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**Prey selection, kill and consumption rates of
Moose by Wolves in central Sweden**
comparison to moose population and human harvest

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Abstract

Predation ecology of radio collared wolves (*Canis lupus*) was studied in three packs of different size during winter in central Sweden. Wolves in all three packs predominantly selected moose calves (*Alces alces*) at similar high rates. Totally calves composed 87% of all moose that were killed. Both kill rates and initial use of carcasses differed between the packs. Kill rates ranged between 15.9-24.7 moose wolf⁻¹ year⁻¹, assuming winter predation to be representative all year. These numbers were high in comparison to similar studies in North America. Initially use of carcasses and handling times were comparatively low. High kill rates, short handling time and poor initial utilisation of kills could result from a combination of relatively high prey densities and high prey vulnerability due to inexperience from predators. Food availability ranged from 0.09-0.17 kg kgwolf⁻¹ day⁻¹. Avian and mammalian scavengers frequently occurred at kill sites, and were probably causing reduction in food intake. High tendency of scavenging old kills was detected for one of the studied packs concluding this was an important source of energy. Predation rates, 4-15% of the winter moose population, indicate that small-scale regulations of the annual moose harvest may have to be accomplished to preserve local moose populations at current densities.

Introduction

Predation ecology of wolves (*Canis lupus*) have been studied in many parts of the northern hemisphere (Filonov 1980; Mendelsson 1983; Shahi 1983; Cuesta *et al.* 1991; Ballard *et al.* 1997; Hovens *et al.* 2000). The patterns of predation including prey selection, kill and consumption rates and its effects on prey populations have been one of the major questions of concern (Van Ballenberge 1987; Skogland 1991; Messier 1995; Okarma 1995).

Kill and consumption rates have been found to vary in time and between locations due to differences in wolf and prey densities (Messier and Crete 1985; Ballard *et al.* 1987), prey species composition (Kolenosky 1972; Messier and Crete 1985; Bjorge and Gunson 1989), snow conditions (Peterson *et al.* 1984a; Nelson and Mech 1986) and pack sizes (Hayes *et al.* 1991; Dale *et al.* 1994).

Wolf predation is often argued to be selective, (Carbyn 1983; Ballard *et al.* 1987; Huggard 1993a) i.e. disproportional predation on different prey categories. However the extent of selection show large variation with the highest degree of selectivity found in colonising and low density wolf populations (Fritts and Mech 1981; Huggard 1993b; Boyd *et al.* 1994).

Wolves are known to prey on a variety of different animals (Cuesta *et al.* 1991; Okarma 1995), with ungulates being by far the most important prey in most systems (Filonov 1980; Fuller and Keith 1980; Gao 1990; Jedrzejewski *et al.* 1992; Marquad-Petersen 1998). In many areas of the northern boreal regions moose (*Alces alces*) is often one of the primary prey species (Filonov 1980; Olsson *et al.* 1997; Hayes *et al.* 2000).

In North America, prey selection, kill and consumption rates have been studied from the arctic to the northern states of USA, covering a wide range of wolf and moose densities (Messier and Crete 1985; Turber and Peterson 1993; Mech *et al.* 1995).

Similar studies from other regions are scarce. In northern Europe, e.g. Fennoscandia, where wolves almost were extirpated for approximately one hundred years (Persson and Sand 1998), few studies of wolf predation have been carried out (Pulliainen 1963; Olsson *et al.* 1997; Gade-Jorgensen and Stagegaard 2000). On the Scandinavian peninsula (Sweden and Norway) wolves became fully protected 1966 in Sweden and 1973 in Norway, a time when less than 10 animals were assumed to remain (Persson and Sand 1998). Although several reproductions were documented from 1983 onwards, population numbers during the 1980s probably never exceeded 8-10 individuals (Wabakken *et al.* 2001). After twenty years of poor recovery, the Scandinavian wolf population started to increase and displayed a stable annual growth of 20-30%, which endured throughout the 1990s (Wabakken *et al.* 2001). In 1998 the wolf population was estimated to a total of 62-78 individuals (Aronsson *et al.* 1999).

During the last 50 years the moose population on the Scandinavian peninsula experienced a dramatic growth caused by modern forestry practice, absence of predators, and major changes in harvest strategies (Markgren 1984). Moose became regarded as an economically very important species, not only as a large game but also as the major species causing large-scale forest damage (Bergström 1992). On what densities the moose population should be kept and what harvest strategies to use have been largely debated among hunters and forest owners. The recent re-colonisation of wolves may alter the conditions for a desirable harvest strategy of moose in wolf areas. Knowledge of wolf predation ecology is therefore a fundamental tool in developing appropriate moose management strategies in the future.

The aim of the following study was to monitor three wolf packs in central Sweden during winter, where moose were assumed to be the primary prey, and to address the following questions:

1. Do wolves show preference for any particular category of moose?
2. What are the kill and consumption rates of moose?
3. What is the current wolf predation rate compared to moose population density and to human harvest rates?

Study Area

The study was accomplished in two wolf territories in central Sweden in the county of Dalarna. The wolf territories are known as the Leksand territory, which was studied for two winters, 1998-1999 and 1999-2000 (core area: 60°40' N, 14°30' E) and the Grangärde territory, which was studied during one winter, 1999-2000 (core area: 60°20' N, 14°50' E) (Fig. 1).

The area is mainly covered with boreal coniferous forest with elements of lakes and mires and with a topography ranging from 155 to 596 m a.s.l. The forest consist to an equal proportion of Norway spruce (*Picea abies*) and Scotch pine (*Pinus sylvestris*) with a 5% mixture of birch (*Betula pendula*, *B. pubescens*), aspen (*Populus tremula*), willow (*Salix ssp*) and alder (*Alnus incana*) (Nilsson 1990).

The vegetation period proceeds about 175 days with an average temperature of 15 °C during July and -9 °C during January. Yearly precipitation is 700-800 mm and the period with snow cover usually lasts 100 days with a maximum average snow depth of 50-60 cm (Raab and Vedin 1995).

Intensive silviculture with clear-cuts and monocultures is conducted through out the area and a dense forest road system (1.5 km road/km²) makes the area highly accessible. Elements of agriculture and enclosed pastures, which amount to about 2 % of the land area, are found in the surroundings of villages (Classon and Granström 1992). Besides a population density of 2-3 inhabitants 100 km⁻² (Öberg and Springfeldt 1991) the area annually experience a high number of people taking part in outdoor activities such as hunting, fishing, skiing and trekking. During summer numerous cabins are used for keeping sheep and cows on their summer pastures and as residences for humans during vacations.

Mammal species such as moose (*Alces alces*), roe deer (*Capreolus capreolus*), lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), badger (*Meles meles*), beaver (*Castor fiber*), mountain hare (*Lepus timidus*) and brown bear (*Ursus arctos*) are all found in the area. Avian species like capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), and raven (*Corvus corax*) are common.

