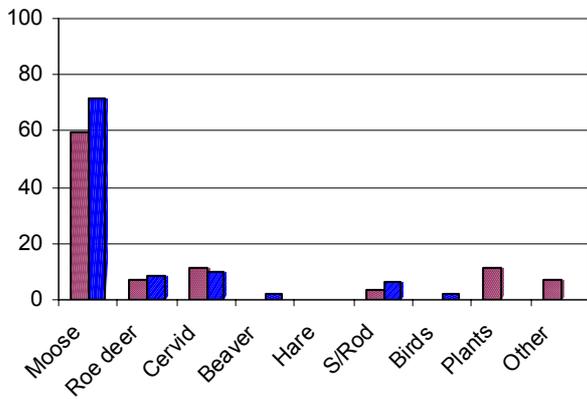
Figure 5: Correlation between moose density [Ind/1000 ha] and Levin's standardized food niche breadth in summer and winter.



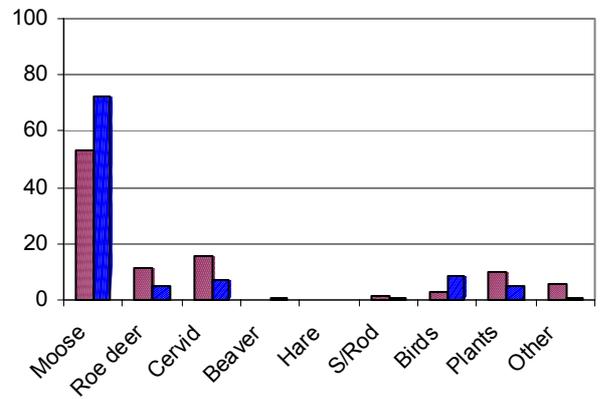
Bograngen



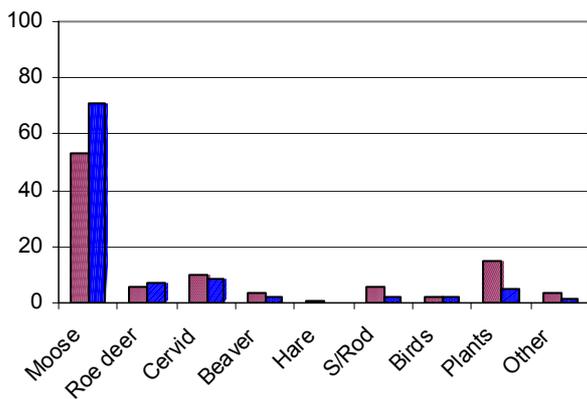
Dals-Ed



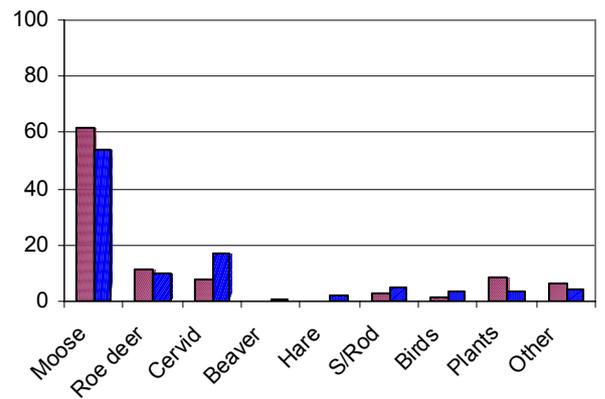
Filipstad



Grangärde



Hagfors



Hasselfors

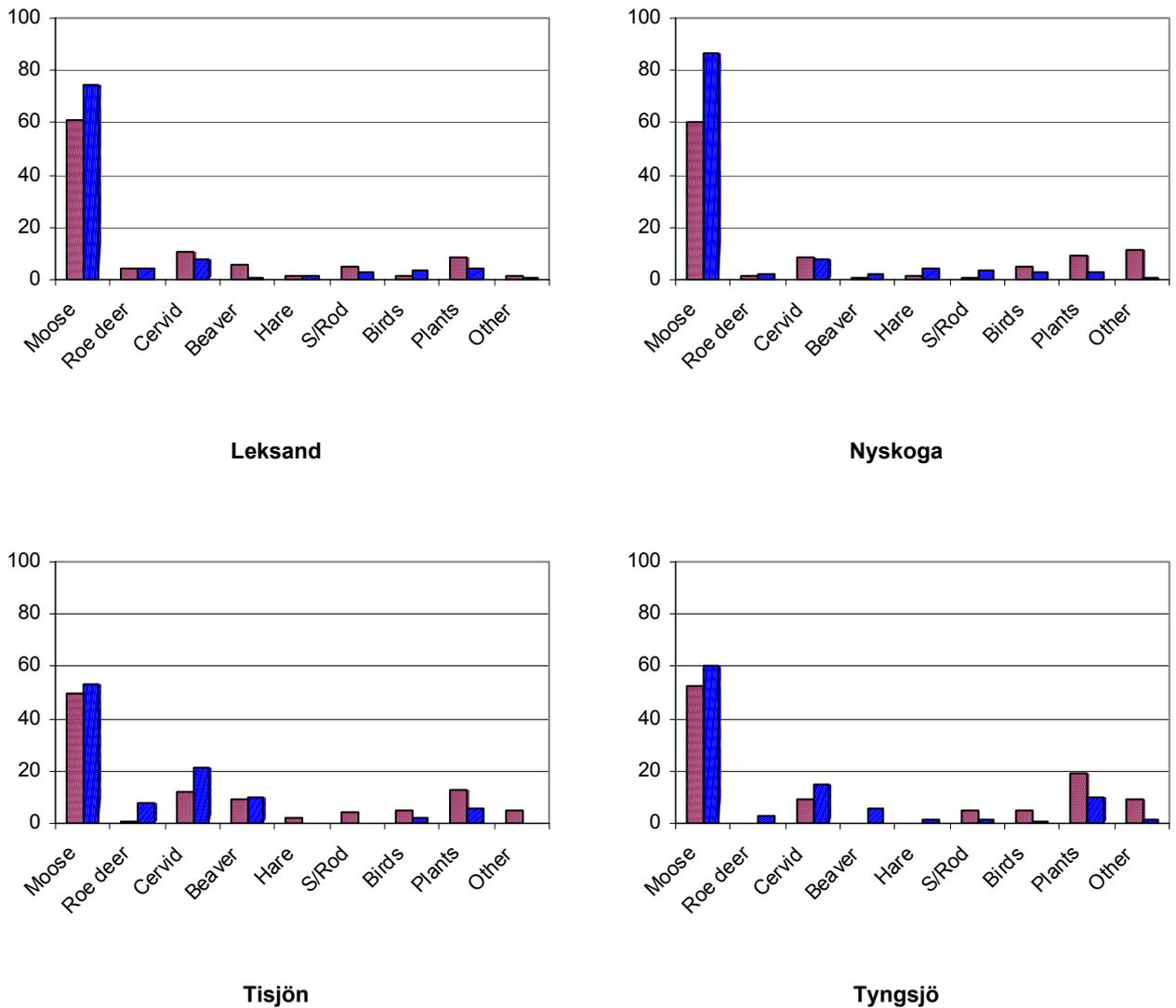


Figure 6: Seasonal %FO / I in 10 Scandinavian wolf territories during summer (red) and winter (blue). ‘Plants’ include berries and grasses. ‘Other’ includes wolf, badger, undetermined carnivores, undetermined mammals, insects and domestic animals. The category ‘Cervid’ contains moose and roe deer that 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 the winter months where roe deer occurred with 51,6%FO in the scat sample. 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 of those items in summer in Bograngen 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 could be 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.

