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Wolf predation and habitat use in relation to moose density during winter

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Abstract

The wolf (*Canis lupus*) predation on moose and roe deer was studied during winter in the west-central parts of Sweden (Nyskoga territory). The wolf distribution and predation in relation to moose density was studied in five different wolf territories in the central parts of Sweden (Nyskoga 2000-2001, Grangärde 1999-2000, Grangärde 2000-2001, Leksand 1998-1999 and Hagfors 1998-1999).

The Nyskoga pack was established during the winter of 1999-2000 (Aronsson *et al*. 2000) and consisted of four animals, two adults forming a alpha pair and one male and one female pupp, during the study period.

During the predation study period, a total of nine mooses and one roe deer were classified to have been killed by wolves. Additionally, one moose and one roe deer were assumed to have been killed by wolves. Kill rate on moose in the Nyskoga study ranged from 10.9 moose/wolf/year to 13.6 ungulates/wolf/year. Sex distribution of the moose carcasses was 89 % female and 11 % males. The age distribution was 30 % calves, 50 % yearlings and 20 % adults among the moose killed by wolf. The consumption rate was 3.6-kg/kg wolf/day and the initial utilization on moose carcasses was 76 % of the consumable parts.

The spatial distribution pattern of wolves in the study was aggregated in four and random in one of the five territories. Moose density was higher inside the 50 % kernel of the wolf territory in Nyskoga ($p<0.001$), but no other territory showed a positive difference that were significant. In Leksand and Grangärde 00-01, ($p<0.05$), were moose density higher outside the 75 % kernel of the territories. A Spearman rank test on moose density and wolf telemetry positions showed no significant correlation between the parameters. This shows that there is no connection between the moose density and the habitat usage of wolves.

No significant relationship was detected between moose density at the location of moose carcasses and moose density in general.

Introduction

Most studies on feeding ecology of wolves have been conducted in North America (e.g. Cook *et al*. 1999; Bergerud and Elliott 1998; DelGiudice 1998; Thurber and Peterson 1993; Kunkel and Pletscher 2000). Recently, several studies on wolf predation have been conducted in Scandinavia as well, (Gade-Jorgensen and Stagegaard 2000; Olsson *et al*. 1997; Palm 2001; Wabakken *et al*. 2001; Wikenros 2001).

Wolves are known to prey on a variety of animal species (Custa *et al*. 1991; Okarma 1995) and in most areas large ungulates are the most important prey (Filonov 1980; Fuller and Keith 1980; Marquad-Petersen 1998). In northern boreal regions are moose (*Alces alces* L.) often the primary prey specie (Filnov 1980; Olsson *et al*. 1997; Hayes *et al*. 2000). In their search for prey, wolves are often assumed to be selective (Carbyn 1983; Ballard *et al*. 1987; Huggard 1983a), meaning that there is a disproportional predation on different prey categories. The selectiveness varies a lot, with the highest degree of variation found in colonizing and low-density wolf populations (Fritts and Mech 1981; Huggard 1993b; Boyd *et al*. 1994). The kill- and consumption rate varies in time and space due to differences in wolf and prey densities (Messier and Crete 1985; Ballard *et al*. 1987), prey species composition (Kolensky 1972; Messier and Crete 1985), snowconditions (Peterson *et al*. 1984) and pack size (Hayes *et al*. 1991; Dale *et al*. 1995).

The moose population on the Scandinavian Peninsula has experienced a dramatic increase during the last 50 years. The increase occurred due to several factors and forest management, lack of predators and changes in the moose harvesting strategies is likely some of them (Markgren 1984). The high increase in the moose population lead to large-scale damages on the forest, but the moose also became an economically important game specie. This has started a debate among hunters and forest owners, mainly arguing about the size on the moose population.

During the 1990`s the wolf population on the Scandinavian Peninsula (Sweden and Norway) has increased annually with a growth of 20-30% (Wabakken *et al*. 2001). In spring 2001, the wolf population in Scandinavia was estimated to consist of 87-97 individuals (Aronsson *et al*. 2001). Despite a substantial increase during the last decade, the population is still small and threatened. Since one of the major threats is lack of local human acceptance, among other things caused by competition for important game, it is of great importance to understand the influence that wolf predation has on it's prey species. Primarily the conflict with humans concern moose (*Alces alces*), roe deer (*Capreolus capreolus*) and with the semi-domesticated reindeer (*Rangifer tarandus*) in the nothern parts of Sweden.

This study is divided into two parts, one predation study and one habitat selection study. The aim of the predation study was to locate as many moose and roe deer carcasses as possible within the Nyskoga territory to determine kill rate and prey selection.
The habitat selection study included documentation of wolf distribution in relation to the distribution of ungulates (moose and roe deer). It was based on my own data from the Nyskoga territory and data collected in three other territories by the Scandinavian wolf project (Skandulv). The specific aims of the study were:

1. What is the age and sex distribution of moose killed by wolf in Nyskoga territory?
2. What are the initial utilization, consumption and kill rate in the Nyskoga territory?
3. How are wolves spatially distributed in the territory?
4. Is the wolf located to areas with locally higher moose densities in the territory and is there a relationship with wolf spatial distribution and moose density?
5. Is there a relationship between moose kill site location and moose density?

Material and Methods

Study areas

The predation study was conducted in Nyskoga territory (60°50´N, 12°90´E) in the northern part of the county of Värmland. The area is dominated by coniferous forest, consiting mainly of Norway spruce *(Picea abies*) and Scotch pine (*Pinus sylvestris*). Deciduous species like birch (*Betula sp.)* willows *(Salix sp.)* aspen *(Populus tremula)* and alders *(Alnus sp.)* occur interspersed in the area. Large predators, accept from wolf, in the area is lynx (*Lynx lynx*) and brown bear (*Ursus arctos*). Other important mammalian species occuring in the area are moose (*Alces alces*), roe deer (*Capreolus capreolus*), red fox (*Vulpes vulpes*), beaver (*Castor fiber*), mountain hare (*Lepus timidus)* and badger (*Meles meles*). Avian species, such as capercaillie (*Tetrao uroguallus*), black grouse (*Tetrao tetrix*) and raven (*Corvus corax)* are common and occasionally the golden eagle (*Aquila chrysaetos*) has been seen in the area.
The altitude ranges from 128 to 593 m. a. s. l. The average temperature in January and July is –7°C and 14°C respectively, with a year around average of 3°C. The snow cover in this area of Sweden usually persists for 150 days (Raab and Vedin 1995).