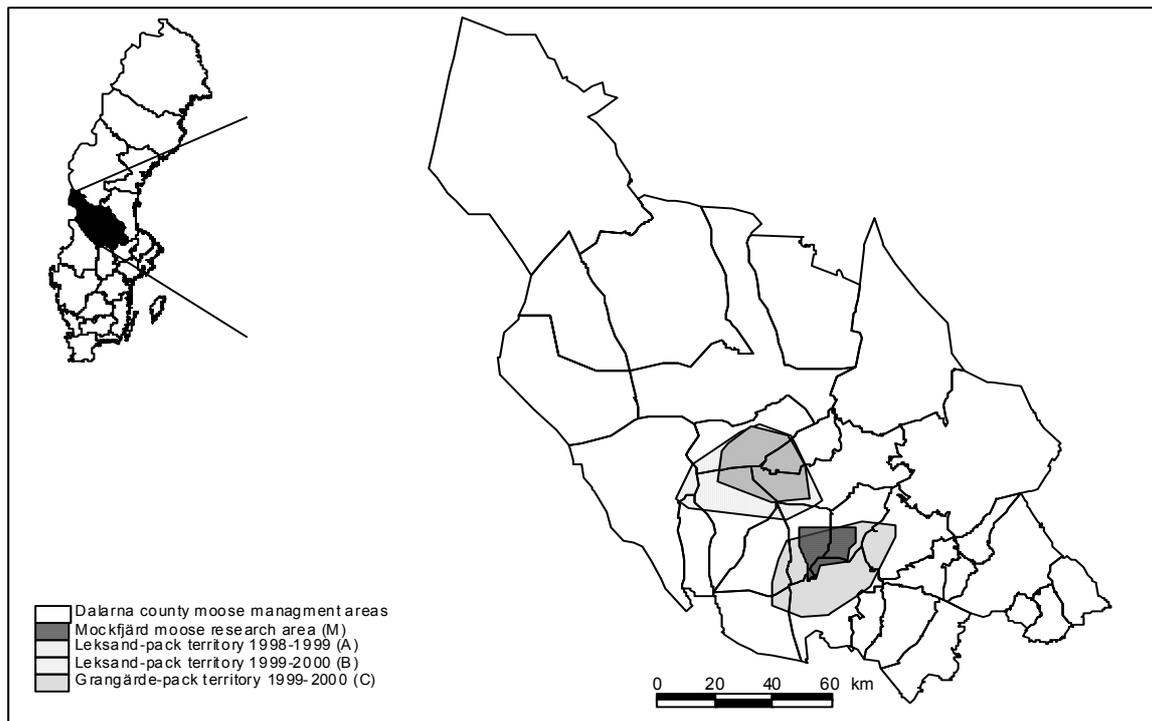


FIG. 1. Dalarna county and the studied wolf territories in central Sweden during 1998 through 2000.

Methods

Monitoring of wolves

Predation in three wolf packs were studied during two winters: the Leksand-pack in the winter of 1998-1999 (A), and in the winter of 1999-2000 (B), and the Grangärde-pack in the winter of 1999-2000 (C). Size of pack A ranged from 4 to 8 individuals with an average of 6, including one alpha pair and 4 pups (Aronson *et al.* 1999). The size of pack B was 3 wolves, one adult female and two yearling males, while pack C consisted of one alpha pair (Aronson *et al.* 2000). The number of wolves radio-collared in each pack was 2, 3, and 2 respectively.

Since wolves often spend more than 48 hours handling a moose carcass (Messier and Crete 1985; Ballard *et al.* 1987; Hayes *et al.* 2000) radio collared wolves were relocated on average once every 24-48 hours in pack A and B, and every 12 hours in pack C. The more intense radio tracking in pack C was due to more resources being available. Wolf relocation was made through triangulation by car, by foot or by skis if necessary, and was conducted on varying times throughout the day.

Snow tracking was made regularly throughout the study to confirm the number of wolves in each pack and search for prey killed which was not indicated from telemetry relocations. Pack size was defined as the average number of wolves tracked in each pack during the whole study period. The number of tracks from ungulates crossing the wolf trail and to what extent wolves, moose, and roe deer, sank in the snow were recorded during every tracking event. Precipitation, temperature and snow depth were measured for each day of the study.

Wolf territory size, during the study period and for the whole year, was estimated by using all relocations calculating a minimum convex polygon (White and Garrott 1990), using the geographic information system ESRI Inc ArcView 3.1 with the extension of Animal movement (U.S.G.S. Alaska Biological Science Center). Relocations located more than 10

km away from any other location were excluded in order not to influence the actual size of the wolf territories. Whole year territory size was estimated by using locations from May 1 to April 30 the following year. Relocations for pack A were only available from December 15 1998 to April 30 1999.

Wolf kills

When radio collared wolves spent, at least 24 hours in a defined area in pack A and B and at least 12 hours in pack C the location was searched for ungulate kills. Kills were found by backtracking wolves and/or by localising ravens present in the area. Locations were investigated no less than 24 hours after the radio-collared wolves had abandoned the location to minimise the risk for disturbance of wolves suddenly returning to the carcass.

When prey were found they were classified in to five different mortality categories:

1. Prey were classified as *dead prior to study period* when carcasses were found laying on bare ground since snow covered the ground before the start of each study period.
2. Prey were classified as *being killed by other causes* than wolves, e.g. when wounds from bullets or traffic accidents could be identified.
3. Prey were classified as *positively killed by wolves* when tracks from a wolf attack and/or marks of heavy bleedings were found in the snow near the carcass (Hayes et al. 2000; Thurber and Peterson 1993; Messier and Crête 1985).
4. Prey were classified as *assumed to be killed by wolves* when tracks from wolves and any amount of fresh blood was found near the carcass.
5. Prey were classified as *possibly killed by wolves* when only tracks from wolves were found at the carcass.

Mandibles from moose positively killed by wolves (prey category 3) were collected for age determination, and was performed by section the first molar (M1) tooth and counting the annual cementum layers, as described by Sergeant and Pimlott (1959). Due to the fact that wolves often remove mandibles from prey, size of skull and/or skeleton were also used for age determination between calves or adults (Markgren 1969). Sex were determined by antler rudiments or sexual organs. The proportion of consumable tissue removed from prey after initial utilisation (e.g. when wolves had abandoned the prey) by wolves was visually estimated to the nearest 5%. Eatable tissue of moose was assumed to be everything but the fur, rumen, spinal, pelvis and bones from extremity.

At the place of the carcass occurrence of tracks from scavengers of different species were noted. Initial handling time was defined as the number of days (24 hours) between kill and abandonment of the carcass and was calculated as the number of days between the last relocation, ≥ 1 km from carcasses, prior to kill and to the first relocation after abandonment. Abandonment of carcasses were assumed when wolves continuously were observed moving further away from carcasses at a distance of ≥ 1 km. When determining time of kill and abandonment of carcasses data from snow tracking and snow conditions at kill sites were considered. Moose initially utilised by 10% or less were arbitrarily assigned a handling time of 0.1 days to minimise overestimation of handling time due to longer time intervals between relocations.

Prey selection

Prey selection for moose and roe deer were calculated for pack C, both by density and by encounter. The number of moose and roe deer tracks crossed while snow tracking were used as an indices of prey encounter. Selection were also calculated when only moose calves were regarded as available prey using 27% as the proportion of calves in the winter moose population (Svensk Viltförvaltning AB 1998, 2000).

Calculation of kill and consumption rates

Kill rate (days/moose) was calculated as:

$$(ND) / (NK - 1) \quad (1)$$

ND = number of days between the first and last kill

NK = number of moose killed

Kill rate calculations was based on prey numbers from three different prey combinations, *i*) mortality category 3, *ii*) mortality category 3+4 and *iii*) mortality category 3+4+5 (see previous sections).