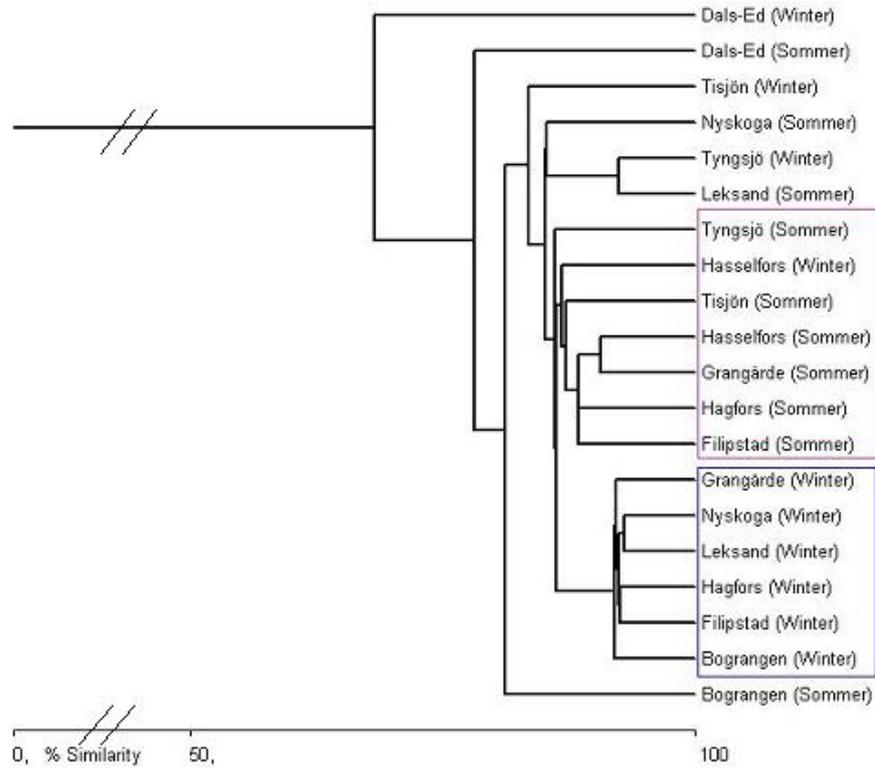


Figure 7: Clustering tree of wolf diet in 10 Scandinavian territories in summer and winter.

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 the FNB was almost equal in both seasons. It was apparent that the difference among summer and winter values varied among the territories, whereas Bograngen shows the largest variation with $\Delta = 0,25$.

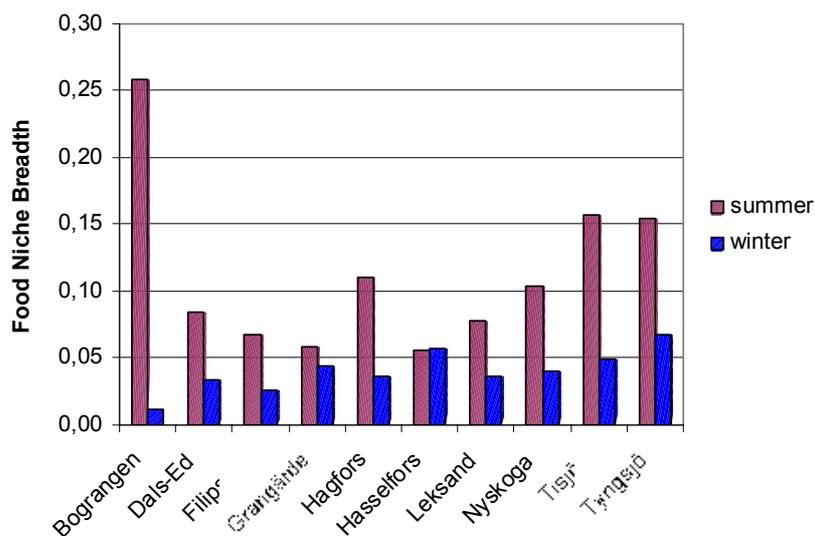


Figure 8: Levin's standardized food niche breadth calculated for 10 territories in summer (red) and winter (blue).

