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Wolf winter predation on moose and roe deer in relation to pack size

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Abstract: Wolf (*Canis lupus*) winter predation on moose (*Alces alces*) and roe deer (*Capreolus capreolus*) were studied in the small, but fast growing wolf population on the Scandinavian Peninsula. Wolves in one territory were radio- and snow-tracked during two successive winters. The wolf pack consisted of an adult pair during the first winter (1999–2000), and of an adult male and three pups the following winter. Kill rate on moose was 7.4–9.2 days/kill for the adult pair and 4.0–4.8 days/kill for the pack of four wolves. The consumed proportion of wolf-killed moose at first feeding occasion was relatively low during both winters (44% and 51%) but wolves utilized carcasses by revisits at previous kill sites. Wolves did not select to kill malnourished moose as nutritional condition of wolf-killed moose was comparable to moose harvested by hunters. Handling time at first feeding occasion did not differ with increased pack size, but were longer for the pups as compared to the adult male. The adult male and pups were solitary in 61–68% of all locations during the second year of study while the adult pair was solitary in 13% during the first year of study. Hunting success of the adult male on moose (60%) and roe deer (100%) during the second year of study was higher as compared to the first year (21% and 55%). Chasing distances during successful attacks by wolves on roe deer were longer than on moose.

Introduction

Gray wolf (*Canis Lupus*) is a protected species since 1966 in Sweden and 1972 in Norway (Persson and Sand 1998). The wolf population on the Scandinavian Peninsula (Sweden and Norway) consisted of eight or nine wolves during winter of 1977–1978 (Bjärvall and Nilsson 1978). The population did not grow until 1991 when wolf breeding in two territories was first documented, but has increased since then with on average 29% per year (Wabakken *et al*. 2001). Wolf territories with newly formed pairs have been established each year since 1994 (Wabakken *et al*. 2001). During winter of 2000–2001 the number of wolves on the Scandinavian Peninsula ranged between 87 and 97 individuals (Å. Aronson *et al*., unpublished data). The Swedish authorities has decided that the Swedish wolf population should reach 200 individuals as a first management goal, and then an evaluation of the situation should be performed whether the population should be let to grow further or be controlled.

With the fast growing wolf population in Sweden, knowledge of how wolves influence populations of moose (*Alces alces*) and roe deer (*Capreolus capreolus*), which are important game species, is of importance for effective management of wolves and their prey populations. Hunters control annual growth rate of moose and roe deer populations through harvest. In order to compensate for wolf predation as the wolf population increase, moose hunting quotas may need to be reduced.

On the Scandinavian Peninsula, only a couple of studies have been performed on wolf predation ecology (Olsson *et al*. 1997, Palm 2001). Olsson *et al*. (1997) reported that wolves killed 5% of the moose population each year, during a 5-year study of wolf scats in one territory. Palm (2001) used observed kills by wolves in three packs and showed that wolves killed 4–15% of the winter moose population annually.

Of further interest while considering moose management in Sweden are facts about how wolf pack size influence kill rate. Studies in North America have shown that the size of packs affect predation rates more than the total number of wolves in a population, as kill rate per wolf in small packs is higher than in large packs (Carbyn 1983, Ballard *et al*. 1987, Thurber and Peterson 1993, Hayes *et al*. 2000). Promberger (1992) explained a higher kill rate per wolf in small packs by the fact that the loss of edible biomass to scavengers are higher than in large packs, and therefore wolves in small packs have to kill more prey per wolf to gain the same quantity of food. Several studies in North America have also reported that wolf handling time on adult moose carcasses decrease as pack size increase, as more wolves consume prey faster (Messier and Crête 1985, Ballard *et al*. 1987, Hayes 1991). However, kill rate are also shown to increase in severe winters due to moose being more vulnerable to predation (Peterson 1977, Peterson *et al*. 1984), and wolves consumption of killed ungulates are shown to be less when prey is easy to kill (Carbyn 1983, Bobek *et al*. 1992, DelGiudice 1998). Thurber and Peterson (1993) suggested as an alternative explanation that kill rate do not reflect pack size because of the predominant influence of adult wolves, which probably eat more than subordinate wolves.

A selection for moose calves by wolves that prey primarily on moose are presented in North American studies (Fuller and Keith 1980, Hayes *et al*. 1991, Hayes *et al*. 2000) and on the Scandinavian Peninsula (Olsson *et al*. 1997, Palm 2001). Fuller and Keith (1980) explained a selection for calves by the fact that young moose are easier to kill than animals in their prime age. Animals in poor nutritional condition should also be an easier prey for wolves, and several studies in North America report that wolves tend to prey on moose in poor condition (Fritts and Mech 1981, Peterson *et al*. 1984, Ballard *et al*. 1987, Mech *et al*. 1995). However, Franzmann and Arneson (1976) and Gasaway *et al*. (1983) showed that wolves did not select to kill malnourished moose.

In spring 1999, a one-year-old, radio-collared male wolf established a territory with a resident adult female wolf northwest of Grangärde in the county of Dalarna, in south-central Sweden. A study examining predation ecology of this pair was conducted between December 1999 and March 2000 (Palm 2001). The adult female was radio-tagged in February 2000. The pair reproduced during spring and four pups was confirmed in autumn the same year by visual observations. Radio telemetry contact was lost with the adult female for unknown reason in the middle of November 2000, and snow tracking confirmed that she was not present in the territory during the current study.

The objective of this study was to examine if, and how, wolf predation on moose and roe deer changes in a pack during a winter following wolf breeding. The parameters of interest were:

- *(i)* kill and consumption rates,
- *(ii)* age and sex of wolf-killed moose and roe deer,
- *(iii)* nutritional condition of wolf-killed moose,
- *(iv)* feeding behaviour of the adult male and pups, as measured by handling time and number of revisits at previous kill sites,
- *(v)* hunting success and chasing distances, and
- *(vi)* pack cohesion.

Study area

The Grangärde wolf territory is located in the province of Dalarna (the centre of the territory is situated at: 66º80'N, 14º40'E) in south-central Sweden (Fig. 1). The study area is hilly with altitudes from 190 to 440 m. a. s. l. and is mainly covered with boreal forest of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Other occurring tree species are birch (*Betula spp*.), willows (*Salix spp*.), and aspen (*Populus tremula*). Forest gravel roads penetrate the whole territory.

Potential prey for wolves in the Grangärde territory included moose, roe deer, beaver (*Castor fiber*), badger (*Meles meles*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*). Other carnivores such as brown bear (*Ursus arctos*), lynx (*Lynx lynx*), and red fox (*Vulpes vulpes*) were also present in the wolf territory. Winter densities of moose and roe deer were 1.1 moose/km^2 during 1999–2000, 1.0 moose/km^2 the following year, and 0.2 roe deer/km^2 during both years, according to fecal pellet group counts during springs of 2000 and 2001 (H. Sand, unpublished data).