Food availability and consumption was calculated as $\text{kg wolf}^{-1} \text{day}^{-1}$ or $\text{kg kgwolf}^{-1} \text{day}^{-1}$. Consumption was also calculated with adjustments for effects of scavengers. Promberger (1992) concluded that interspecific competition between wolves and ravens resulted in a reduction of the actual amount of meat consumed by wolves. The amount of meat lost were found to be negatively correlated to pack size. Wolf portions of the total consumable fraction of a moose carcasses were set to 50%, 60% and 80% respectively at the actual packs sizes of 2 (pack C), 3 (pack B) and 6 (pack A).

Food availability was calculated as:

$$(ab (ef + gh + ij + kl) + (mno)) / (pq) \text{ or } /(pqr) \quad (2)$$

Consumption was calculated as:

$$(abc (ef + gh + ij + kl) + (mno)) / (pq) \text{ or } /(pqr) \quad (3)$$

Consumption adjusted for effects of scavengers was calculated as:

$$(abcd (ef + gh + ij + kl) + (mno)) / (pq) \text{ or } /(pqr) \quad (4)$$

a = number of moose killed –1

b = consumable fraction of moose biomass (65%)

c = average proportion of carcasses consumed during initial utilisation

d = wolf portions at actual pack size

e = proportions of calves of the total number of moose killed

f = calf weight (kg)

g = proportion of yearlings of the total number of moose killed

h = yearling moose weight (kg)

i = proportion of adult females of the total number of moose killed

j = adult female moose weight (kg)

k = proportion of adult males of the total number of moose killed

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 = wolf pack size

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

r = wolf total pack weight (kg)

Estimation of winter body weights

Adult male, adult female, yearling and calf moose live weight during fall were set to 370, 330, 310 and 170 kg respectively (Svenska Jägareförbundet, unpublished data) using data from 318 moose harvested 1997-2000 within the wolf territory of pack C ((Mockfjärd moose research area (M)) (Fig. 1). Estimation of average total live weight of moose was done by adjusting the actual measures of carcass body weight. The correction factor for adjusting carcass to total live weight was received from the Grimsö Research Area from where data on total live weight and carcass weight existed for a larger sample of harvested moose. Carcass weight of adult, yearling and calf moose from the Grimsö Research Areas was on average 55%, 50%, and 45% of live body weight, respectively (Sand et al. unpublished data). Moose live weight reduction from fall to mid February was assumed to be 5%, 6% and 9% for adults yearlings and calves, respectively (Cederlund et al. 1992, Sand et al. unpublished data). Moose average live weight during the study periods were therefore adjusted to 353, 314, 291 and 155 kg for adult males, adult females, yearlings, and calves, respectively. Adult roe deer live weight during winter was assumed to 22.5 kg (Cederlund and Liberg 1995). Consumable fraction of moose was assumed to 65% of live weight (Promberger 1992) and 80% for roe deer (Glowacinski and Profus 1997). Small prey like roe deer are readily consumed and the loss to scavengers were assumed to be negligible. Wolf weights were set to 51, 39 and 35 kg during winter for adult male, adult female and pups respectively (Sand et al. 2000).

Wolves re-visiting old prey

Rate of wolf scavenging, in terms of wolves re-visiting prey that was assumed to be killed earlier during the winter, was estimated only for pack (C). When wolves in pack (C) were located near an earlier known moose carcass, investigation at the carcass was made. Scavenging was assumed to have occurred when tracks from wolves were present at the carcass. Wolves were considered to be scavenging when using all categories (1-5) of moose carcasses. Handling time during scavenging was calculated the same way as handling time for fresh wolf kills.

Ungulate census

According to previous fecal pellet group counts, the Leksand territory 1998-1999 (pack A) and 1999-2000 (pack B) showed a moose winter density of 0.9 moose km⁻² and a roe deer winter density of 0.05 roe deer km⁻² (Sand et al. 2000). The Grangärde territory 1999-2000 (pack C) had somewhat higher prey densities with 1.1 moose km⁻² and 0.2 roe deer km⁻² (Sand, unpublished data). Three aerial winter moose counts in the wolf territories during 1998 and 2000 showed that calves constituted with 27% (pack C 1998), 25% (pack B 2000), and 30% (pack B 2000), averaging 27 % in the standing moose population (Svensk Viltförvaltning AB 1998, 2000).

Human harvest

Human harvest of moose in each of the wolf territories was estimated by calculating the average number of moose shot year⁻¹ km⁻² (1997-1999) using data from all moose management areas (Fig. 1) that primarily composed core areas of the wolf territories.

Results

Monitoring of wolves

The radio-collared wolves in the three packs were intensively monitored for 310 pack days, or 1091 wolf days, with a total of 424 relocations, and 1015 km of snow tracking (Table 1).

TABLE 1. Total number of days in each study period, number of days with 0, 1, 2 or ≥ 3 telemetry relocations, and the total length of snow tracking of wolves made during the study for the Leksand-pack 1998-1999 (A), Leksand-pack 1999-2000 (B) and Grangärde-pack 1999-2000 (C).

Pack	Study period (n days)	Number of days with 0, 1, 2, or ≥ 3 relocations				Relocations (n total)	Snow tracking (km)
		0	1	2	≥ 3		
A	95	35	49	11	0	71	462
B	91	19	59	12	1	86	278
C	124	6	23	66	29	267	275
Total	310	60	131	89	30	424	1015

During the two winters of study, temperature ranged from +4 to -22 °C with an average day temperature of -5 to -10 °C. Snow depth varied from 5 cm in early December to 80 cm in late February. The highest track depth recorded to which moose, roe deer, and wolves sank in the snow was 50, 20 and 40 cm respectively. Because of frozen crust in February in both winters the median depth to which moose, roe deer and wolves sank during successful hunting attempts was 10-30 (n=30), 1-10 (n=37) and 1-10 (n=5) cm respectively.

Territory size during the study period of pack A was calculated to 535 km² while the territories of pack B and C covered areas of 1142 km² and 1036 km² respectively. Whole year territory sizes were somewhat larger, (A=719 km², B=1311 km² and C=1175 km²)(Fig. 1) than during the study periods.

Carcasses

During the 3 study periods, a total of 72 moose and 7 roe deer carcasses utilised by wolves were found (Table 2). Of all moose classified as positively killed by wolves, 77% were found by the aid of telemetry, i.e. clustering of successive locations, and 23% by continues snow tracking. Three of the 7 roe deer (43%), classified as positively killed by wolves, were found by the aid of telemetry while the other 4 were found during snow tracking. An additional 19 moose carcasses, 7 of which could be classified as positively killed by wolves, was found prior to and after the study periods (Appendix 1).

TABLE 2. The number of moose and roe deer carcasses utilised by wolves during each study period and the number of days between first and last kill. The number of roe deer are presented within brackets.