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 the 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, SMIETANA 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 the diet composition among summer and winter in our study area is mainly based on the increased use of those 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 the 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 the 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 resource (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 that roe deer offers in comparison to red deer or moose. Therefore roe deer appears to be of comparatively inferior quality in view of effective foraging. Particularly in agricultural and non-forested areas the importance of roe deer as

prey increases due to higher population densities and 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 of plants 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 the killed domestic animals 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 remaining domestic animal items were observed in summer scats collected in Norwegian territories (Rømskog: n = 2; Våler: n = 10), in Dals-Ed that is located in the Norwegian-Swedish border country (n = 1) and Grangärde (n = 1) in Sweden. The seasonal variation in the consumption of domestic animals can be explained by the fact that sheep are only found on pastures or free-grazing 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. Remains of domestic animals are detected with 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 seem to 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 per 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. Because of 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).

Another reason for the preference of moose and the avoidance of roe deer in summer and winter might be the coexistence of wolves with lynx in Scandinavia. MOSHØJ (XXXX) in Sweden and SUNDE et al. (2000) in Norway describe that roe deer is an important prey for lynx. Hence the prey selection by wolves might also be explained by food niche separation

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 the 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 the Food Niche Breadth is influenced by the density of large ungulates. They described that wolves specialise on large ungulates if those prey species are available in high numbers. Therefore the density of the main prey species has an influence on the 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 density is high.

Consequently during winter time the wolves seem to prefer the prey category whose availability is highest (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. It is possible that the wolves supplement their summer diet with alternative prey items, 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 the 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 abiotic factors (e.g. snow depth, landscape management, clear cutting, road density). Additionally we described that always 6 territories can be pooled in summer and winter clusters, respectively. Therefore we assume that the similarities among the territories are mainly caused by the seasonal availability of given food resources.

Bogranen 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 the winter months. 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 Bogranen. The evident difference between summer and winter diet seems to be caused by the concentration on cervids and in particular moose as prey during winter. It is possible that the wolves indeed do not resort to secondary prey items because of the high availability of moose during winter. Bogranen 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 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 the seasonal diet composition.

We could also show 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 the 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 the preferences and the utilization of different prey items in the studied territories were influenced by the prey densities as well as by the 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 the biomass consumed by carnivores. 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 the 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 chose 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 the moose biomass consumed as it would have been the case when choosing the Floyd or Rühle equations.

Table 4 shows that the 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 the 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 the 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 criterions, it is be 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.

However, when selecting the study area and study period one has to take into consideration that we are dealing with an open system with fluctuating territories, and prey and predator densities. Nevertheless it seems to be meaningful to concentrate on only a few territories and depending on the research question to provide all the necessary biotic as well as a biotic extra information (e.g. prey density, snow depth, road density).

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. Hence 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 the winter months 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 choose 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 Andréén 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.