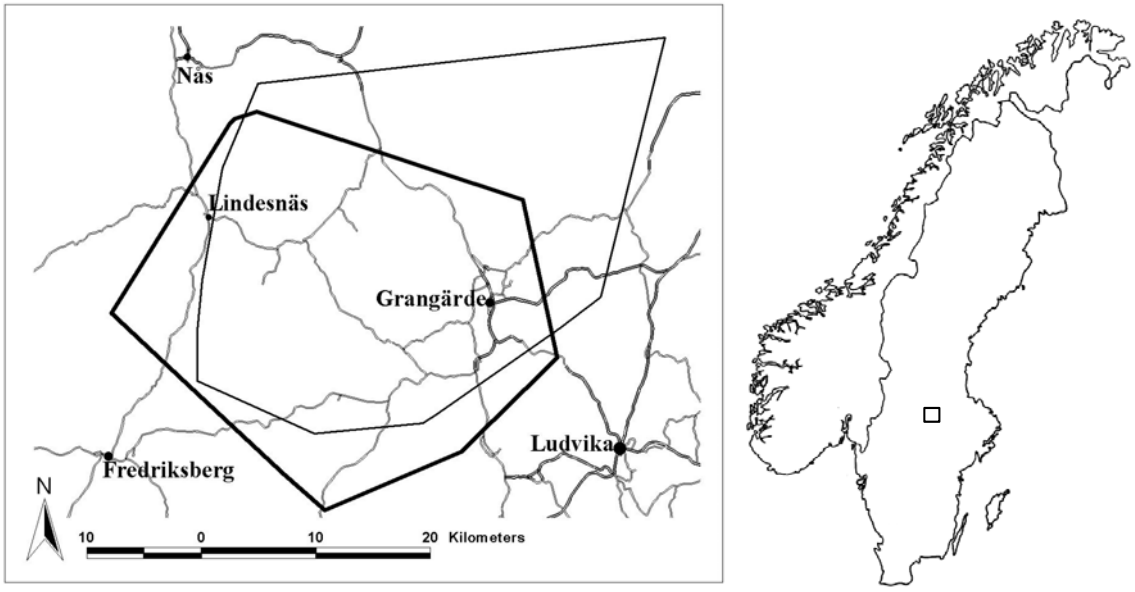

Figure 1. Boundaries of the Grangärde territory during winters of 1999–2000 (thin lines) and 2000–2001 (thick lines), and the study areas location on the Scandinavian Peninsula.

Maximum snow depth during winters of 1999–2000 and 2000–2001 were 80 cm (Palm 2001) and 60 cm, respectively. Temperature ranged between +4 and -22 °C during winter of 1999–2000 (Palm 2001) and between +4 and -32 °C in the following winter.

Methods

Radio tracking

The field study was carried out between 29 November 2000 and 3 April 2001. Two pups, a male and a female, were tagged with mortality-sensing radio-collars (151 MHz; Telonics, Inc., Ariz.) on 9 February 2001. Wolves were radio tracked from ground, using standard telemetry triangulation technique (Kenward 1987). At least three bearings were used for each location, but if the wolf was under fast movement during radio telemetry, only two bearings were obtained. Locations were obtained 1 to 10 times each day between 6:15 AM and 11:30 PM, and on average 4 times per day for the adult male and twice a day for the pups. Territory sizes were determined from radio telemetry locations by using the 100% minimum convex polygon method (Mohr 1947).

Snow tracking

During the period of continuous snow cover (18 December 2000–1 April 2001), wolves were snow tracked by foot, with the aid of snowshoes, or cross country skies in order to find their kills and register failed wolf attacks on moose and roe deer. Snow tracking was also made by car when wolves had travelled on forest roads for distances > 1 km.

When one or more wolves had been stationary, according to clustering of locations within an area of < 5 km^2 for > 24 hours, the area was searched for wolf-killed prey. To ensure that wolves were not disturbed, search for carcasses was not initiated until wolves were radio-located at least 5 km away from the suspected site of kill. Before pups were fitted with radio-collars, searching for wolf kill was avoided until it was concluded, on the basis of wolf tracks, that the pups had left the assumed area of kill. If it was not possible to search and find killed prey after the wolves had left, due to heavy snowfall, the area was searched after the next time one of the radio-collared wolves was located close to the suspected area of kill.

Wolves were snow tracked almost every day even if locations from radio tracking did not indicate that a killing had occurred. This was done in order to find recently killed prey that were consumed quickly, or prey abandoned before totally consumed by the wolves (Palm 2001), and previously killed prey that were revisited by wolves. Presence of ravens (*Corvus corax*) was often used as an indicator of kill sites. Kills were also found on the basis of information from local people, not connected to the research project.

A wolf attack on prey was defined as gait-tracks from both wolf and moose or roe deer occurring together (moose and roe deer are hereafter refereed to as ungulates). Length, number of wolves involved, and outcome (successful or failed) of chase were registered for every confirmed attack.

Carcasses

To determine the cause of death of found ungulates, kill sites were searched for tracks from a wolf attack and for heavy bleeding or fresh blood from prey. Carcasses were then categorized into three groups:

1. *Wolf-killed prey* – had either tracks from a wolf attack at the site of kill, or heavy bleeding/fresh blood from prey in the snow in combination with wolf tracks at kill site (Messier and Crête 1985, Thurber and Peterson 1993, Hayes *et al*. 2000).
2. *Possibly wolf-killed prey* – had wolf tracks at kill site, but it could not be excluded that the ungulate was not wolf-killed, as prey was found > 1 month after assumed time of death.
3. *Other carcasses* – ungulates known to have died from other causes than wolf predation (for example shot by hunters) or of unknown reason prior to the first snowfall (if a carcass was found on bare ground), but utilized by wolves.

Visual observations and tracks or scats from scavengers were registered at kill sites. Carcasses were examined in order to identify species and sex, and to estimate the consumed proportion of available biomass at first feeding occasion, and time of death. Sex was determined by the sexual organ or by presence of antlers or antler pedicels. The proportion consumed was estimated visually to the nearest 5% of the edible part of ungulates, rumen, guts, bones, and hide excluded (Promberger 1992). Assumed time of

death of wolf-killed ungulates was set to the midpoint in time between the first location of the adult male within 1 km from the actual carcass and the previous location. In three cases of wolf-killed moose and five cases of wolf-killed roe deer, wolves were not radio tracked within a radius of 1 km. The possible time period of death was then estimated by comparing existence or lack of snow cover on carcass, with daily registrations of precipitation and snow depth during the study period. The middle day of this period (≤ 3 days) was set as date of kill. It was possible to roughly determine time of death on previously killed ungulates because hair layers at different snow depths indicated earlier occasions of consumption. The location of a carcass was obtained by using a handheld GPS-unit (GARMIN GPS 12/12XL, accuracy: 15 meters).

Ungulates consumed < 95% at first feeding occasion, were examined again, roughly every 10^{th}, 20^{th} and 30^{th} day after assumed date of death, or when wolves had been radio-located < 1 km from a previously found kill site. Consumed proportion of edible biomass, visual observations of scavengers, and presence of tracks and scats from wolves and scavengers were then registered at kill site.

Mandibles and leg bones were collected from wolf-killed ungulates, for determination of age and nutritional condition. Collected material was kept frozen until analyses in laboratory were conducted, in order to prevent bone marrow from drying (Peterson *et al*. 1982). Age was determined for moose by sectioning the 1^{st} molar (M1) tooth and counting cementum annuli (Wolfe 1969). For roe deer, age was determined by comparing tooth eruption of mandibles from wolf-killed roe deer with tooth eruption of mandibles from roe deer of known age (Cederlund and Liberg 1995).