Pack	Mortality category					Carcasses (n total)	Number of days between first and last moose kill
	1	2	3	4	5		
A	9		16	6	2	33	88
B	5	1	14 (1)	1	0	21 (1)	72
C	3	1	13 (6)	0	3	20 (6)	111
Total	17	2	43 (7)	7	5	74 (7)	271

- 1) prey dead prior to study period
- 2) prey killed by other causes than wolves
- 3) prey positively killed by wolves
- 4) prey assumed killed by wolves
- 5) prey possibly killed by wolves

Prey selection

Forty-seven of the moose positively killed by wolves were determined by age, or age class (31 from sectioned molar teeth, and 16 from size of skull and/or skeleton). Only 6 (13%) of the 47 moose positively killed by wolves were classified as older than 1 year. Two of them were 1.5 years and two were 7.5 years. The remaining two adults were of unknown age. The proportion of calves killed by wolves was 87% (all positive wolf kills pooled), and differed significantly from their average distribution in the standing winter population, 27%, (Normal approximation $Z = 11.7$ $df=1$, $P < 0.001$) (Fig. 2). Twenty of the moose positively killed by wolves could be determined by sex. Ten (63%), of the 16 calves and 3, (75%), of the 4 adults (≥ 1 years) were females. Both moose older than 2.5 year were females. Only one roe deer positively killed by wolves could be determined by age and sex and was a female fawn. During snow tracking of pack C a total of 592 tracks from moose and 16 from roe deer were crossed. Pack C preferred roe deer both by density ($\chi^2 = 3.7$, $df=1$, $P < 0.01$) and encounter ($\chi^2 = 45.6$, $df=1$, $P < 0.001$). Roe deer were preyed upon almost half (0.46) as often as moose despite moose being 5.5 times more abundant and 37 times more often encountered. Roe deer was also preferred by encounter when only moose calves were regarded as available prey ($\chi^2 = 10.5$, $df=1$, $P < 0.05$). Roe deer was not preferred by density when only moose calves were regarded as available prey ($\chi^2 = 0.2$, $df=1$, $P > 0.25$). On five occasions carcasses from small game positively killed by wolves were found, four black grouse and one capercaillie.

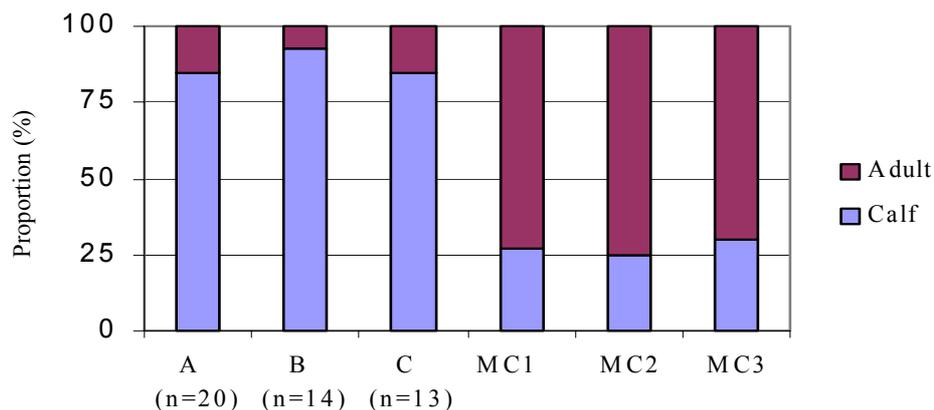


FIG. 2. The proportion of calf and adults (≥ 1 years) among moose positively killed by wolves by the Leksand-pack 1998-1999 (A), 1999-2000 (B) and by the Grangärde-pack 1999-2000 (C). Bars to the right shows the proportion of calves and adults in the standing moose winter population as observed during aerial moose counts in the Grangärde-pack territory 1998 (MC1) and in the Leksand-pack territory 2000 (MC2 and MC3).

Kill rate

Kill rate differed between the packs (Table 3). The highest and lowest pack kill rate was found in pack A with 62.2-95.4 and C with 39.5-49.3 moose year⁻¹ respectively (using prey combination *i-iii*) and assuming constant kill rates all year. In contrast, kill rate per wolf year⁻¹ was lowest in pack A (10.4-15.9) but similar between pack B (22.0-23.7) and C (19.7-24.7).

TABLE 3. Kill rate calculated for different combinations of prey (*i-iii*) and for each of the three packs (A-C) within the study.

Pack (<i>pack size</i>)	A (6)			B (3)			C (2)		
	<i>i</i>	<i>ii</i>	<i>iii</i>	<i>i</i>	<i>ii</i>	<i>iii</i>	<i>i</i>	<i>ii</i>	<i>iii</i>
Prey category.									
Days moose ⁻¹	5.9	4.2	3.8	5.5	5.1	5.1	9.3	9.3	7.4
Moose 100 days ⁻¹	17.0	23.9	26.1	18.1	19.4	19.4	10.8	10.8	13.5
Moose year ⁻¹	62.2	87.1	95.4	65.9	71.0	71.0	39.5	39.5	49.3
Moose 100 days ⁻¹ wolf ⁻¹	2.8	4.0	4.4	6.0	6.5	6.5	5.4	5.4	6.8
Moose year ⁻¹ wolf ⁻¹	10.4	14.5	15.9	22.0	23.7	23.7	19.7	19.7	24.7

i) prey positively killed by wolves

ii) prey positively killed + prey assumed to be killed by wolves

iii) prey positively killed + prey assumed to be killed + prey possibly killed by wolves

Handling time

Moose handling time did not differ significantly between the wolf packs (Kruskal-Wallis test, $df=2$, $H=3.25$, $P=0.20$). The lowest average handling time was found in pack C, 2.3 ± 0.32 (mean \pm SE) ($n = 13$) days and with 5 out of 13 carcasses (38 %) handled in less than 2 days and 2 out of 13 (15%) in less than one day. Average handling time in pack B was 2.4 ± 0.46 ($n = 11$) days and with 6 of 11 carcasses (55 %) handled in less than 2 days and 2 out of 11 (18%) in less than one day. Handling time in pack A was 3.8 ± 0.84 ($n = 13$) days with 4 out of 13 carcasses (31%) handled in less than 2 days and 3 out of 13 (23 %) in less than one day. Handling time for 6 of the moose carcasses could not be measured because of too few relocations. Handling time for roe deer could only be measured in pack C and was estimated to 1.1 ± 0.36 ($n = 5$) days.

Initial carcass utilisation and consumption

The proportion of moose consumable fraction consumed during initial utilisation differed (Kruskal-Wallis test, $df=2$, $H=7.61$, $P=0.002$) between the packs, A (73 ± 7.53 %, mean \pm SE), B (57 ± 6.7 %) and C (43 ± 8.0 %) (Fig.3). The proportion of roe deer consumable fraction consumed by the wolves were 100% ($n=1$) in pack B and 95% ($n=5$) in pack C, excluding one kill by which the wolves were disturbed by humans. Observations and/or tracks from scavengers were detected at 87% of the moose carcasses, where records of scavengers were registered ($n = 82$). Raven, red fox and golden eagle were the most common species but jay (*Garulus glandarius*), siberian jay (*Perisoreus infaustus*), marten (*Martes martes*) and lynx were also detected at some of the carcasses. The highest number of ravens simultaneously estimated at a given moose carcass was 20.

Food availability calculated as total consumable weight of meat from of all prey killed during the study periods ranged from 3.3 kg to 7.8 kg wolf⁻¹ day⁻¹ (Table 4). Consumption was highest in pack B, both without ($3.8-4.0$ kg wolf⁻¹ day⁻¹) and with ($2.3-2.5$ kg wolf⁻¹ day⁻¹) adjustments for scavengers (Table 4).