References

- AANES, R.; LINNELL, J.D.C.; PERZANOWSKI, K.; KARLSEN, J.; ODDEN, J. (1998): Roe deer as prey. In: Andersen, R.; Duncan, P.; Linnell, J.D.C. (eds.). *The European Roe Deer: The Biology of Success*. Scandinavian University Press, Oslo. 139-159.
- ANDERSONE, Ž.; OZOLIŅŠ, J. (2004): Food habits of wolves *Canis lupus* in Latvia. *Acta Theriol.* 49(3): 357-367.
- ANGERBJÖRN, A.; TANNERFELDT, M.; ERLINGE, S. (1999): Predator – prey relationships: arctic foxes and lemmings. *J. Anim. Ecol.* 68: 34-49.
- ANSORGE, H.; KLUTH, G.; HAHNE, S. (2006): Feeding ecology of wolves *Canis lupus* returning to Germany. *Acta Theriol.* 51(1): 99-106.
- BALLARD, W.B.; WHITMAN, J.S.; GARDNER, C.L. (1987): Ecology of an exploited wolf population in south-central Alaska. *Wildl. Monogr. No. 98*: 54pp.
- BERGER, J.; SWENSON, J.E.; PERSSON, I.-L. (2001): Recolonizing carnivores and naïve prey: conservation lessons from pleistocene extinctions. *Science* 291: 1036-1039.
- BERNELIND, T. (2006): Winter prey selection of moose (*Alces alces*) by Scandinavian wolves (*Canis lupus*). Examensarbete. Grimsö Research Station, Swedish University of Agricultural Sciences, Uppsala. 28pp
- CAPITANI, C.; BERTELLI, I.; VARUZZA, P.; SCANDURA, M.; APOLLONIO, M. (2004): A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystems. *Mamm. Biol.* 69(1): 1-10.
- CHAVEZ, A.S.; GESE, E.M. (2005): Food habits of wolves in relation to livestock depredations in Northwestern Minnesota. *Am. Midl. Nat.* 154: 253-263.
- CHESEMORE, D.L. (1968): Notes on the food habits of arctic foxes in northern Alaska. *Can. J. Zool.* 46: 1127-1130.
- CIUCCI, P.; BOITANI, L.; PELLICIONI, E.R.; ROCCO, M.; GUY, I. (1996): A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. *Wildl. Biol.* 2(1): 37-48.
- CUESTA L.; BARCENA, F.; PALACIOS, F.; REIG, S. (1991): The trophic ecology of the Iberian Wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. *Mammalia* 55(2): 239-254.
- DALERUM, F.; ANGERBJÖRN, A. (2000): Arctic fox (*Alopex lagopus*) diet in Karupelv Valley, East Greenland, during a summer with low lemming density. *Arctic* 53(1): 1-8.
- DEBROT, S.; FIVAZ, G.; MERMOD, C.; WEBER, J.-M. (1982): *Atlas des poils de mammifères d'Europe*. Institut de Zoologie, Université de Neuchâtel, Suisse. 208pp.

- ELMHAGEN, B.; TANNERFELDT, M.; VERUCCI, P.; ANGERBJÖRN, A. (2000): The arctic fox (*Alopex lagopus*): an opportunistic specialist. *J. Zool., Lond.* 251: 139-149.
- ELMHAGEN, B.; TANNERFELDT, M.; ANGERBJÖRN, A. (2002): Food-niche overlap between arctic and red foxes. *Can. J. Zool.* 80: 1274-1285.
- FLOYD, T.J.; MECH, L.D.; JORDAN, P.A. (1978): Relating wolf scat content to prey consumed. *J. Wildl. Manage.* 42(3): 528-532.
- FORBES, G.J.; THEBERGE, J.B. (1996): Response by wolves to prey variation in central Ontario. *Can. J. Zool.* 74: 1511-1520.
- FRENZEL, L.D. (1974): Occurrence of moose in food of wolves as revealed by scat analyses: a review of North American studies. *Naturaliste can.* 101: 467-479.
- FRITTS, S.H.; MECH, L.D. (1981): Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildl. Monogr. No. 80*: 79pp.
- GADE-JØRGENSEN, I.; STAGEGAARD, R. (2000): Diet composition of wolves *Canis lupus* in east-central Finland. *Acta Theriol.* 45(4): 537-547.
- GARROTT, R.A.; EBERHARDT, L.E.; HANSON, W.C. (1983): Summer food habits of juvenile arctic foxes in northern Alaska. *J. Wildl. Manage.* 47: 540-545.
- GAZZOLA, A.; BERTELLI, I.; AVANZINELLI, E.; TOLOSANO, A.; BERTOTTO, P.; APOLLONIO, M. (2005): Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. *J. Zool., Lond.* 266: 205-213.
- GOSZCZYNSKI, J. (1974): Studies on the food of foxes. *Acta Theriol.* 19: 1-18.
- HAYES, R.D.; BAER, A.M.; WOTSCHIKOWSKY, U.; HARESTAD, A.S. (2000): Kill rate by wolves on moose in the Yukon. *Can. J. Zool.* 78: 49-59.
- JAMES, D.D. (1983): Seasonal movements, summer food habits, and summer predation rates of wolves in northwest Alaska. Master of Science Thesis, University of Alaska, Fairbanks. 90pp.
- JĘDRZEJEWSKI, W.; JĘDRZEJEWSKA, B.; OKARMA, H.; SCHMIDT, K.; ZUB, K.; MUSIANI, M. (2000): Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. *J. Mammal.* 81(1): 197-212.
- JOHANSSON, Ö. (2004): Summer predation patterns of the Scandinavian wolf. Examensarbete. Grimsö Research Station, Swedish University of Agricultural Sciences, Uppsala. 28pp.
- KJØRSTAD, M. (2005): Abstract from "Seminar on the transboundary management of large carnivore populations", Osilnica, Slovenia.
- KOHIRA, M.; REXSTAD, E.A. (1997): Diets of wolves, *Canis lupus*, in logged and unlogged forests of southeastern Alaska. *Can. Field-Nat.* 111(3): 429-435.