Analysis of nutritional condition of moose

Analysis of nutritional condition of moose were conducted by removing bone marrow, which was weighed and dried at 70ºC for 14 days, then weighed again, and fat content was calculated as the ratio of dry weight/wet weight (Neiland 1970). To investigate if nutritional condition differed between wolf-killed moose and moose harvested by hunters, a comparison between fat content in mandibles from wolf-killed moose and moose harvested by hunters was performed (Ballard *et al*. 1981). Moose harvested by hunters were assumed to represent the average condition of moose in the population. In seven wolf-killed moose the mandible could not be found at kill site but a leg bone was. Mandible fat content was then estimated from fat content in the collected leg bone, using a constructed statistical relationship between mandible and leg bone fat content (Table 1). The relationship between fat content in the mandible and various leg bones from the same moose was constructed by using bone marrow from wolf-killed moose in the Grangärde territory during winters of 1999–2000 (n = 8) and 2000–2001 (n = 17). In addition, a reference material consisting of 15 moose from Grimsö Wildlife Research Area (10 calves, 3 yearlings and 2 adults) harvested by hunters in autumns of 1999 (n = 9) and 2000 (n = 6), and 1 adult moose that was assumed to have died from natural causes in spring 2001 (H. Sand, unpublished data) were used in this analysis.

Table 1. Regressions between fat content in mandibles (*X*) and various leg bones (*Y*). Results are calculated from wolf-killed moose in the Grangärde territory during winters of 1999–2000 and 2000–2001, a reference material from moose harvested in the Grimsö Wildlife Research Area during autumns of 1999 and 2000, and one moose that was assumed to have died from natural causes in spring 2001.

Leg bone (*Y*)	Regressions between fat content in mandibles (*X*) and leg bones (*Y*)			
	r	d. f.	p	Equation
Femur	0.64	20	< 0.001	$X = 32.72 + (0.51 \times Y)$
Tibia	0.86	22	< 0.001	$X = 22.58 + (0.59 \times Y)$
Metatarsus	0.71	16	< 0.001	$X = 31.90 + (0.48 \times Y)$
Humerus	0.61	14	0.020	$X = 44.93 + (0.31 \times Y)$
Radius	0.87	20	< 0.001	$X = 26.07 + (0.57 \times Y)$
Metacarpal	0.62	19	0.004	$X = 48.05 + (0.26 \times Y)$

Kill and consumption rates

Minimum kill rates were calculated for both wolf-killed moose and wolf-killed ungulates by estimating the true time interval between consecutive kills. Time of death was more uncertain for possibly wolf-killed prey and maximum kill rates were therefore calculated as:

$$K_{moose} = \frac{H}{J}$$

$$K_{ungulates} = \frac{G}{T}$$

where

K = maximum kill rate,
H = number of days between the first and last wolf-killed/possibly wolf-killed moose,
J = number of wolf-killed and possibly wolf-killed moose (excluding the first killed moose during the study period),
G = number of days between the first and last wolf-killed/possibly wolf-killed ungulate, and
T = number of wolf-killed and possibly wolf-killed ungulates (excluding the first killed ungulate during the study period).

Food availability (*A*) was calculated as kg/wolf/day, maximum consumption by wolves at first feeding occasion (*C*) and minimum consumption by wolves with adjustment for food loss to scavengers (*S*), were estimated as kg/wolf/day and kg/kg_{wolf}/day according to the following formulas:

$$A_i = R_i \times N_i \times P_i$$

$$A = \frac{\left(\sum_{i=1}^{4} A_i\right)}{(G \times F)}$$

$$C = \frac{\left(\sum_{i=1}^{4} (A_i \times D_i)\right)}{(G \times F)} \quad \text{or} \quad C = \frac{\left(\sum_{i=1}^{4} (A_i \times D_i)\right)}{(G \times F \times W)}$$

$$S = C \times E$$

where

i = four categorizes of wolf-killed ungulates: adult female moose, yearling moose, calf moose and roe deer,
A_i = biomass available from ungulates in prey category i,
R_i = live weight of ungulate in prey category i,
N_i = number of carcasses in prey category i (excluding the first wolf-killed ungulate during the study period),
P_i = wolves consumable part of ungulate biomass in prey category i,
F = wolf pack size,
D_i = average proportion consumed during first feeding occasion of prey in category i,
W = wolf pack weight, and
E = consumed proportion by wolves after adjusting for food loss to scavengers.

Live weights of wolf-killed adult, yearling and calf moose were estimated by using carcass body weight from moose harvested by hunters in the Mockfjärd Moose Research Area which is partly covered by the Grangärde territory (Svenska Jägareförbundet, unpublished data). The moose were harvested in October 2000 and live weights were obtained by correcting carcass body weight to live weight, using a known relationship between carcass body weight and live weight (H. Sand *et al*., unpublished data), and then correct for weight loss during winter (Table 2). The weight loss from October to February were assumed to be 5, 6 and 9% for adults, yearlings and calves, respectively (Cederlund *et al*. 1991, H. Sand *et al*., unpublished data). Average live weight of roe deer in winter was 23 kg, calculated from a weight loss of 8% on autumn live weight (25 kg; Cederlund

Table 2. Linear regression model between live weight (L) and carcass body weight (B) of moose in Grimsö Wildlife Research Area (H. Sand *et al*., unpublished data). Also shown are calculated average live weights of moose in Mockfjärd Moose Research Area during October (M), and average live weights adjusted for reduction during winter (R).

Moose category	Linear regression model	Live weight in October (M)	Live weight during winter (R)
Adult females[a]	$L = 1.75B + 46.18$	360	342
Yearlings	$L = 1.89B + 16.72$	308	290
Calves	$L = 2.04B + 10.67$	176	160

[a]No adult male moose was killed by wolves during the study period.

and Liberg 1995). Edible biomass of moose and roe deer consumed by wolves were estimated to 65% (Promberger 1992) and 80% (Glowacinski and Profus 1997), respectively, of live weights. Scavengers, such as red fox and raven, were often noted to consume edible biomass from wolf-killed ungulates. Minimum consumption by wolves (*S*) was 65% of maximum consumption (*C*) for a pack of four wolves, when adjusted for food loss to scavengers (Promberger 1992). Average wolf body weights during winter were set to 51 kg for the adult male and 35 kg for the pups (Sand *et al*. 2000).

Handling time

Handling time is the number of days that wolves spent at or near a kill site, according to Walters *et al*. (1981). Only wolf-killed ungulates were wolves had been radio-located within 1 km from kill site were used when calculating handling time at first feeding occasion. Distances between locations of radio collared wolves and site of carcass were calculated by using the geographic information system (GIS), ArcView 3.2 (ESRI 1996), without consideration of location error from radio tracking (Kenward 1987). Handling time equalled the number of days between assumed time of death of prey, and midpoint in time between the first location exceeding 5 km from kill site and the previous location. The 5 km distance was used because wolves often moved back and forth to a carcass during the first feeding occasion, but on all occasions after exceeding this distance, wolves continued to travel further away from the carcass. If it was known from snow tracking that wolves did not return to a carcass, even when radio-located within a 5 km radius, then a radius of 1 km was used to define the end of handling time (n = 5). Handling time for revisits to wolf-killed prey and utilization of possibly wolf-killed prey and other carcasses (revisits to wolf-killed prey and utilization of possibly wolf-killed prey and other carcasses are hereafter refereed to as revisits and scavenging) that were detected with the aid of telemetry was calculated the same way as handling time at first feeding occasion. Handling time for revisits and scavenging that were only detected during snow tracking were set to half the estimated time between the location prior to and the first location after the known revisit or scavenging event.