The habitat selection study was preformed with an GIS approach. Information from following territories was used:

- The Hagfors territory (core area: 60°20`N, 13°80`E) was studied during the winter of 1998-99 and is situated in the northern parts in the county of Värmland. Hagfors territory was not used in the analysis of the relationship of moose carcasses and moose density since no predation study was preformed here.
- The Leksand territory (core area: 60°40´N, 14°30´E) this area was studied during the winter of 1998-99.
- Grangärde territory (core area: 60°20´N, 14°50´E), studied during the winters of 1999-00 and 2000-01.

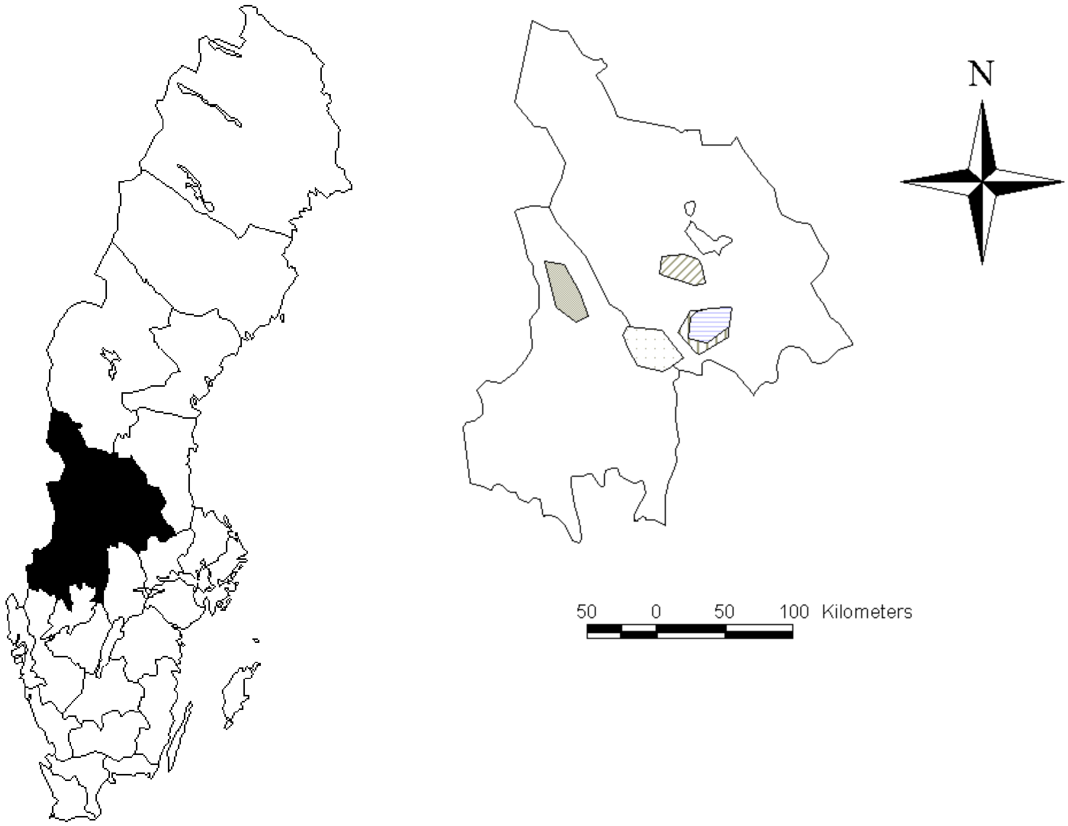

Figure 1. Sweden with the counties of Värmland and Dalarna marked in black. The map to the right shows the locations of the four different territories. Nyskoga is located to the left and is marked with a squared pattern; the dotted one in the lower central part is the Hagfors territory 1998-1999. Grangärde territory is located slightly to the right of Hagfors, observe that the territory boundaries of Grangärde 2000-2001 (vertical stripes) lay beneath Grangärde 1999-2000 (horizontal stripes). Leksand 1998-1999 (diagonal stripes) is situated between Grangärde lake Siljan (non-filled)

Monitoring radiomarked wolves

The predation study in Nyskoga was conducted during the winter and spring of 2001, from 25th of January to 7th of April, a total of 74 days. The wolves were monitored by ground-based radio-telemetry, using an Rx-98 Televilt receiver and snow-tracking along wolf trails. During each day of observation the goal was to locate the wolves position at least twice a day, but as many positions as possible during the 24 hour period was preferred. Positioning was spaced in time, preferably one in the morning and one in the evening. In total 175 positions were collected during the predation study period in Nyskoga. To determine the position of the wolves (accuracy of 100 meter), standard telemetry triangulation method (Kenward 1987) was used, and at least three different bearings were used. Snow tracking was conducted as often as time and weather allowed.

Search for carcasses

Locations where the wolves were stationary for a longer period, or repeatedly returned to, were investigated for carcasses. Messier and Crête (1985) found that wolves often spend more than 48 hours on handling a moose carcasses. Palm (2001) found that the handling time for a roe deer was 1.1 days. Therefore we searched for ungulate carcasses on places where the wolves had stayed for a time period of 24 hours or more. We also used observations of scavenging ravens flying towards or hovering over a specific area. Tracks from red fox, and in a few cases, sightings of golden eagles helped us find kills. Wolf trails were followed as often as possible to find kills that we did not have indications of. All ungulate carcasses were investigated *in situ* and at the kill site we took positions using a Garmin 12 xl GPS calibrated to Swedish Grid (RT 90).