- KOJOLA, I.; HUITU, O.; TOPPINEN, K.; HEIKURA, K.; HEIKKINEN, S.; RONKAINEN, S. (2004): Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland. *J. Zool., Lond.* 263: 229-235.
- KUNKEL, K.E.; PLETSCHER, D.H.; BOYD, D.K.; REAM, R.R.; FAIRCHILD, M.W. (2004): Factors correlated with foraging behavior of wolves in and near Glacier National Park, Montana. *J. Wildl. Manage.* 68(1): 167-178.
- LEŚNIEWICZ, K.; PERZANOWSKI, K. (1989): The winter diet of wolves in Bieszczady Mountains. *Acta Theriol.* 34(27): 373-380.
- LIBERG, O. (2006): Genetic aspects of viability in small wolf populations with emphasis on the scandinavian wolf population. Swedish Environmental Protection Agency, Report No. 5436. 67pp.
- LINNELL, J.D.C.; ANDERSEN, R. (1995): Site tenacity in roe deer. Short-term effects of logging. *Wildl. Soc. Bull.* 23: 31-36.
- MATTIOLI, L.; APOLLONIO, M.; MAZZARONE, V.; CENTOFANTI, E. (1995): Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. *Acta Theriol.* 40(4): 387-402.
- MATTIOLI, L.; CAPITANI, C.; AVANZINELLI, E.; BERTELLI, I.; GAZZOLA, A.; APOLLONIO, M. (2004): Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north-eastern Apennine, Italy. *J. Zool., Lond.* 264: 249-258.
- MECH, L.D. (1966): The wolves of Isle Royale. U.S. Nat. Park Serv. Fauna Ser. No. 7: 210pp.
- MECH, L.D. (1970): The wolf. The ecology and behaviour of an endangered species. University of Minnesota Press, Minneapolis, USA. 384pp.
- MECH, L.D.; BOITANI, L. (eds.) (2003): Wolves: Behavior, ecology, and conservation. University of Chicago Press. 465pp.
- MERIGGI, A.; BRANGI, A.; MATTEUCCI, C.; SACCHI, O. (1996): The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography* 19(3): 287-295.
- MERIGGI, A.; LOVARI, S. (1996): A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *J. Appl. Ecol.* 33: 1561-1571.
- MOORE, T. D.; SPENCE, L.E.; DUGNOLLE, C.E. (1974): Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Dept. Bull. No. 14: 177pp.
- MOSHØJ, C.M. (XXXX): Foraging behaviour, predation and diet of European lynx (*Lynx lynx*) in Sweden. M.Sc. Thesis, Dept. of Population Ecology. University of Copenhagen. Manuscript II. 42pp.