Statistical methods

Only wolf-killed prey (category 1) was used for all statistical analyses, with exceptions for calculations of maximum kill rates and analyses of wolves revisits and scavenging. Chi-square (two-way classification) analyses were performed to test if age structure of prey and hunting success of wolves, differed between years. Simple linear regression was used to estimate the relationship between fat content in bone marrow of mandible and various leg bones. Mann-Whitney U-test were used to examine variation in fat content between wolf-killed moose and moose harvested by hunters, and to determine if chasing distances differed between failed and successful attacks, between years and prey species. Kruskal-Wallis test was performed to determine if the number of days between revisits or scavenging differed between adult and subordinate wolves. Unpaired t-tests were used to determine if kill rate and consumption differed between years, and if handling time differed between the adult male and pups, age of prey, and between years.

Results

Pack cohesion

According to snow tracking, four wolves, an adult male and three pups, permanently occupied the territory in Grangärde during winter of 2000–2001. The adult male (9804), the female pup (0101), and the male pup (0102) were radio-located 504, 121, and 123 times, respectively. A total of 493 km of snow tracking was performed (449 km by skiing or foot and 44 km by car), of which 360 km was tracks from the adult male, alone or in company with one, two, or three pups. The radio-collared wolves in the pack were solitary in 61–68% of all locations (Fig. 2), and in 59–84% of the total distance of snow tracking. During winter of 1999–2000 the adult pair were in company in 87% of all locations (n = 126) and solitary during 13% (n = 18; H. Sand, unpublished data). Territory size for the Grangärde pack during winter of 1999–2000 was 1036 km^2 (Palm 2001), and 857 km^2 during the following winter.

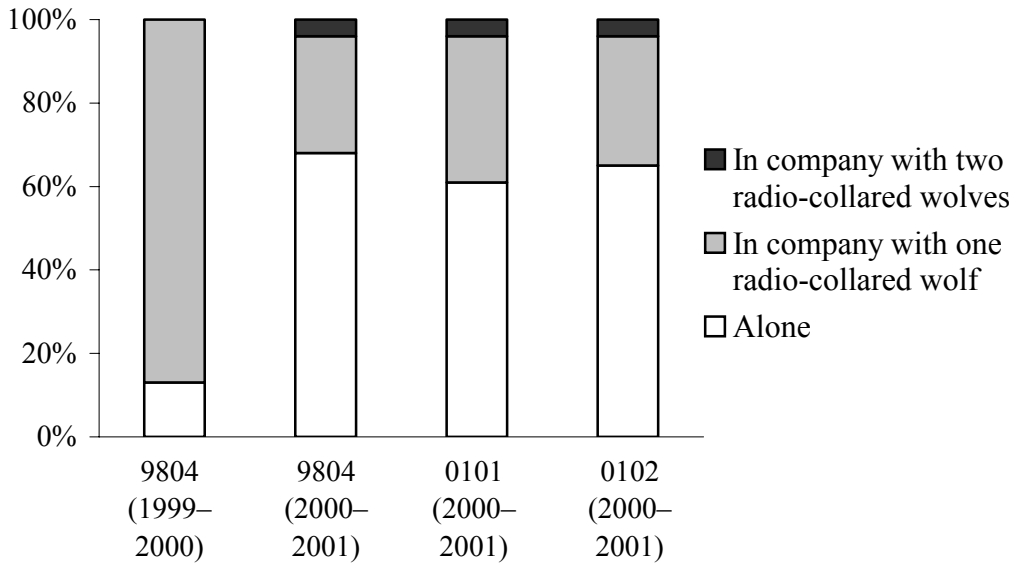

Figure 2. Percentages of locations in which the adult male (9804), the female pup (0101), and the male pup (0102) were solitary and in company with other radio-collared wolves in the Grangärde pack, during winters of 1999–2000 and 2000–2001.

Feeding ecology

During the study period, 34 moose carcasses and 9 roe deer carcasses were found (Appendix 1). Among moose carcasses, 21 were wolf-killed, 3 were possibly wolf-killed, and 7 died before the start of the study period (found during snow tracking when wolves revisited previous kill sites or scavenged). Wolves were also scavenging remains of three hunter-killed moose, which was left in the forest during autumn of 2000. Eight of nine roe deer were wolf-killed and one had died from unknown causes. Small game killed by

wolves were also found and these consisted of five capercaillie, one male and four females, and four black grouse, two males and two females.

Of the 21 wolf-killed moose, 4 were killed by the adult male alone, and 14 by the adult male in company with one or two pups. For the remaining three moose, the numbers of wolves involved in the killings were unknown. Of the eight wolf-killed roe deer, three were killed by the adult male alone, and two by the adult male in company with two pups. At two kill sites the numbers of wolves involved in the killings were unknown. From what could be detected from snow- and radio-tracking, the two radio-collared pups killed their first ungulate on 25 March 2001, a roe deer.

Age and sex of wolf-killed ungulates

Moose calves (n = 14), yearlings (n = 4), and adults (n = 3) comprised 67, 19 and 14% of wolf-killed moose. Age of adult moose averaged 14 ± 2.3 (mean ± SD) years. Age structure of wolf-killed moose did not differ significantly ($\chi^2 = 4.50$, d. f. = 2, p = 0.105) from winter of 1999–2000, when wolf-killed moose consisted of 85% calves (n = 11) and 15% adults (n = 2); adults were both 7 years of age (Palm 2001).

The 14 wolf-killed moose calves consisted of 5 males (36%), 3 females (21%) and 6 that were not possible to determine to sex (43%). Of the four yearlings, two were males (50%), one was a female (25%), and one was of unknown sex (25%). All adult moose were females. In winter of 1999–2000 the 2 adults were both females and the 11 calves consisted of 6 males (55%), 2 females (18%) and 3 of unknown sex (27%; Palm 2001).

Of the eight wolf-killed roe deer, four were determined to age and three to sex. Two males were 4 and 5 years old, one female had the age of 2 years, and one of unknown sex was a 1-year old. It was possible to determine age and sex of one of six wolf-killed roe deer during winter of 1999–2000, and it was a female fawn (Palm 2001).

Nutritional condition of wolf-killed moose

Moose mandible fat content did not differ significantly between wolf-killed calves (median = 56%, range = 28–73%) and calf harvested by hunters (median = 56%, range = 51–65%, U = 120.00, $n_{\text{wolf-killed}} = 24$, $n_{\text{reference}} = 10$, p > 0.999) or between wolf-killed adults (≥ 1-year-old, median = 72%, range = 47–79%) and adults harvested by hunters (median = 67%, range = 66–83%, U = 20.00, $n_{\text{wolf-killed}} = 9$, $n_{\text{reference}} = 5$, p = 0.740, Fig. 3).