The carcasses were examined for specie, cause of death, age, sex and degree of consumption. Age classification was determined in following classes: calf, yearling and older than 2 years of age. The ageing was made on basis of tooth replacement and colour. Calves have 3 premolars and one molar, while individuals older than 1 year have three of each. The three premolars are whiter than the three molars for yearlings, but not for adults. Sex was determined by the occurrence of pedicel on the skull or by sexual organs.

Ungulate census

Moose density inside wolf territories during winter was determined by counting faecal pellet groups in small sample plots (Neff 1968). The size and location of the census area was determined by the core area of wolves. For every second kilometer within each census area, a square of 1000*1000 m were placed. Every 100 m along each census line a sample plot of 100 m^2 were placed, making up a total of 40 plots for each square. In Leksand 1998-1999 and in Grangärde 1999-2000, moose census were also conducted from the air during winter. The moose density at different location was calculated and added to the GIS program.

Found prey was classified in three different mortality categories:

- Prey were classified as dead prior to the intensive study period if the carcass was know to have been killed prior to the intensive study period and the wolves came back to scavenge.
- Prey was classified as positively killed by wolves when tracks from wolf attacking and/or heavy bleedings were found in the snow near the carcass (Hayes et al. 2000; Thurber and Peterson 1993; Messier and Crête 1985).
- Prey were classified as assumed to have been killed by wolves when tracks from wolves and any small amount of blood were found near the carcass**.**

According to unpublished data from the Swedish Hunter organisation, the live body mass of calves, yearlings and adult female moose is 170, 310 and 330 kilos respectively.Their data were collected during the autumn moose hunt in the southern parts of the county of

Dalarna). The Nyskoga territory is situated not far from southern Dalarna, why it is assumed that moose body weights are similar. The live weight reduction from fall to mid February is 5 %, 6% and 9% for adults, yearlings and calves respectively (Cederlund *et al*. 1992; Sand *et al*. unpublished data). This means that live weights were reduced to 314 kg for adult females, 291 kg for yearlings and 155 kilos for calves. The average roe deer live weight during winter was assumed to 22.5 kg (Cederlund and Liberg 1995). The consumable biomass of the moose was estimated to be 66 % (Hayes *et al*. 2000) and 80 % of the live weight for roe deer (Glowacinski and Prufus 1997). For large prey such as moose, the loss to scavenger is negativly correlated to pack size. According to Promberger (1992), the amount of meat consumed of a moose carcass by a wolf pack of 4 is 67 %. For small prey such as roe deer the loss to scavengers was regarded as zero. The proportion of consumable tissue removed after the first utilisation by wolves was visually estimated to the nearest 10 %. Edible tissue of moose and roe deer was assumed to be everything except fur, rumen, and bones in the skull, spinal chord, pelvis and legs.

Wolf weight during winter were set to 51, 39 and 35 kg during winter for adult male, adult female and pups respectively (Sand *et al*. 2000)

Consumption- and kill rates

Daily consumption rate (kg/wolf/day, kg/kgwolf/day) was determined by taking the total amount of meat consumed by the pack between the first and last kill, divided with number of days during the period (ND) and the number of wolfs in the pack (giving kg/wolf/day), or the weight (kg) of the pack (giving kg/kgwolf/day). When the effect of scavengers was adjusted for, the total amount of meat consumed was multiplied with the wolf portion factor 0.67 (see the chapter: Ungulate census). The formulas used are presented in appendix 3.

Territorial utilization

During the winter period, from October 15th to the first of April, the wolves were located by radio telemetry every second/third day in the territories. The wolves positions and the faecal group count of moose were added into the Geographical Information System program Arc View 3.2 (ESRI 1996) with the following extensions: Animal Movement SA v 2.03 beta (U.S.G.S Alaska Biological Science Centre), The Analysis Extension and Spatial Analyst (ESRI 1996). Wolf territory sizes were calculated using minimum convex polygon (MCP) (White and Garrott 1990). The core areas of wolves during winter were calculated with a fixed kernel using both 50 % and 75 % levels.

Table 1. Number of telemetry positions (wolf positions) during the winter period, moose density / 1000ha (mean;S.D.) territory size (MCP) and core areas calculated by using 50 % and 75 % kernel in the five territories.

Territory	**No. Positions**	**Moose density**	**Territory size (km^2) MCP**	**Core area (km^2) Kernel 50%**	**Core area (km^2) Kernel 75%**
Grangärde 99-00	121	11.7±4.9	812.0	95.6	446.1
Grangärde 00-01	155	10.0±4.3	880.7	92.5	249.5
Hagfors	67	10.7±4.3	926.5	54.3	280.9
Leksand	125	9.0±4.6	1738.6	440.5	545.1
Nyskoga	84	11.5±4.9	712.5	184.2	399.5

The spatial distribution pattern of wolves was calculated by using the Index of Dispersion method[1] (Krebs 1989) and then statistically tested by using the chi-square method with a two-way classification. The Index of Dispersion is based on the theory behind Poisson distribution, where the expected value always is 1.0 and therefore all situations are supposed to be without deviations. The formula thus is

$$I = \frac{s^2}{m} \qquad \chi^2 = I(n-1)$$

where **I** is the Index of Dispersion, **s** is the observed variance and **m** is the observed mean. **n** is the number of quadrates counted and χ^2 is the value of chi-square with n-1 degrees of freedom. The Index of Dispersion creates a two tailed χ^2 test since there are two possible directions of deviation. If the organisms are uniformly spaced, the variance will be less than the mean, and the index value will be less than 1. If organisms are aggregated, the observed variance will be greater than the mean and the index value will be larger than 1.