- NOWAK, S.; MYŚLAJEK, R.W.; JĘDRZEJEWSKA, B. (2005): Patterns of wild wolf *Canis lupus* predation on wild and domestic ungulates in the Western Carpathian Mountains (S Poland). *Acta Theriol.* 50(2): 263-276.
- OKARMA, H. (1995): The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta Theriol.* 40(4): 335-386.
- OLSSON, O.; WIRTBERG, J.; ANDSSON, M.; WIRTBERG, I. (1997): Wolf *Canis lupus* predation on moose *Alces alces* and roe deer *Capreolus capreolus* in south-central Scandinavia. *Wildl. Biol.* 3(1): 13-25.
- ØSTRENG, O.-C. (2000): Wolves (*Canis lupus*) in the counties of Akershus and Østfold – diet in the summer and prey selectivity. Institutt for Biologi og Naturforvaltning. Norges Landbrukshøgskole. 41pp.
- PALM, D. (2001): Prey selection, kill and consumption rates of moose by wolves in central Sweden. Examensarbete. Grimsö Research Station, Swedish University of Agricultural Sciences, Uppsala. 21pp.
- PEDERSEN, H.C.; WABAKKEN, P.; ARNEMO, J.M.; BRAINERD, S.M.; BRØSETH, H.; GUNDERSEN, H.; HJELJORD, O.; LIBERG, O.; SAND, H.; SOLBERG, E.J.; STORAAS, T.; STRØMSETH, T.H.; WAM H.; ZIMMERMANN, B. (2005): Rovvilt og Samfunn (RoSa). Det skandinaviske ulveprosjektet – SKANDULV. Oversikt over gjennomførte aktiviteter i 2000-2004. NINA Rapport 117. 78pp.
- PETERSON, R.O.; WOOLINGTON, J.D.; BAILEY, T.N. (1984): Wolves of the Kenai Peninsula, Alaska. *Wildl. Monogr.* No. 88: 52pp.
- POTVIN, F.; JOLICOEUR, H.; HUOT, J. (1988): Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. *Can. J. Zool.* 66: 1274-1279.
- REYNOLDS, J.C.; AEBISCHER, N.J. (1991): Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. *Mammal Rev.* 21(3): 97-122.
- SALVADOR, A.; ABAD, P.L. (1987): Food habits of a wolf population (*Canis lupus*) in León province, Spain. *Mammalia* 51(1): 45-52.
- SAND, H.; WIKENROS, C.; WABAKKEN, P.; LIBERG, O. (2006): Cross-continental differences in patterns of predation: Will naive moose in Scandinavia ever learn? *Proc. R. Soc. Lond. B.*
- SAND, H.; WIKENROS, C.; WABAKKEN, P.; LIBERG, O. (in press): Wolf (*Canis lupus*) hunting success on moose (*Alces alces*) in Scandinavia: The effect of hunting group size, snow depth, and age of breeding wolves. *Anim. Behav.*
- SAND, H.; ZIMMERMANN, B.; WABAKKEN, P.; ANDRÉN, H.; PEDERSEN, H.C. (2005): Using GPS technology and GIS cluster analyses to estimate kill rates in wolf – ungulate ecosystems. *Wildl. Soc. Bull.* 33(3): 914-925