Fat content value in various leg bones ranged between 10–69% (median = 35%, n = 23) and 50–91% (median = 82%, n = 9) for wolf-killed calves and adults, respectively. Fat content in leg bones of harvested moose ranged between 21–50% (median = 40%, n = 10) for calves, and 60–89% (median = 76%, n = 5) for adults. The adult in the reference material that was assumed to have died from natural causes had a fat content of 6% in mandible and 7% in leg bone (Appendix 2).

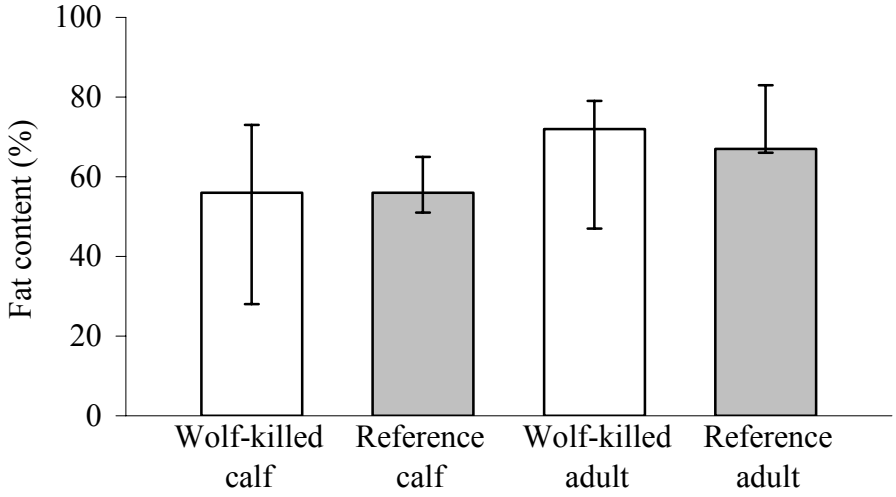

Figure 3. Median and range of fat content in mandibles of wolf-killed moose in the Grangärde territory during winters of 1999–2000 and 2000–2001, and a reference material from Grimsö Wildlife Research Area consisting of moose harvested by hunters during autumns of 1999 and 2000.

Kill and consumption rates

Kill rates in the Grangärde pack differed significantly between winters of 1999–2000 and 2000–2001 (Table 3) for both moose ($t = 2.79$, $n_{1999–2000} = 12$, $n_{2000–2001} = 20$, $p = 0.009$) and ungulates ($t = 2.04$, $n_{1999–2000} = 18$, $n_{2000–2001} = 28$, $p = 0.047$).

Table 3. Minimum and maximum kill rates (days/kill) on moose and ungulates, in the Grangärde territory during winters of 1999–2000 and 2000–2001.

Year	Kill rate (mean ± SD)			
	Wolf-killed moose		Wolf-killed ungulates	
	Positively[a]	Possibly[b]	Positively[a]	Possibly[b]
1999–2000	9.2 ± 6.22	7.4	6.1 ± 5.83	5.3
2000–2001	4.8 ± 2.59	4.0	3.6 ± 2.33	3.2

[a]True time intervals between consecutive kills based on the actual date of kills.
[b]Calculated time intervals between consecutive kills based on the total study period.

Food availability, consumption by wolves at first feeding occasion, and consumption by wolves at first feeding occasion with adjustment for food loss to scavengers, were 7.2, 3.7, and 2.4 kg/wolf/day, respectively, during winter of 2000–2001, and 6.8, 3.2 and 1.8 kg/wolf/day, respectively, during the previous winter (Palm 2001). Wolves consumption were 0.10 and 0.08 kg/kg_{wolf}/day, and 0.06 and 0.05 kg/kg_{wolf}/day when adjusting for food loss to scavengers, during winters of 2000–2001 and 1999–2000, respectively.

Handling time

Handling time of all moose by the adult male during the entire winter of 2000–2001, 1.1 ± 0.93 (mean ± SD) days, and by the adult pair during the previous winter, 1.9 ± 0.59 days, did not differ significantly between years ($t = 1.84$, $n_{1999–2000} = 7$, $n_{2000–2001} = 18$, $p = 0.080$). There was no significant difference in handling time by the adult male (handling

time during winters of 1999–2000 and 2000–2001 pooled), for adult moose (≥ 1-year-old), 1.7 ± 1.17 days, as compared to calf moose, 1.2 ± 0.71 days ($t = 1.55$, $n_{adults + yearlings} = 8$, $n_{calves} = 17$, $p = 0.134$). Handling time of moose killed after the two pups were radio-tagged differed significantly between the adult male, 0.8 ± 0.39 days, and the radio collared pups, 3.4 ± 2.73 days ($t = 2.85$, $n_{9804} = 9$, $n_{0101, 0102} = 6$, $p = 0.010$, Fig. 4). Handling time of roe deer by the adult male were 0.2 and 1.5 days for two roe deer during winter of 2000–2001, and 1.9 days for one roe deer during the previous winter.

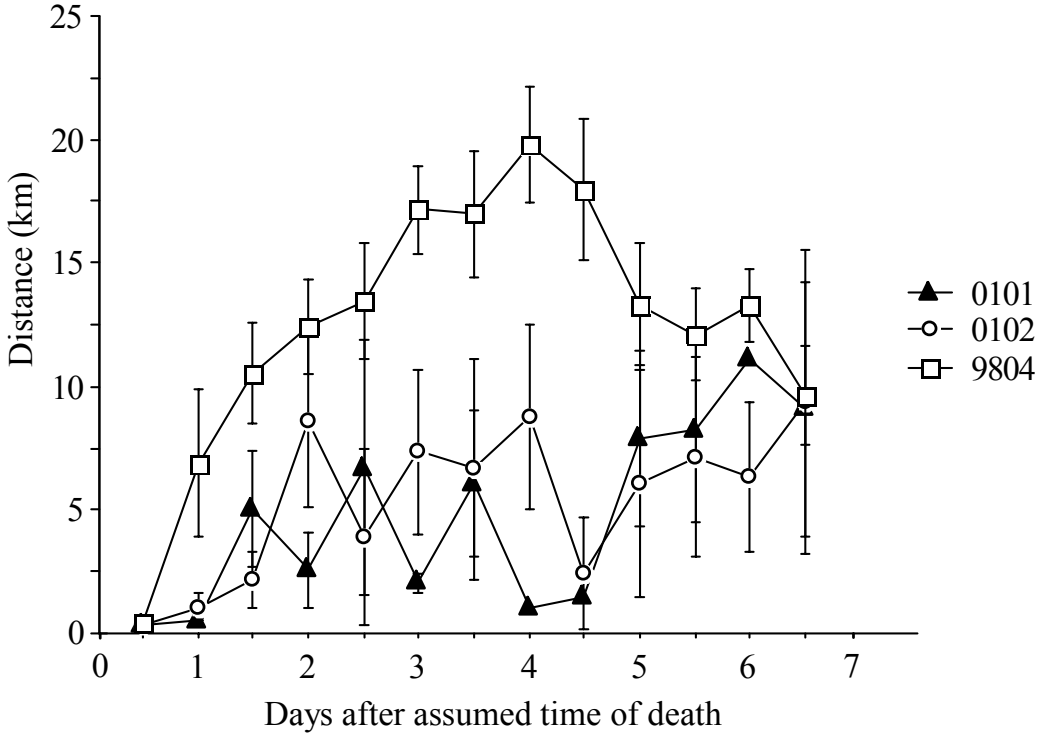

Figure 4. Distances (mean ± SE) between sites of wolf-killed moose and consecutive locations of the adult male (9804, n = 9), the female pup (0101, n = 2), and the male pup (0102, n = 4), in the Grangärde territory during 12 February 2001 and 24 March 2001.