To determine the moose density in- and outside wolf utilization area, an interpolated grid of the moose density and Kernels of 50 and 75 % were used. The interpolation was created in Arc View 3.2b and cell size was fixed to 5000*5000 meters. Moose density was calculated in three different ways, using the value of the four and twelve nearest neighbouring cells and the values within a radius of 3000 meters from the location. This was tested statistically by using an unpaired t-test.

To test if there was a relationship between the time wolf spend in an area and moose density, the same grid, created in the former test, was used. For each cell, moose density

[1] Also called "Coefficient of Dispersion" in Sokal and Rohlf,1989

and the number of wolf telemetry positions were calculated. Correlation between these values was tested statistically by using a Spearmann Rank (Spearmann's Rho) correlation.

The predation pressure in relation to moose density was determined by linking each location of a moose kill to the moose density (determined through the interpolations made in the test above). All carcasses, inside the moose census areas including those found at a maximum distance of 2 kilometres outside censused areas, were added to this specific study. The territories used were Grangärde 99-00, 00-01 and Nyskoga. Leksand was rejected because only four moose carcasses were found within the moose census area (se table 2), and Hagfors due to circumstances mentioned earlier. These values were tested statistically by using an unpaired t-test.

Table 2. Number of killed moose in each territory during winter. Total number of killed moose (T) and number of killed moose in the fecal inventory area (F).

T erritory	Study year	No. moose carcass (T)	No. moose carcasses in (F)
Grangärde	1999-2000	21	20
Grangärde	2000-2001	31	31
Nyskoga	2000-2001	10	9
Leksand	1998-1999	14	4

Results

Wolf monitoring and carcass findings

The wolves were tracked 130 km on ski and 71 km by either car or snowmobile, giving a total of 201 km. During the study period, carcasses of 10 moose, 2 roe deer, one mountain hare and two black grouse were found. Of the 10 moose, were 9 killed during the study period, and one prior to its start. Nine moose and one roe deer were positively identified as killed by wolf, and one roe deer was assumed to have been killed by wolves. The hare and the black grouses were all positively identified as killed by wolf. The average time between an ungulate was killed and it was found was 3.9 ± 2.6 days. The interval between the first and the last killed moose found during our study was 67 days.

Prey selection

The total biomass available (all ungulates assumed and positively identified as killed by wolves) was 2593 kg. The proportion of moose was 2548 kg (98.3 %) and roe deer 45 kg (1.7%). The age distribution of killed moose (N=10) was 30% calves, 50% yearlings and 20% adults. The sex distribution among the killed mooses was 89 % females and 11 % males. The age and sex of the roe deer could not be determined since the wolves did not leave mandibles, skulls or sexual organs.

Consumption and kill rate

The average proportion consumed of adults (n=7) was 65.7 ±15.5% and calves (n=3) 100% with an average of 76 ± 15.1 %. The average amount of meat consumed from an adult moose was 126.0± 28.6 kg and 100.75 kg of the calves. The roe deer killed in the study (n=2) was totally consumed and each provided 18 kilos of meat.

To each wolf the total available amount of meat per day was 8.5 kilo (mortality category 2 and 3) and 7.9 kilo (mortality category 2). Each wolf consumed 5.3-5.84 kilos of meat/day and the amount per kgwolf/day was 0.13-0.15 kg without the effect of scavengers. With the effect of scavengers included in the calculations, each wolf in the pack consumed 3.6-3.9 kilo and the amount per kgwolf/day was 0.09 kg.

Table 3. Food availability, consumption and consumption with effects of scavengers adjusted for, calculated as kg/wolf/day, and kg/kgwolf/day within brackets. (a) Ungulate positively killed by wolf, (b) ungulates positively and assumed killed by wolf.

Total biomass		**Consumable**		**Consumption adjusted for loss to scavengers**	
(a)	(b)	(a)	(b)	(a)	(b)
7.9 (0.19)	8.5 (0.21)	5.3 (0.13)	5.84 (0.15)	3.6 (0.09)	3.9 (0.09)

The kill rate ranged from 8.4 days/moose (positively identified as killed by wolves) to 6.7 (assumed and positively killed by wolves) days/ungulates. In a period of 100 days, wolves killed 11.9 mooses, for assumed and positively killed ungulates, the number is 14.9. Observations and/or tracks from scavengers were found at al kill sites of both moose and roe deer (N= 12).

Table 4. Wolf kill rate in moose and ungulates in different units and prey combinations from Nyskoga territory 2000-2001.

Unit	**Moose (n=8)**	**Positively killed ungulates (n=9)**	**Positively + assumed killed ungulates (n=10)**
Days/ind.$^{-1}$	8.4	7.4	6.7
No./100 days^{-1}	11.9	13.5	14.9
No./ year^{-1}	43.5	49.3	54.4
No./100 days^{-1} wolf^{-1}	3.0	3.4	3.7
No./year^{-1} wolf^{-1}	10.9	12.3	13.6

Territorial distribution

The distribution patterns in the different territories during winter were aggregated in four territories and random in one (table 5). In Nyskoga, Grangärde 00-01 and Hagfors the significance level was <0.01 and in Grangärde 99-00 <0.05.

Table 5. The spatial distribution pattern of wolf, determined by using Index of Dispersion method, in the different wolf territories.

Territory	Index of Dispersion	Chi-square	Degree of freedom	Spatial pattern	Level of significance
Nyskoga	2.126	36.14	17	Aggregated	<0.01
Grang. 00-01	1.693	52.49	31	Aggregated	<0.01
Grang. 99-00	1.549	51.12	33	Aggregated	<0.05
Leksand	1.294	54.70	50	Random	N.S
Hagfors	2.283	91.34	40	Aggregated	<0.01

Wolf habitat usage in relation to moose density

The moose density in- and outside 50 and 75 % fixed Kernel made from wolf habitat utilization shows that the density was higher in both Nyskoga and Grangärde 99-00, but the difference was only significant in Nyskoga (50 %)($p<0.01$). In Grangärde 00-01 and in Leksand territory the moose density was significantly larger outside the 75 % Kernel ($p<0.05$).