- SAND, H. (2005): Abstract from the „International Wolf Conference“, Colorado, USA.
- SCOTT, B.M.V.; SHACKLETON, D.M. (1980): Food habits of two Vancouver Island wolf packs: a preliminary study. *Can. J. Zool.* 58: 1203-1207.
- SIDOROVICH, V.E.; TIKHOMIROVA, L.L.; JĘDRZEJEWSKA, B. (2003): Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. *Wildl. Biol.* 9(2): 103-111.
- ŚMIETANA, W. (2005): Selectivity of wolf predation on red deer in the Bieszczady Mountains, Poland. *Acta Theriol.* 50(2): 277-288.
- SPAULDING, R.L.; KRAUSMAN, P.R.; BALLARD, W.B. (1997): Calculation of prey biomass consumed by wolves in northwest Alaska. *J. Wildl. Res.* 2(2): 128-132.
- SPAULDING, R.L.; KRAUSMAN, P.R.; BALLARD, W.B. (1998): Summer diet of Gray Wolves, *Canis lupus*, in northwestern Alaska. *Can. Field-Nat.* 112(2): 262-266.
- SUNDE, P.; KVAM, T.; BOLSTAD, J.P.; BRONNDAL, M. (2000): Foraging of lynxes in managed boreal-alpine environment. *Ecography* 23: 291-298.
- SVENSKA JÄGAREFÖRBUNDET (2005): Jägareförbundets Viltövervakning [www.jagareforbundet.se].
- SWEDISH WILDLIFE DAMAGE CENTRE (2004): Viltskadestatistik 2003. [www.viltskadecenter.se].
- SWEDISH WILDLIFE DAMAGE CENTRE (2006): Nyhetsbrev Nr. 1. [www.viltskadecenter.se].
- TEERINK, B.J. (1991): Hair of west european mammals. Cambridge University Press, Cambridge. 224pp.
- THEBERGE, J.B.; COTTRELL, T.J. (1977): Food habits of wolves in Kluane National Park. *Arctic* 30: 189-191.
- THEBERGE, J.B.; OOSENBURG, S.M.; PIMLOTT, D.H. (1978): Site and seasonal variations in food of wolves, Algonquin Park, Ontario. *Can. Field-Nat.* 92(1): 91-94.
- THEUERKAUF, J. (2003): Impact of man on wolf behaviour in the Białowieża Forest, Poland. Ph.D. Thesis. Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt, Technische Universität München. 96pp.
- TRAVES, J.L. (1983): An assessment of quantity of prey consumed by wolves through analysis of scats. M.Sc. Thesis, Northern Michigan Univ., Marquette. 32pp.
- TREMBLAY, J.-P.; JOLICOEUR, H.; LEMIEUX, R. (2001): Summer food habits of Gray Wolves in the boreal forest of the Lac Jacques-Cartier highlands, Québec. *Alces* 37(1): 1-12.
- TRITES, A.W.; JOY, R. (2005): Dietary analysis from fecal samples: how many scats are enough? *J. Mammal.* 86(4): 704-712.
- VALDMANN, H.; KOPPA, O.; LOOGA, A. (1998): Diet and prey selectivity of wolf *Canis lupus* in middle- and south-eastern Estonia. *Baltic Forestry* 4(1): 42-46.

- VOIGT, D.R.; KOLENOSKY, G.B.; PIMLOTT, D.H. (1976): Changes in summer foods of wolves in central Ontario. *J. Wildl. Manage.* 40(4): 663-668.
- VOS, J. (2000): Food habits and livestock depredation of two Iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. *J. Zool., Lond.* 251: 457-462.
- WABAKKEN, P.; SAND, H.; LIBERG, O.; BJÄRVALL, A. (2001): The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. *Can. J. Zool.* 79: 710-725.
- WEAVER, J.L.; ARVIDSON, C.; WOOD, P. (1992): Two wolves, *Canis lupus*, killed by a moose, *Alces alces*, in Jasper National Park, Alberta. *Can. Field-Nat.* 106(1): 126-127.
- WEAVER, J.L. (1993): Refining the equation for interpreting prey occurrence in gray wolf scats. *J. Wildl. Manage.* 57(3): 534-538.
- WIKENROS, C. (2001): Wolf winter predation on moose and roe deer in relation to pack size. Examensarbete. Grimsö Research Station, Swedish University of Agricultural Sciences, Uppsala. 24pp.
- ZABALA, J.; ZUBEROGOITIA, I. (2003): Badger, *Meles meles* (Mustelidae, Carnivora), diet assessed through scat-analysis: a comparison and critique of different methods. *Folia Zool.* 52(1): 23-30.