Handling time during revisits and scavenging (after pups were radio-tagged) did not differ significantly for the adult male, 0.2 ± 0.11 days, and the radio-collared pups, 1.2 ± 2.22 days ($t = 1.50$, $n_{9804} = 11$, $n_{0101, 0102} = 17$, $p = 0.145$).

Consumption at first and subsequent feeding occasion

At first feeding occasion, 51% ± 38 (mean ± SD, n = 21) and 82% ± 30 (n = 8) of wolf-killed moose and roe deer, respectively, were consumed. Consumption of moose at first feeding occasion did not differ significantly from the previous winter, 44% ± 29 (Palm 2001; $t = 0.63$, $n_{1999–2000} = 13$, $n_{2000–2001} = 21$, $p = 0.535$). During the second year of the study, consumption at first feeding occasion differed significantly between moose killed and consumed by the adult male alone, 10% ± 4, and moose killed and consumed by the adult male in company with one or two pups, 58% ± 38 ($t = 2.51$, $n_{9804} = 4$, $n_{pups} = 14$, $p = 0.020$).

Of the 21 wolf-killed moose, 6 (28%) were consumed ≥ 95% at first feeding occasion, and another 10 (48%) were revisited one, two or three times by wolves (Table 4). During the study period, wolves never revisited 5 (24%) of the carcasses, but 1 of these was killed only 11 days before the end of the study period and may have been revisited later. The time between date of kill and the first revisit of the same moose by wolves was 31 ± 24 (mean ± SD, n = 10, range = 2–64) days. Of the eight wolf-killed roe deer, five (63%) were 100% consumed at first feeding occasion. Two roe deer carcasses (25%) were consumed to 25 and 45% at first feeding occasion and revisited by wolves one and two times, respectively. One roe deer carcass (12%), consumed to 90% at first feeding occasion, was never revisited by wolves.

Table 4. Consumption (mean ± SD) by wolves and scavengers on moose carcasses at first and subsequent feeding occasion by wolves, in the Grangärde territory during winter of 2000–2001.

Wolf-killed moose	Proportion consumed (%)				
	1st	2nd	3rd	4th	n
First feeding	51 ± 38	–	–	–	21
Consumed ≥ 95% at first feeding	98 ± 3	–	–	–	6
Carcasses revisited once	35 ± 28	72 ± 19	–	–	5
Carcasses revisited twice	37 ± 34	62 ± 33	100 ± 0	–	3
Carcasses revisited three times	40 ± 21	55 ± 7	95 ± 0	100 ± 0	2
Carcasses never revisited	26 ± 33	–	–	–	5

Tracks, scats or visual observations of scavengers were recorded in 67% of first feeding occasion of wolf-killed moose (n = 21), and in 50% of wolf-killed roe deer (n = 8). At subsequent examinations of wolf-killed prey consumed < 95%, utilization by scavengers were noted in 55% (n = 44) of moose carcasses and in 67% (n = 6) of roe deer carcasses. Red fox and raven were the most common scavengers, but lynx, crow (*Corvus corone*), jay (*Garrulus glandarius*), and magpie (*Pica pica*) also utilized wolf-killed ungulates. During the first month after date of kill, moose carcasses never revisited by wolves were consumed to a similar extent as carcasses revisited by wolves, due to utilization by scavengers (Table 5).

Table 5. Proportion of edible biomass (mean ± SD) of wolf-killed moose consumed < 95% after wolves first feeding occasion, at subsequent examinations after date of kill. A comparison between carcasses revisited by wolves and carcasses probably only utilized by scavengers after wolves first feeding occasion, in the Grangärde territory during winter of 2000–2001.

Wolf-killed moose	Proportion consumed (%) after							
	1st feeding	n	10 days	n	20 days	n	30 days	n
Revisited	36 ± 26	10	54 ± 27	10	60 ± 27	10	74 ± 28	7
Never revisited	26 ± 33	5	27 ± 33	5	52 ± 30	4	75 ± 22	3

During the study period, 23 revisits and 17 occasions of scavenging (including moose and roe deer carcasses consumed ≥ 95%) by wolves were confirmed. The number of days (median) between revisits or scavenging (after pups were radio-tagged) did not differ significantly between the adult male (4 days, range = 0–11), the female pup (2 days, range = 0–11), and the male pup (6 days, range = 2–11, $H = 3.55$, $n_{9804} = 10$, $n_{0101} = 10$,

$n_{0102} = 5$, $p = 0.170$). At the end of the study period (3 April 2001), 82 ± 26% (mean ± SD, n = 21) and 98 ± 4% (n = 8) of wolf-killed moose and roe deer, respectively, were consumed by wolves and scavengers.

Hunting success and chasing distances

Hunting success per snow-tracked kilometre for the adult male on moose was significantly lower during winter of 1999–2000, 13 of 61 (21%) attacks during 275 km of snow tracking (Palm 2001), as compared to 21 of 35 (60%) attacks during 360 km of snow tracking during winter of 2000–2001 ($\chi^2 = 16.52$, d. f. = 1, $p < 0.0001$). Hunting success per snow-tracked kilometre for the adult male on roe deer was also significantly lower during winter of 1999–2000, 6 of 11 (55%) attacks as compared to 8 out of 8 (100%) during the following winter ($\chi^2 = 4.79$, d. f. = 1, $p = 0.029$).

There were no significant differences in chasing distances between years (winters of 1999–2000 and 2000–2001) in neither failed ($U = 218.00$, $n_{1999–2000} = 43$, $n_{2000–2001} = 14$, $p = 0.120$) nor successful ($U = 52.50$, $n_{1999–2000} = 13$, $n_{2000–2001} = 11$, $p = 0.270$) attacks on moose (Table 6). Also, there was no difference in successful hunting distance on roe deer between years ($U = 8.50$, $n_{1999–2000} = 4$, $n_{2000–2001} = 5$, $p = 0.710$, Table 7). No failed wolf attack on roe deer was snow tracked during winter of 2000–2001, but there were five failed attacks registered the previous winter. There were no significant differences in failed versus successful chasing distances (chasing distances during winters of 1999–2000 and 2000–2001 pooled) on moose ($U = 529.00$, $n_{failed} = 57$, $n_{successful} = 24$, $p = 0.100$), or on roe deer ($U = 21.00$, $n_{failed} = 5$, $n_{successful} = 9$, $p = 0.840$).

Table 6. Length (m) of failed and successful attacks by the adult male (9804) on moose, in the Grangärde territory during winters of 1999–2000 and 2000–2001.