Table 6. Moose density in and outside (mean±SD) 50 % fixed kernels.

Territory	Moose density (inside)	Mosse density (outside)	Degree of freedom	t-value	p-value
Nyskoga	12.7±5.4	8.1±3.2	61	4.207	<0.001
Grang. 00-01	8.9±4.0	10.6±4.5	89	-0.140	0.8886
Grang. 99-00	13.8±6.0	9.7±3.4	103	0.344	0.7313
Hagfors	8.2±3.3	13.2±4.8	53	-0.457	0.64940
Leksand	8.4±4.1	10.1±5.4	56	-0.345	0.7317

Table 7. Moose density in and outside (mean±SD) 75 % fixed kernels.

Territory	Moose density (inside)	Moose density (outside	Degree of freedom	t-value	p-value
Nyskoga	17.8±6.4	8.1±2.7	62	1.709	0.0924
Grang. 00-01	9.7±3.6	10.1±4.4	103	2.195	0.0304
Grang 99-00	12.7±3.9	11.6±5.0	89	-0.890	0.3761
Leksand	8.5±4.0	9.4±4.8	53	-2.259	0.0280
Hagfors	9.4±3.8	10.9±4.4	55	-0.649	0.5188

A Spearmann Rank correlation were preformed to see if there was a correlation between moose density and wolf distribution in the studied territories. No correlation between the two parameters was detected in the test. To rule out any effect in calculating the interpolation, three different calculations was used.

Table 8. Results from a Spearmann rank correlation between no. wolf monitoring positions and moose density.

Location	Interpolation calculation	Rho	p-value
Nyskoga	4	0.17	0.41
Nyskoga	12	0.25	0.21
Nyskoga	Radius	0.21	0.24
Grangärde 99-00	4	0.25	0.11
Grangärde 99-00	12	0.29	0.12
Grangärde 99-00	Radius	0.22	0.25
Grangärde 00-01	4	0.03	0.85
Grangärde 00-01	12	-0.07	0.68
Grangärde 00-01	Radius	-0.14	0.39
Leksand	4	-0.05	0.81
Leksand	12	-0.02	0.91
Leksand	Radius	-0.14	0.51
Hagfors	4	-0.08	0.97
Hagfors	12	3.76E-4	0.99
Hagfors	Radius	-0.13	0.50

Moose density at kill site locations in relation to moose density

Three territories were used (Nyskoga and Grangärde, both years) in the study to determine if there is a relationship between density of moose and the moose density at kill sites of moose. None of the territories used showed a connection between the parameters (se table 10). To rule out any effect in calculating the interpolation, three different calculations was used.

Table 10. Results from a un-paired t-test of moose density at the location of a moose carcass and the moose density at inventory points for faecal inventories with different calculation methods

Territory	Study year	Interpolation calculation	Degrees of freedom	p-value
Nyskoga	2000-2001	4	70	0.1758
Nyskoga	2000-2001	12	70	0.2200
Nyskoga	2000-2001	Radius	70	0.3022
Grangärde	1999-2000	4	123	0.5316
Grangärde	1999-2000	12	123	0.5249
Grangärde	1999-2000	Radius	123	0.7706
Grangärde	2000-2001	4	120	0.9418
Grangärde	2000-2001	12	120	0.8598
Grangärde	2000-2001	Radius	120	0.9638

Discussion

Age and sex of ungulate killed

The age distribution among killed moose in Nyskoga indicatse a preference in wolves for yearlings (50%). This deviates from the general opinion that wolves prefer calves and older animals (i.e. Mech 1970, Fritts & Mech 1981, Peterson *et al*. 1984, Ballard *et al.* 1987, Bjorge & Gunson, 1989). There are several possible reasons for this. Snow conditions have an effect on the selection of the age category (Huggard 1993c) According to Peterson (1977), the risk of being killed increased at a snow depth of 75 cm. Also Peterson and Allen (1974) found that moose vulnerability to wolves started to increase at a moose track depth of 50 cm. During this study, snow depth was not often recorded to more than 40 cm for longer periods, and since crust occurred during winter it is not likely that snow was a problem for moose. Therefore is it not likely that snow dept was the reason for this unexpected result. The only likely reason I could find then was a skewed age ratio with an overrepresentation of yearlings in the moose population .

The amount of females killed in the study was much higher than the amount of males. This correlates with the result from Olsson *et al*. (1994) that was conducted in the northern parts of the county of Värmland. Peterson *et al*. (1984) also found a prey selection preference on females. Female moose could bee easier to kill for a wolf since they are smaller and that they don't have antlers. The predation preference on female could also depend on a skewed sex ratio in the moose population.

Consumption- and kill rate

The consumption rate (kg/kgwolf/day) in this study (0.09 kg) was higher than in the found by Palm in another Swedish wolf territory (2001) (0.04-0.05 kg), but not compared with studies in North America (Messier and Crête 1985, Ballard *et al*. 1997, Fuller and Keith 1980, Peterson and Page 1988, Haber 1977, Peterson et *al*. 1984). The different results of this study and the one conducted by Palm (2001) are likely to depend on a higher initial utilization of the moose carcass and also a higher preference for yearlings and adult moose rather than predating on calves as the [illegible] was in Palms (2001) study.

The large number of ravens seen at the kill sites could depend on the fact that the city of Torsby, and other parts of Torsby municipality, deposits their garbage in the southern parts of the wolf territory. This dump is providing an excellent opportunity for ravens to gather in large numbers. This could bias the amount of kg meat that each wolf can utilize, since it attracts birds to the area, increasing the local population of scavenging birds.

Territorial distribution

There are three main types of distribution. (**i**) Random, occurs when there is an equal probability of an organism occupying any point in space, and when the presence of one individual does not influence the presence of another. (**ii**) Regular, occurs either when each individual has a tendency to avoid all other individuals, or when individuals that are too close to other individuals die or leave the population altogether. (**iii**) Aggregated, occurs either when individuals all tend to be attracted to particular parts of the environment, or when the presence of one individual at a location attracts or gives rise to other individuals at the same location (Begon *et al*. 1996).