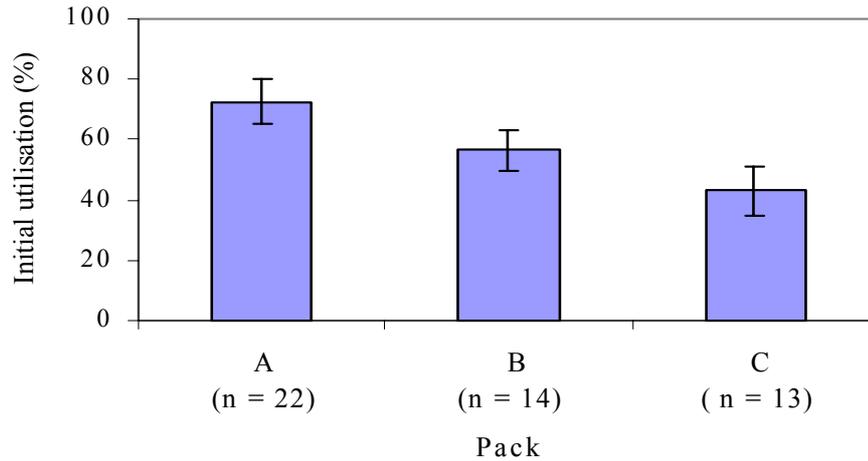


FIG. 3. Consumption (%) of moose (mean \pm SE) positively killed by wolves during initial utilisation in the different wolf packs A-C.

TABLE 4. Food availability, consumption, and consumption were the effects of scavengers are adjusted for, calculated as $\text{kg wolf}^{-1} \text{day}^{-1}$, and $\text{kg kgwolf}^{-1} \text{day}^{-1}$.

Pack	Food availability			Consumption			Consumption (effects of scavengers adjusted for)		
	<i>i</i>	<i>ii</i>	<i>iii</i>	<i>i</i>	<i>ii</i>	<i>iii</i>	<i>i</i>	<i>ii</i>	<i>iii</i>
Prey combination									
A	3,3 0,09	4,6 0,12	5,0 0,13	2,5 0,07	3,5 0,09	3,8 0,10	2,0 0,05	2,8 0,07	3,1 0,08
B	6,5 0,14	7,0 0,15	7,0 0,15	3,8 0,08	4,0 0,09	4,0 0,09	2,3 0,05	2,5 0,05	2,5 0,05
C	6,8 0,15	6,8 0,15	7,8 0,17	3,2 0,07	3,2 0,07	3,6 0,08	1,8 0,04	1,8 0,04	2,1 0,05

i) prey positively killed by wolves

ii) prey positively killed + prey assumed to be killed by wolves

iii) prey positively killed + prey assumed to be killed + prey possibly killed by wolves

Scavenging by wolves

A total of 18 occasions were detected when wolves in pack C scavenged earlier known moose carcasses. The ratio between kill and scavenge of moose was calculated to 1: 1.1-1.4 (prey category *i-iii*) which means, on every moose killed 1.1-1.4 moose carcasses was scavenged. The number of days between individual occasions of scavenging were 5.9 ± 1.37 (mean \pm SE) ($n = 17$) with an average handling time of 1.6 ± 0.39 ($n = 18$) days. Six out of all 13 moose definitely killed by wolves during the study period were revisited and scavenged once and only one was scavenged twice. The average time between kill and first occasion of scavenge on the same moose were 28.4 ± 11.33 ($n = 6$) days with an average handling time of 1.3 ± 0.14 ($n = 6$) days.

Moose harvest, winter population and wolf predation

Wolf territories covered parts of 12 different moose management areas from which 8 composed the primary territory core areas (Fig. 1). The highest number of moose shoot $\text{km}^{-2} \text{year}^{-1}$ calculated for the period 1997-1999 was found in the moose management areas covered by pack A and B, with an annual harvest of $0.44 \text{ moose km}^{-2}$ (Svenska Jägareförbundet 2000, unpublished). The proportion of calves among harvested moose ranged between 46% and 0.49% (Table 5).

TABLE 5. The average annual number of moose harvested in each territory and per km², and the average proportion of calves.

Pack	Moose year ⁻¹	Moose year ⁻¹ km ⁻²	Proportion of calves
A	316	0.44	49%
B	577	0.44	49%
C	482	0.41	46%

The highest predation rate (moose km⁻² year⁻¹) (prey combination *iii*) compared to the standing moose winter population was observed in the area used by pack A both as total predation rate (15%), of adults (≥ 1 year) = 3% and of calves = 48% (Table 6). Predation rate on adult moose only amounted to 1% in both pack B and C.

TABLE 6. Moose winter population density (moose km⁻²)(M), wolf predation (moose killed km⁻² year⁻¹)(Pr) as calculated from prey combination *iii*, and wolf predation rate (Pr/M) for the three wolf packs A-C. Estimates are given for the total population, adults only, and calves only.

Pack	Total			Adults (≥ 1 year)			Calves		
	M	Pr	Pr/M(%)	M	Pr	Pr/M(%)	M	Pr	Pr/M(%)
A	0.9	0.13	15	0.67	0.02	3	0.23	0.11	48
B	0.9	0.05	6	0.67	0.00	1	0.23	0.05	21
C	1.1	0.04	4	0.81	0.01	1	0.29	0.04	12

The highest predation (moose km⁻² year⁻¹) compared to the total number of moose harvested by humans, was found in the territory of pack A (30 %)(Table 7). Regarding the predation on adults (≥ 1 year) and calves, pack A again showed the highest values with 9% and 52 % respectively.

TABLE 7. Human harvest (moose km⁻² year⁻¹)(H), wolf predation (moose km⁻² year⁻¹)(Pr) calculated from prey combination *iii*, and the rate of predation to harvest (Pr/H) given for the total population, adults only, and calves only.

Pack	Total			Adults (≥ 1 year)			Calves		
	H	Pr	Pr/H(%)	H	Pr	Pr/H(%)	H	Pr	Pr/H(%)
A	0.44	0.13	30	0.22	0.02	9	0.22	0.11	52
B	0.44	0.05	12	0.22	0.00	2	0.22	0.05	23
C	0.41	0.04	10	0.22	0.01	3	0.19	0.04	19

Discussion

Predation selectivity

The high proportion of calves, 85-93%, among moose killed by wolves, compared to the proportion of calves in the population, 27% (Fig. 4), indicates a strong predation selectivity. High proportions of calves among moose killed by wolves are also found in other winter predation studies (Fuller and Keith 1980; Peterson *et al.* 1984a; Ballard *et al.* 1987; Ballard *et al.* 1997; Hayes *et al.* 2000). Hayes *et al.* (1991) found that calves were represented up to 2.9 times more often than their occurrence in the population compared to 3.2 in the present study. High preference for juvenils have also been observed in systems where wolves prey on elk (*Cervus elaphus*) (Huggard 1993b; Kunkel *et al.* 1999), white-tailed deer (*Odocoileus virginianus*) (Voigt *et al.* 1976; Fuller 1991), red deer (*Cervus elaphus*) (Bobek *et al.* 1992; Jedrzejewski *et al.* 2000), wildboar (*Sus scrofa*) (Okarma 1995; Glowacinski and Profus 1997) and bison (*Bison bison*) (Mech 1970; Smith *et al.* 2000). Previous studies on prey selection in Scandinavia showed that 51% of moose killed by wolves were calves (Olsson *et al.* 1997). Still the observations in the present study is the highest yet recorded.