Year	Chasing distances (m), moose							
	Failed attacks				Successful attacks			
	Median	Max.	Min.	n	Median	Max.	Min.	n
1999–2000	50	500	5	43	30	200	0	13
2000–2001	95	450	30	14	65	900	0	11

Table 7. Length (m) of failed and successful attacks by the adult male (9804) on roe deer, in the Grangärde territory during winters of 1999–2000 and 2000–2001.

Year	Chasing distances (m), roe deer							
	Failed attacks				Successful attacks			
	Median	Max.	Min.	n	Median	Max.	Min.	n
1999–2000	150	200	50	5	150	300	100	4
2000–2001	–	–	–	0	600	1100	50	5

There was a significant difference in successful chasing distances between the two ungulate prey species, with significantly shorter chasing distances for moose than for roe deer (chasing distances during winters of 1999–2000 and 2000–2001 pooled, $U = 41.00$, $n_{moose} = 24$, $n_{roe\ deer} = 9$, $p = 0.007$).

Discussion

Wolf predation on ungulates in relation to pack size

Kill rate
Kill rates on moose in the Grangärde pack was in the higher range compared to studies with similar pack sizes (Thurber and Peterson 1993, Hayes *et al*. 2000), and consumption of carcasses at first feeding occasion lower (Messier and Crête 1985, Mech *et al*. 1995, Jedrzejewska and Jedrzejewski 1998). Calculated kill rates in the Grangärde pack should be viewed as minimum estimates because some kills where radio-collared wolves spent < 24 hours at first feeding occasion might not have been found. Four moose carcasses were abandoned by the adult male in < 14 hours and were never revisited during the 360 km of snow-tracking in winter of 2000–2001. According to snow tracking, the average distance travelled by the adult male was 17 km per day. Assuming that the adult male abandoned killed moose regularly, kill rate on moose could have been as high as 2.6–2.8 days/kill. When handling time is as short as shown by the adult male in the Grangärde pack, the only way to obtain data on true kill rates is by regular snow tracking, as carcasses abandoned quickly cannot be detected by the aid of radio telemetry.

Thurber and Peterson (1993) reported kill interval to decrease with approximately 33% as pack size doubled. After the recruitments of pups in the Grangärde territory, kill interval decreased with 48%. While including roe deer, the time interval between consecutive kills was reduced with 41%, as the proportion of wolf-killed roe deer was higher during winter of 1999–2000 compared to the following winter. Kill rates on ungulates in the current study was similar to those in a study of wolf predation on moose and caribou in Alaska, 4.0–4.2 days/kill for packs of four wolves, but higher than for pairs, 9.3–12.5 days/kill (Ballard *et al*. 1997). The results from the Grangärde territory contrast to previous studies in North America, where kill rate per wolf on moose in general are lower in large packs as compared to small packs (Carbyn 1983, Ballard *et al*. 1987, Dale *et al*. 1995, Hayes *et al*. 2000). However, lower kill rate per wolf in large packs was shown in the Leksand territory in Sweden, with 4.2 and 5.1 days/moose, for pack sizes of six and three wolves respectively, during two successive winters (Palm 2001).

Promberger (1992) explained a higher kill rate per wolf, in smaller packs compared to larger packs, by a larger loss of biomass to scavengers in small packs. Scavengers utilized wolf-killed ungulates to a great extent in the Grangärde territory. However, during both winters, wolves often left carcasses before they were totally consumed, and consumption of edible biomass by scavengers did probably not have a major impact on the high kill rate.

The high kill rate on ungulates during this study is probably best explained by the fact that ungulates are relatively easy to kill by predators, due to high vulnerability of prey in combination with high moose density. Naïve prey might result from a previous absence of predators on the Scandinavian Peninsula due to a large reduction in the wolf (Persson and Sand 1998) and brown bear populations (Berger *et al*. 2001) during late 19th and early 20th century. Lack of predators is shown to make prey more vulnerable to attacks,

due to their inexperience of carnivores (Breitenmoser and Haller 1993, Berger *et al*. 2001). To what extent the relatively high moose density influenced the kill rate is unknown, but high moose density provides more opportunities for wolves to catch up with, and kill moose. Studies of wolf predation at high moose densities need to be compared with wolf predation at lower moose densities, for knowledge of functional response.

Hunting success

Wolves hunting success was higher during winter of 2000–2001, as compared to the previous winter. This could not be explained by different harshness of the two winters. Moose vulnerability to predation by wolves are shown to increase at snow depths > 75 cm (Peterson 1977), and maximum snow depth in the Grangärde territory was 80 cm in winter of 1999–2000 and 60 cm in the following winter. Instead, the high hunting success in winter of 2000–2001 was most likely due to increased hunting experience of the adult male, as compared to the previous winter when he was a yearling. Increased hunting experience may also have contributed to the high kill rate during the second year of the study.

Hunting success in the Grangärde territory in winter of 2000–2001 was 60% on moose and 100% on roe deer. This was higher than reported from Alaska (26% on moose, Mech *et al*. 1998) and Canada (46% on white-tailed deer, Kolenosky 1972). The higher hunting success rate in the Grangärde territory could result from prey being more inexperienced to predators (Berger *et al*. 2001) but more data need to be gathered from other wolf packs. This study was accomplished to compare hunting behaviour between years and not to investigate an overall hunting success, and is likely biased to higher success, because kills may be easier to detect than failed attacks. To further study hunting success, more efforts need to be put down on snow tracking (following entire paths of wolves' travel between kills).

Consumption rate

Consumption at first feeding occasion was relatively low during both winters and did not differ significantly when pack size increased twofold. This may have been a consequence of the fact that prey are easy to kill and abundant. Wolves are found to utilize carcasses less if prey is easily available (Potvin and Jolicoeur 1988), for example at increasing snow depth (Carbyn 1983, Bobek *et al*. 1992, DelGiudice 1998). When wolves' primary prey are domestic animals, wolves often leave before kills are completely consumed (Pullianen 1965). This is thought to happen because the killings of domestic animals are easy and wolves eat only what they consider the most tasteful parts of carcasses (Mech 1970). In the Grangärde pack, the adult male while together with the male pup, killed two moose within 24 hours, 1200 meters apart. Only 10% of the first moose was consumed at the time when the other one was killed. Mech (1970) also reported that whenever wolves catch up with a moose they try to kill it, regardless of whether wolves recently had eaten or not.

Food availability for wolves in the Grangärde territory was similar (6.8 and 7.2 kg/wolf/day) in winters of 1999–2000 and 2000–2001, respectively. These figures are of

the same magnitude as shown in other studies in North America where wolves feed mainly on moose, 4.4–14.9 kg/wolf/day (Ballard *et al*. 1987, Thurber and Peterson 1993, Ballard *et al*. 1997). Wolves consumption in both winters (0.08 and 0.10 kg/kg_{wolf}/day) was in the lower range as compared to other wolf packs preying on moose in winter, 0.09–0.19 kg/kg_{wolf}/day (Fuller and Keith 1980, Peterson *et al*. 1984, Messier and Crête 1985, Ballard *et al*. 1987), and clearly lower when adjusting for food loss to scavengers, 0.05–0.06 kg/kg_{wolf}/day. Ravens were the most common scavenger on wolf-killed ungulates in the Grangärde territory, followed by red fox, which is similar to studies in Alaska (Ballard *et al*. 1987), Canada (Promberger 1992) and Poland (Jedrzejewska and Jedrzejewski 1998). Calculations of consumption by wolves in the Grangärde pack should be viewed as a minimum estimate. Food gained at wolves' revisits and scavenging were not included in the calculations. This was due to lack of knowledge of wolves' food intake at those feeding occasions, as moose carcasses never revisited by wolves were consumed almost to the same extent as carcasses revisited by wolves, due to utilization by scavengers. The radio-collared wolves in the Grangärde pack revisited or scavenged carcasses on average every fourth day during winter of 2000–2001, which indicate a non-negligible intake of edible biomass from those carcasses.