This study shows that wolves are located to specific areas within the territory limit, meaning that wolves are aggregated in their distribution. The reason for that could be linked to feeding behaviour, social interests or other aspects as disturbance by people i.e. hunting, that makes the wolves prefer or reject specific areas within the territory. The aggregation patterns found among wolves in this work supports what Cook *et al*. 1999 found at Algonquin Park in a wolf-deer ecosystem.

There are various types of behaviour underlying the aggregative response of a consumer, but they fall into two broader categories: those involved with the location of profitable patches, and those that represent the response in which consumers perceive, at a distance, the existence of heterogeneity in the distribution of their prey (Begon *et al.* 1996).

Wolf habitat usage in relation to moose density

In this work, three connections between wolf territory utilization and moose density was found. One positive and two negative relations was found, the positive was relationship was found in Nyskoga at the 50 % kernel and the negative correlation in Grangärde 00-01 and in Leksand, both in the 75 % kernel study. In no other case was there a connection between moose density and wolf territorial utilization. Several studies show that prey abundance has an effect on the habitat selection of wolf i.e. Ballard *et al*. 1997, Massolo and Meriggi 1998, Kunkel and Pletscher 2000. This study shows that there probably is a connection between moose density and wolf spatial distribution within the territory limits.

Studies have been conducted in the North America and Europe and they conclude that locations of wolf territories are determined of not only prey abundance, but instead they depend on several factors. (**i**) Prey abundance (Massolo and Meriggi 1998, Kunkel and Pletscher 2000, Ballard *et al*. 1997). (**ii**) Human disturbance / presence (Massolo and Meriggi 1998, Ciucci *et al* 1997, Mladenoff *et al* 1995). (**iii**) Forest cover (Massolo and Meriggi 1998, Kunkel and Pletcher 2000 and Ciucci *et al* 1997).

There are several factors that seems to interact on the wolfs habitat choice, and they can vary over the year, i.e. Ballard *et al*. 1997, found that wolf packs did not follow migrating caribou, but instead the stayed at year-round resident territories. However if the migration caribou were absent and the moose density was low, up to 17 % of the packs followed migrating caribou, but then returned to their original territory for denning (Ballard *et al*. 1997). In Sweden, as a general, the winter population of moose is very high in general (10-15 moose/1000 ha). This means that the moose distribution dosen't attract wolves to certant areas and thereby no connection with moose density is found. With a lower moose population in the area, perhaps, wolf will be more dependent on its food source and thereby spend more time in areas with higher moose densities. This would lower the handling time since they will reduce the time spent to search for a feeding opportunity.

A study conducted in central Ontario revealed that even though moose were relatively constant in availability, and a major food item, the wolf population was responding primarily to the availability of deer (*Odocoileus virginianus*). Even a small population of deer 0.02/km^2 prompted movement of wolves toward the deer yard (Forbes and Theberge 1996). In the studied areas there were small populations of roe deer, they could have an attracting force on the wolf. Thereby wolves would spend time in an area with a population of roe deer instead of areas with locally higher moose populations.

A lot of people hunt during the study period, from the middle of October to the beginning of April, this gives a high disturbance / presence of people. A special case is during the moose hunt, this is a period of more or less constant disturbance for a week or two in the forest by both, people and dogs. This could have an effect on the wolf distribution. Also, a lot of forest management actions are conducted during this time period.

The wolf is a territorial animal, this means that it defends its territory against other wolfs from nearby packs. To sustain the borders, wolf has to been in areas with, perhaps, low moose density to defend the territory. This gives telemetry positions in areas that wolves may not use as hunting areas. In the short perspective, this could effect the outcome of this test and maybe a longer time perspective is needed to make sure that there are or aren't a connection between the wolves and the moose abundance on the Scandinavian peninsula.

Conclusion

- The wolf pack in Nyskoga has a kill rate of 10,9 moose/wolf/year to 13,6 ungulates/wolf/year
- The proportion of moose that was consumed were in average 76 ± 15.1 %. The utilization of adults (n=7) was lower (65,7 ±15.5%) than of the calves (n=3, 100%)
- Each wolf consumed 5,84 kilos of meat/day and the amount per kgwolf/day was 0,15 kg without the effect of scavengers. With the effect of scavengers, each wolf consumed 3,9 kilos and per kgwolf/day the amount was 0,09 kilo.
- The spatial distribution pattern was aggregated in four of five studied territories.
- The moose density was higher inside the 50 % kernel made in Nyskoga, no other test showed a positive relation between moose density and wolf habitat utilization
- No connection between moose density and moose density at the kill site was found.