Snow conditions may effect prey selection, both at the species level (Mech *et al.* 1998; Smith *et al.* 2000) and at the age category level (Mech *et al.* 1987; Huggard 1993c) due to differences in prey vulnerability. Even though the snow depth at which moose calf vulnerability readily increases (75 cm) (Peterson 1977) was exceeded during some periods of the study, the effects were probably negligible. From snow tracking data neither moose or roe deer were recorded to sink more than 30 and 10cm respectively into the snow for any longer periods as a result from the frozen crust both winters. Increased prey vulnerability are probably first likely to occur at track depth of more than 50 and 20cm for moose and white tailed deer respectively (Peterson and Allen 1974; Fuller 1991).

Wolf preyed primarily on moose (n= 47-55) (prey combination *i-iii*) but carcasses of 7 roe deer killed by wolves were also found (Table 2). The number of roe deer killed could be underestimated since smaller prey, like caribou (Hayes *et al.* 2000) and white tailed deer, (Fuller 1989) are consumed much more readily compared to moose and will therefore not be detected as easily by telemetry. Olsson *et al.* (1997) found that roe deer was killed twice as often as moose despite the fact that moose density was three times as high.

Using the roe deer predation data from pack C, where telemetry were more intensively used (Table 1), roe deer were clearly preferred compared to moose. The only case when roe deer were not preferred was selection calculated by density and only moose calves were regarded as available prey. Selection for smaller prey in wolf-ungulate systems are reported elsewhere (Dale *et al.* 1995; Kunkel *et al.* 1999). Small prey selection could be a result of moose being a dangerous prey that occasionally kill attacking wolves (Weaver *et al.* 1992). A high degree of predation selectivity are often found in areas of low wolf densities or in areas newly colonised by wolves (Fritts and Mech 1981, Huggard 1993b, Boyd *et al.* 1994) which is also the case for the Scandinavian Peninsula.

Kill rate, handling time and initial utilisation

Kill rates observed in the present study show higher values compared to the regressions made by Ballard *et al.* (1987), Thurber and Peterson (1993) and Hayes *et al.* (2000) (Fig. 4). Still the observations are within the range of what has been observed in other systems where moose densities have ranged between 0.7-2.5 moose km⁻² (Peterson *et al.* 1984; Peterson and Page 1984; Ballard *et al.* 1987; Turber and Peterson 1993; Messier 1994) (Fig. 5).

Fuller and Keith (1980) found that kill rates are higher when calves are preferred since time intervals between kills is shorter after calf kills (3.6 days) than after adult kill (5.8 days) for a pack of ten wolves due to large differences in the amount of food available. Handling time may also influence kill rates since the proportion of time spent on carcasses will effect the amount of time invested in searching for and killing new prey. Handling time for moose in pack B and C, 2.3-2.4 days, were shorter compared to (Messier Crete 1985; Ballard *et al.* 1987; Hayes *et al.* 2000), who reported handling time of 3.3-4.2 days for calves by packs of similar size as B and C.

Predominantly selection for calves may explain some of the differences but not all. Kill rates can not be influenced due to differences in prey size if not most parts of carcasses is utilised. Initial carcasses utilisation (Fig. 3) was low for all packs compared to Peterson *et al.* (1984a); Messier and Crete (1985); Mech *et al.* (1995) who observed complete consumed carcasses with nothing but fur and bones remaining in most cases. Low carcasses utilisation, referred to as surplus killing, have been documented for wolves (Björvall and Nilsson 1976; Peterson and Allen 1974; DelGiudice 1998) and for other predators (Kruuk 1972). Increased kill rates and surplus killing are often observed when prey suffers increased vulnerability e.g. during periods of deep snow (Bobek *et al.* 1992; Boyd *et al.* 1994). Kolenosky (1972) found white-tailed deer killed by wolves consumed by less than 30% during sever winters.

Kill rates have also been found to increase in areas newly colonised by carnivores since ungulates inexperienced of large carnivores constitute a more vulnerable prey (Berger *et al.* 2001). Moose in most parts of Scandinavia have not experienced wolves or bear for approximately a hundred years and carnivore avoidance behaviour have been noticed to disappear just after a few generations in absence of predators (Berger 1999). High prey vulnerability in combination with low initial utilisation and handling time could be the best explanation for the observed kill rates.

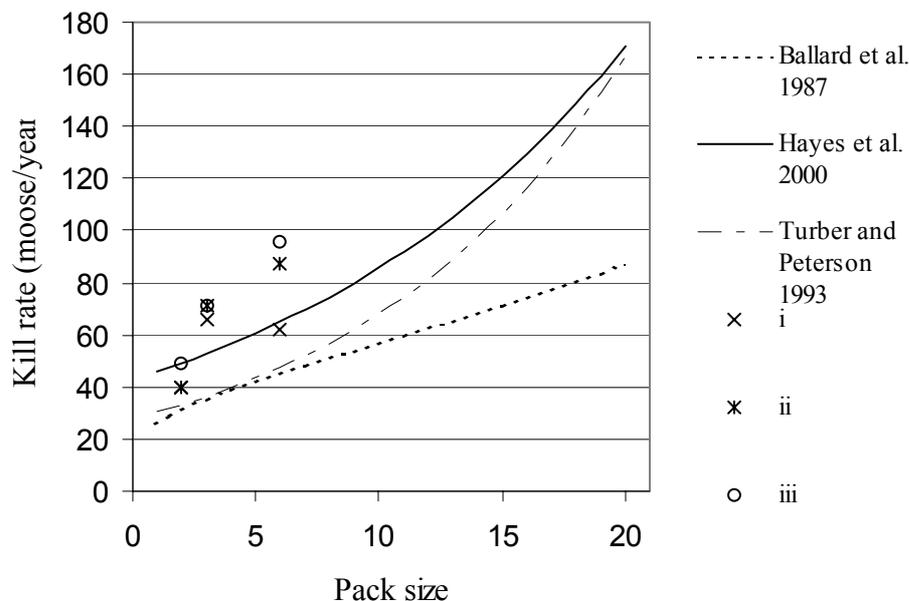


FIG. 4. Kill rates of the three wolf packs in the current study (A-C) compared to estimated kill rates found in three North American studies. Moose densities (moose km⁻²): Ballard *et al.* (1987) 0.59-0.72, Hayes *et al.* (2000) 0.26-0.44, Thurber and Peterson (1993) 0.9-1.9.

i) prey positively killed by wolves

ii) prey positively killed + prey assumed to be killed by wolves

iii) prey positively killed + prey assumed to be killed + prey possibly killed by wolves

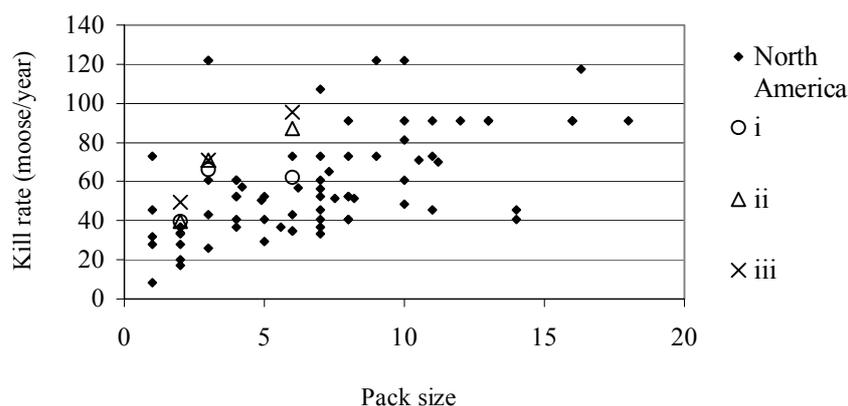


FIG. 5. Kill rates of the three wolf packs in the current study (A-C) compared to kill rates found in five North American studies with moose densities ≥ 0.7 moose km^{-2} (Peterson et al. (1984), Peterson and Page (1984), Ballard et al. (1987), Thurber and Peterson (1993), Messier (1994).