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Appendix 1

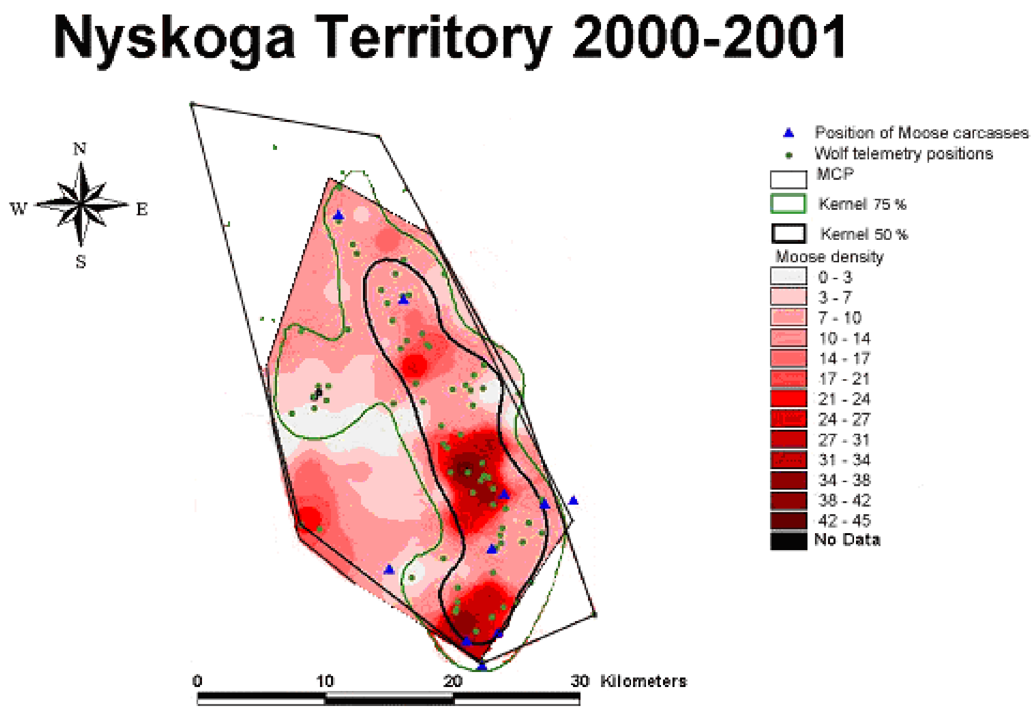
Ungulate carcasses killed and assumed killed by wolf that were found during the predation period in Nyskoga 2001.

Id	**Specie**	**Date of death**	**Age**	**Sex**	**Initial utilization (%)**	**Found during**	**Days after kill until found (days)**
1	Moose	?	Y	F	??	S	??
2	Moose	010208-09	C	F	100	T	1
3	Moose	010131-0202	Y	F	??	T	17-20
4	Moose	010216-17	Y	F	60	T	3
5	Moose	010226-27	Y	F	90	S	4
6	Roe deer	010303-04	?	?	100	S	1
7	Moose	010306-07	A	F	50	T	2
8	Moose	010313	Y	F	30	T	1
9	Moose	010323	A	F	30	S	2
10	Roe deer	010319	?	?	?	S	10
11	Moose	010330-31	C	F	100	T	1-2
12	Moose	010407	C	F	100	T	1

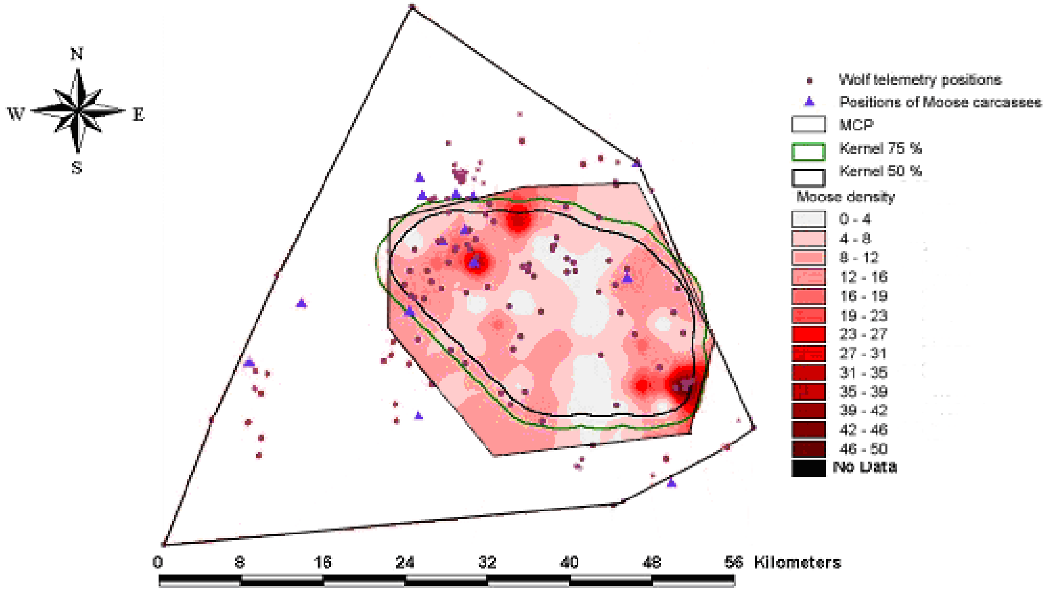
A= Adult
C= Calf
S=Snowtracking
T=Telemetry
Y=Yearling

Appendix 2

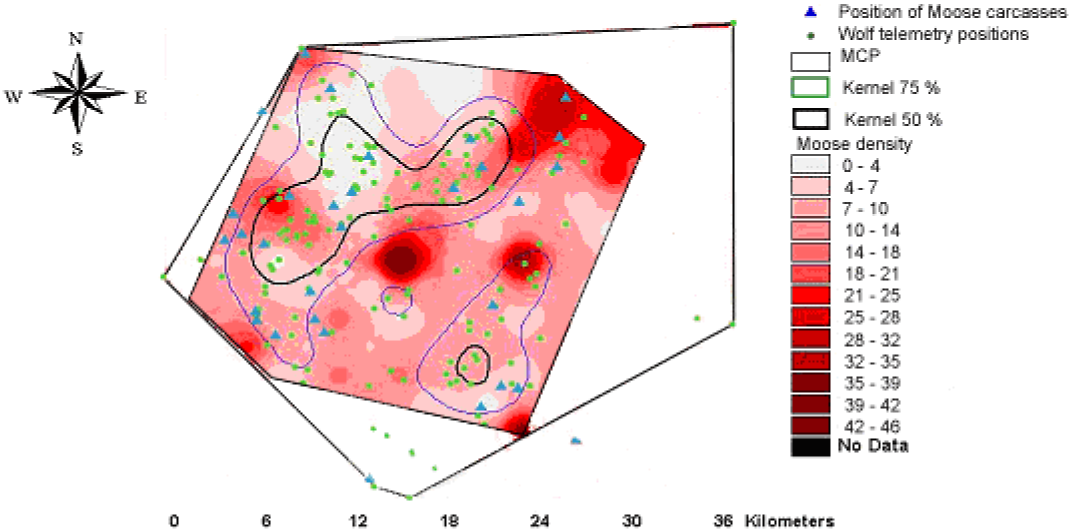
Maps of the different territories, containing; telemetry positions of wolf, killsite of moose and roe deer, moose density within the area of fecal inventory, MCP, Kernel 75 and 50 %.



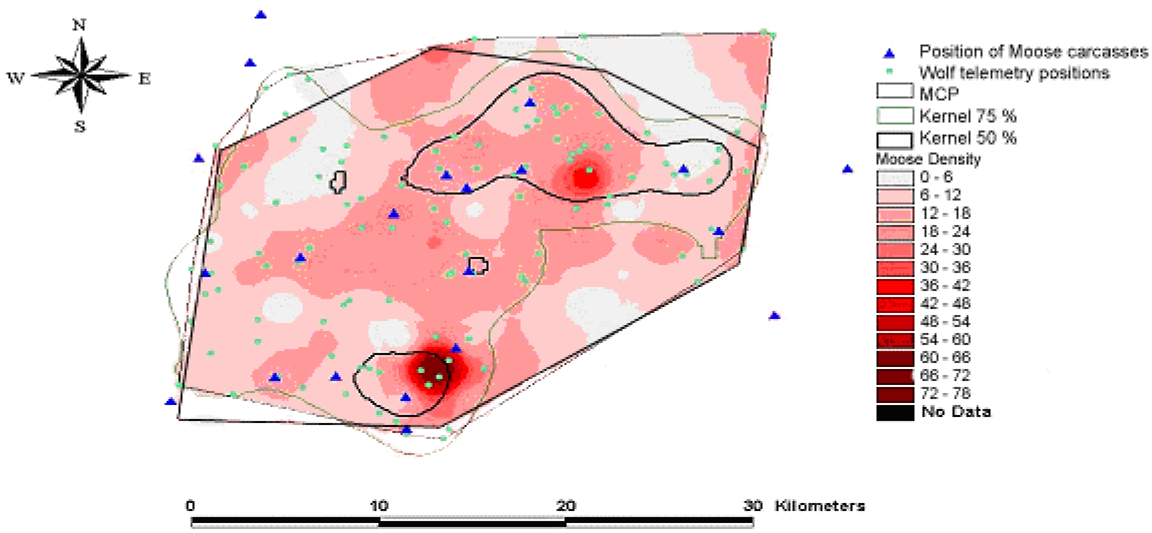
Leksand Territory 1998-1999



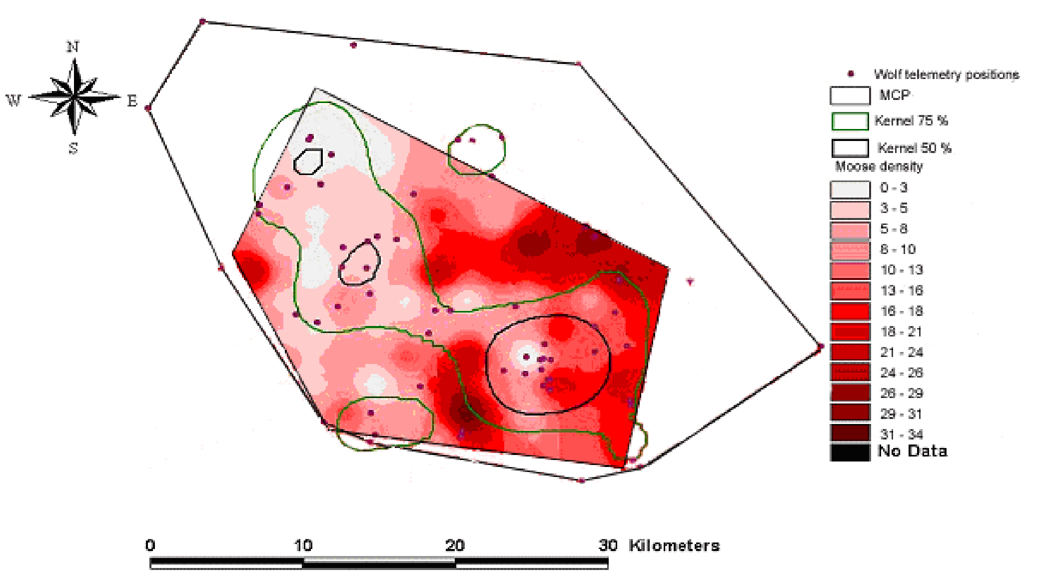
Grangärde Territory 2000-2001



Grangärde territory 1999-2000



Hagfors territory 1998-1999



Appendix 3

Food availability:

(ab(ef+gh+ij+kl) + (mno)) / pq or qr

Consumption rate:

(abc(ef+gh+ij+kl) + (mno)) / pq or qr

Consumption rate with adjustments for scavengers:

(abcd(ef+gh+ij+kl) + (mno)) / pq or qr

a= number of moose killed –1

b= Consumable fraction of moose biomass (0,65%)

c= average proportion of carcasses consumed during initial utilisation

d= wolf portion at actual pack size (0,67%)

e= proportion of calves of total number of moose killed(t.n.m.k.)

f= calf weight 155 (kg)

g= proportion of yearlings of t.n.m.k.

h= yearling moose weight (kg)

i= proportion of adult moose of females t.n.m.k.

j= adult female moose weight (kg)

k= proportion of adult male of t.n.m.k.

l= adult male moose weight (kg)

m= number of roe deer killed

n= weight of adult roe deer (kg)

o= consumable fraction of roe deer biomass (80%)

p= pack size

q= number of days between date of first and last killed

r= wolf total pack weight (kg)

The formula used to calculate kill rate (days/moose) is the same as in Palm (2001), which is: (ND)/(NK-1),ND = number of days between the first and last kill and NK= number of moose killed

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