- i) prey positively killed by wolves
- ii) prey positively killed + prey assumed to be killed by wolves
- iii) prey positively killed + prey assumed to be killed + prey possibly killed by wolves

The method used in this study is probably to course since wolves tend to spend only short periods by their prey and show a low degree of initial utilisation. Twenty-three percent of all moose and 57% of all roe deer were found during snow tracking of the wolves. These were mostly prey that were consumed to only a low degree during a short period of time and the locations was therefore not detected by telemetry as potential kill sites. Kill rates in this study might be underestimated for all of the packs and calculations based on prey category *iii* are therefore probably the ones most likely.

Dale *et al.* (1995) who studied wolf predation on caribou, moose and dalsheep by locating packs from the air once or twice a day found 39% of all prey when backtracking wolves between locations. He suggested that smaller prey that are rapidly consumed will be underestimated during systematic relocating if wolves are not backtracked. Similar observations was made by Fuller (1989), who used fixed-wing aircraft for wolf relocation. He found that kill rate for wolves preying on white tailed deer were underestimated with 50% when packs were only located once every day compared to packs which were located twice every day.

To reduce the risk of not detecting kills and to gain wolf movement information a reduction of the time intervals between relocations would be necessary, especially concerning pack A and B which were relocated only half as often as pack C. In situations of surplus killing, kill rates could possible be calculated on a track length basis e.g. as the number of moose killed km^{-1} of wolf track. It would then be possible to extrapolate the kill rate over a longer time period if data from daily wolf travel length are available. One big advantage using this method would be that all prey would be found, even the ones utilised only to a few percent. A problem would be high variation in daily travel length and kills per unit travel length whereupon large amounts of snow tracking data would be needed. The snow tracking data from this study could not undergo such an analyses due to errors in the design of the snow tracking. Potential feeding sites of the wolves in the present study were detected by radio tracking and investigated separately. Snow tracking was mostly accomplished on sites not regarded as potential feeding sites. Kill rate calculations based on the number of prey found during regular snow tracking would therefore underestimate actual kill rates. A more correct design

would therefore be to perform snow tracking independently from radio tracking data. A second alternative method would be to use radio collars combined with GPS programmed to load waypoints every 30 or 60 minutes. All locations where more than two or more waypoints have been loaded, within a small radius, should then be searched for prey. This method would require a lot of effort since locations with clustered waypoints could be numerous throughout one single day without any prey being killed.

Consumption

Food availability $0.09\text{-}0.17\text{ kg kgwolf}^{-1}\text{ day}^{-1}$ in this study (Table 4) was found to be within the range of what has been observed in other studies, $0.09\text{-}0.29\text{ kg kgwolf}^{-1}\text{ day}^{-1}$ (Fuller Keith 1980; Fritts and Mech 1981; Messier Crete 1985; Ballard *et al.* 1987; Bjorge and Gunson 1989; Hayes *et al.* 1991; Thurber and Peterson 1993; Hayes *et al.* 2000). Wolves in pack B and C acquired more food ($0.14\text{-}0.17$) per wolf per day than did wolves in pack A ($0.09\text{-}0.13$) which in similarity to Schmidt and Mech (1997) indicates that small packs are more optimal from a foraging point of view compared to larger packs.

Six different avian and mammalian species were found to scavenge from moose carcasses, red fox and raven being the most frequent. Interspecific competition between scavengers and large carnivores are also reported by Cooper (1991); Promberger (1992).

Consumption when adjusted for the effects of scavengers was lower, $0.04\text{-}0.08\text{ kg kgwolf}^{-1}\text{ day}^{-1}$ (Table 4), than presented by Hayes *et al.* (2000). Hayes *et al.* (2000) calculated consumption rates (adjusted for scavengers) for packs of different size. Small packs (2-4 individuals) consumed 0.15, medium packs (4-9 individuals) 0.13 and large packs (9-20 individuals) $0.09\text{ kg kgwolf}^{-1}\text{ day}^{-1}$ respectively.

There may be at least three reasons why we underestimate the true consumption rates in this study. First, since wolves did not use all portions of moose carcasses during initial utilisation and the time spent on carcasses were short, scavengers probably did not compete as severe as suggested by Promberger (1992) who refers to situations where wolves did not abandon kills until all of carcasses were totally consumed. The number of days spent on a carcasses influence the rate of loss to scavengers since the number of scavengers present increased with the number of days from the kill (Promberger 1992). Second, the density of ravens could be different from the densities in the Yukon, where Promberger (1992) carried out his study, which would alter the outcome of interspecific competition between ravens and wolves. The effects of differences in densities are hard to estimate since densities of ravens are calculated as the number of breeding pairs per unit area. This type of density calculations do not present the number of subadult ravens that form large flocks during winter (Heinrich 1991) and probably are the ones to perform the greatest influence on the extent of competition (Hayes *et al.* 2000). Third, in spite of a low degree of initial utilisation (Fig. 3), which reduces calculated consumption (Table 4), wolves in pack C showed a high tendency of revisiting old carcasses, on average every 5.9 days, which probably were an important source of food and would increase the total amount of biomass consumed. Calculations of gained biomass from old carcasses could not be done since available and consumed tissue could not be estimated. Wolves in pack (A) and (B) probably also used old carcasses frequently but it was not measured. Extent and importance of scavenging old carcasses are also reported in other studies (Kolenosky 1972; Messier and Crete 1985; Wilton 1986; Fuller 1991; Huggard 1993c). The ratio at which wolves in pack C killed and scavenged moose (1: 1.1-1.4), prey combination *i-iii*, are probably low estimates since occasions of scavenging only could be registered on earlier detected moose carcasses. Forbes and Theberge (1992) found that scavenging supplied a large proportion of the winter food intake since wolves killed and scavenge at a ratio of 1:6 during midwinter which is notable higher compared the present study.

Predation, moose population and human moose harvest

In this study annual wolf predation rates (prey combination *iii*) was 4-15% compared to the moose winter population (Table 6) and 10-30% compared to the annual moose harvest (Table 7). The major part of predation occurred within the calf category, 12-48% compared to the moose winter population (Table 6) and 19-52% compared to the annual moose harvest (Table 7). If annual growth rate of the local moose population are balanced by harvest, future calf harvest in the area occupied by pack A would have to be reduced by at least 50 %, assuming a constant prey selectivity and kill rates from wolves over the year. Regarding the areas occupied by pack B and C calf harvest would only have to be reduced by 25%. Harvest on adults would not have to be changed since the proportion of reproducing adults in wolf kills are comparatively low 1-3% (Table 6) and would therefore probably not effect the population growth substantially.

The territory size, have a large influence on the effects of predation. Territory size for pack B and C was 82 and 63% larger compared to pack A (Fig. 1). High kill rate in combination with a small territory causes higher local predation rate in the territory occupied by pack A compared to the territories occupied by pack B and C. Wolf territory size is influenced by prey density, pack size and wolf density (Fritts and Mech 1981; Ballard *et al* 1997). In a low density wolf population as the Scandinavian, territory size is not limited by any of these parameters and tend to range within 800 - 1200 km² (Sand unpublished data). In an area with wolf territories of this size and relatively high moose density (0,8-0,12 moose km⁻²) wolf predation will probably not cause any large-scale effects on the moose population

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Appendix

Table A1. Ungulate carcasses found in the Leksand-pack territory during the winter of 1998-1999.

Nr	Species	Found during	Date of death	Cause of death	Age	Sex	Consumed proportion (%)	Handling time (days)
1	moose	snow tracking	1998-10-12	3	0		90	
2	moose	snow tracking		1	0		95	
3	moose	snow tracking		1	≥1	F	95	
4	moose	snow tracking		1			100	
5	moose	snow tracking	1998-11-08	3	0	F	1	
6	moose	snow tracking	1998-11-16	3	0		95	
7	moose	snow tracking	1998-11-27	3	0		99	
8	moose	snow tracking	1998-12-06	3	0		5	
9	moose	snow tracking	1998-12-09	3	≥1	F	95	
10	moose	snow tracking		5			100	
11	moose	snow tracking	1998-12-22	3	0		100	
12	moose	snow tracking	1998-12-28	3	0		100	2,19
13	moose	telemetry	1999-01-04	3	0		95	4,08
14	moose	telemetry	1999-01-04	3	0		95	4,08
15	moose	telemetry		4	0		100	
16	moose	snow tracking		1	0		100	
17	moose	telemetry	1999-01-14	3	0	F	20	4,93
18	moose	snow tracking		1			100	
19	moose	snow tracking		1	0		100	
20	moose	telemetry		3			98	12,03
21	moose	snow tracking		1			100	
22	moose	telemetry	1999-01-25	3	≥1	M	70	3,48
23	moose	telemetry	1999-01-24	3	0		50	3
24	moose	snow tracking		4	0		100	
25	moose	telemetry	1999-02-09	3	0		100	0,8
26	moose	snow tracking	1999-02-12	3	0	F	0	0,1
27	moose	snow tracking	1998-12-15	4	0		99	
28	moose	telemetry	1999-01-20	4	0		95	
29	moose	snow tracking		1	0		100	
30	moose	snow tracking		1	≥1	F	100	
31	moose	snow tracking		4		F	99	
32	moose	snow tracking	1999-02-14	3	0	F	85	
33	moose	telemetry	1999-02-19	3	0		70	
34	moose	telemetry	1999-03-02	3	0		95	4,85
35	moose	snow tracking		4	0		97	
36	moose			1	≥1	F	60	
37	moose	snow tracking		1			100	
38	moose	telemetry	1999-03-16	3	0		95	
39	moose	snow tracking		1	0		100	
40	moose	snow tracking		5	0	F	100	
41	moose	telemetry	1999-03-18	3	1		85	6,08
42	moose	telemetry	1999-03-18	3	0	F	50	1,04
43	moose	telemetry	1999-03-26	3	0		95	2,92
44	moose	snow tracking		5	0		100	

Found within study period

- 1) killed by other causes than wolves
- 2) dead prior to study period
- 3) positively killed by wolves
- 4) assumed to be killed by wolves
- 5) possibly killed by wolves

Table A2. Ungulate carcasses found in the Leksand-pack territory during the winter of 1999-2000.

Nr	Species	Found during	Date of death	Cause of death	Age	Sex	Consumed proportion (%)	Handling time (days)
1	moose	telemetry	1999-10-14	2		F		
2	moose	telemetry	1999-10-20	2	≥2	M		
3	moose	telemetry	2000-01-01	3	0		75	5,65
4	moose	Snow tracking		1			100	
5	moose	Snow tracking		1			100	
6	moose	telemetry	2000-01-08	3	1		35	4,4
7	moose	telemetry	2000-01-10	3	0		60	1,95
8	roe deer	Snow tracking	2000-01-21	3			100	
9	moose	telemetry	2000-01-25	3	0	F	30	1,88
10	moose	telemetry	2000-01-30	3	0		80	
11	moose	Snow tracking	2000-02-03	3	0	F	10	0,1
12	moose	Snow tracking		1			100	
13	moose	telemetry	2000-02-05	3	0		60	2,27
14	moose	telemetry	2000-02-10	3	0		95	2,65
15	moose	Snow tracking	2000-02-13	3	0		90	
16	moose	telemetry	2000-02-17	3	0		60	1,92
17	moose	Snow tracking		1	8		100	
18	moose	telemetry	2000-02-25	3	0		55	2,65
19	moose	telemetry	2000-02-28	4	0		95	
20	moose	telemetry	2000-03-07	3	0	F	30	
21	moose	Snow tracking		1			100	
22	moose	telemetry	2000-03-10	3	0		50	0,92
23	moose	telemetry	2000-03-13	3	0		80	1,79

Found within study period

- 1) killed by other causes than wolves
- 2) dead prior to study period
- 3) positively killed by wolves
- 4) assumed to be killed by wolves
- 5) possibly killed by wolves

Table A3. Ungulate carcasses found in the Grangårde-pack territory during the winter of 1999-2000.

Nr	Species	Found during	Date of death	Cause of death	Age	Sex	Consumed proportion (%)	Handling time (days)
1	moose	snow tracking	1999-12-05	3	0	M	50	3
2	moose	telemetry	1999-12-12	3	0	M	60	4,11
3	moose	telemetry		1	0		100	
4	moose	snow tracking	1999-12-31	3	0		35	0,85
5	roe deer	snow tracking	2000-01-01	3			100	0,86
6	moose	snow tracking	2000-01-02	3	0	M	1	0,1
7	roe deer	telemetry	2000-01-03	3			90	1,12
8	moose	telemetry		1	0		90	
9	moose	telemetry	2000-01-19	3	0	M	25	2,01
10	roe deer	telemetry	2000-01-22	3			95	2,5
11	roe deer	snow tracking	2000-01-25	3	0	F	15	
12	moose	snow tracking	2000-01-28	3	0	M	20	1,1
13	roe deer	telemetry	2000-01-31	3			95	0,54
14	roe deer	snow tracking	2000-01-22	3			95	0,54
15	moose	snow tracking		5	0		80	
16	moose	telemetry		5	0	F	100	
17	moose	snow tracking	2000-02-16	3	0	F	10	1,71
18	moose	snow tracking		1	≥1		20	
19	moose	telemetry	2000-02-20	3	0		100	2,54
20	moose	snow tracking		2	≥1	M	20	
21	moose	telemetry	2000-03-05	3	0	F	60	1,81
22	moose	telemetry		5	0	M	100	
23	moose	telemetry	2000-03-09	3	7	F	20	2,44
24	moose	telemetry	2000-03-15	3	0	M	65	2,53
25	moose	telemetry	2000-03-19	3	7	F	40	3,16
26	moose	telemetry	2000-03-25	3	0		80	3,97

Found within study period

- 1) killed by other causes than wolves
- 2) dead prior to study period
- 3) positively killed by wolves
- 4) assumed to be killed by wolves
- 5) possibly killed by wolves

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