Age and sex of wolf-killed ungulates

During both winters, wolves killed more calves than adults, and all adults were ≥ 7 years old. That wolves prey primarily on young-of-the-year and animals in older age-classes, are in accordance with other studies where moose are the primary prey (Pimlott 1967, Hayes *et al*. 1991, Mech *et al*. 1995, Olsson *et al*. 1997, Mech *et al*. 1998, Hayes *et al*. 2000). Fuller and Keith (1980) explained this by the fact that young and old moose most likely are easier to kill than animals in their prime age. Moreover, all wolf-killed adult moose during the study were females. A female biased predation on adult moose is in accordance with Olsson *et al*. (1997) who reported that wolves killed no males older than two years old, during a study in south-central Sweden. Adult female moose is probably easier to kill for wolves than adult male moose due to their smaller size. The female biased predation may also be a consequence of a skewed sex ratio where older males are few, but this remains to be investigated.

Chasing distances

Chasing distances on moose and roe deer in the Grangärde territory did not differ between failed and successful attacks or between the two winters. The distances ranged between 0 to 900 meters for moose and between 50 to 1100 meters for roe deer. Mech (1966) found that wolves most often gave up after < 800 meters when chasing moose, during a study on Isle Royale. Kolenosky (1972) reported from a study in Canada that the average lengths of chasing distances on white-tailed deer were 600 and 1900 m for failed attacks, during two successive winters, and 2100 m for successful attacks. However, in the Grangärde territory, successful chasing distances on moose were significantly shorter than on roe deer. Moose being more difficult to kill if not taken within a shorter distance as compared to roe deer, could explain the fact that all moose, with the exception of two, were killed within 200 meters.

Nutritional condition of wolf-killed moose

The use of fat content in leg bones as an indicator of nutritional condition has been debated since bone marrow fat levels only indicate poor physical condition, and do not show whether an ungulate is in normal or good condition (Mech and Delguidice 1985, Ballard *et al*. 1987). Starvation is assumed to occur at a fat content in bone marrow ≤ 20% for adults and ≤ 10% for calves (Franzmann and Arneson 1976, Petersen *et al*. 1984), but has been documented to occur in adult moose at a marrow fat level of 52% (Ballard *et al*. 1987). Ungulates probably do not die of starvation until their bone marrow fat is almost depleted, but low fat content may cause loss of vitality that will decrease their capability of moving through snow and thereby escaping wolves (Mech *et al*. 1995).

Bone marrow mobilization occurs more quickly in proximal bones compared to distal bones (Peterson 1982). In this study, it was not possible to collect the same type of leg bone at all kill sites as carcasses were consumed differently. To minimize errors that results from using various types of leg bones, mandibles and leg bones that were corrected to mandible fat content (when a mandible was not found at a kill site) were used to evaluate differences in fat content between wolf-killed moose and moose harvested by hunters. However, fat mobilization in mandible and leg bones can vary for different age classes (Ballard *et al*. 1981). Therefore, estimates of correlations between mandible and various leg bones, and comparisons between wolf-killed moose and the reference material ought to be calculated separately for calves, yearlings and adults. In this study the sample size was too small to allow this.

Of the wolf-killed moose in the Grangärde territory during winters of 1999–2000 and 2000–2001, only one calf had a leg bone fat content ≤ 10%, but calves had overall less bone marrow fat content than adults. Peterson *et al*. (1984) explained a lower fat content among calves than adults in winter as a result of lower fat reserves among calves because of rapid growth requirements. The nutritional condition of wolf-killed moose, as reflected by mandible bone marrow fat content, was similar to that of moose harvested by hunters in autumn; the latter were assumed to represent the average condition of moose in the population. Therefore it was concluded that the wolves in the Grangärde pack did not select to prey on moose in poor nutritional condition, as earlier shown in North American wolf packs by Franzmann and Arneson (1976) and Gasaway *et al*. (1983).

Feeding behaviour of adult and subordinate wolves

Feeding ecology

Although wolves most commonly hunt together in packs, single wolves are known to kill large prey such as adult moose (Cowan 1947, Hayes *et al*. 1991, Thurber and Peterson 1993). The adult male in the Grangärde territory participated in all known killings of ungulates, alone or in company with one or two pups, until 25 March 2001 when the first ungulate killed by the radio-collared pups alone was found. Mech (1966) reported that even in large packs, it is the adult pair that starts the attacks. During a study in Alaska, adult males were involved in 92% of the fresh kills of calf moose or larger prey, and although yearlings hunt alone, they are almost always unsuccessful and scavenge, or kill

smaller prey (Ballard *et al*. 1997). The pups in the Grangärde pack fed on fresh kills while together with the adult male, and revisited or scavenged carcasses when alone. Consumption of ungulates killed by the adult male in company with pups was also significantly higher than of prey killed by the adult male alone.

Handling time
Several studies in North America have shown that handling time by wolves on adult moose decrease as pack size increase, as more wolves consume prey faster (Messier and Crête 1985, Ballard *et al*. 1987, Hayes 1991). In the Grangärde pack, there was no difference in handling time by the adult male between adult moose and calf moose, and handling time on all moose did not differ between years even though pack size increased two-fold. This is best explained by the fact that the kill rate also increased two-fold and the pack members did not feed on the same carcass simultaneously during the second year of the study.

When together with the radio-collared pups, the adult male almost always left kill sites earlier than pups, which often stayed until the carcasses were totally consumed. Thus, handling time at first feeding occasion was shorter for the adult male, but similar among the two radio-collared pups, as presented by studies in North America for packs of four wolves (Peterson *et al*. 1984, Ballard *et al*. 1987, Hayes *et al*. 2000). A longer handling time for the pups as compared to the adult male, was best explained by the pups incapability of killing large prey by themselves. However, handling time at revisits and scavenging did not differ significantly for the adult male and pups in the Grangärde pack. The adult male and the radio-collared pups revisited and scavenged carcasses on average every forth day. Revisits were more frequent by the wolves in the Grangärde pack than compared to a two-year study in Alberta where pack members revisited previous kill sites on only four occasions per year (Fuller and Keith 1980). Scavenging by wolves is shown in other studies (Kolenosky 1972, Bjorge and Gunson 1989, Hayes 1991, Huggard 1993, Mech *et al*. 1998), but revisits at old kill sites may not be as common as compared to the Grangärde territory because the majority of wolf-killed prey in North America is totally consumed at first feeding occasion (Fritts and Mech 1981, Messier and Crete 1985, Mech 1995).

Pack cohesion

The Grangärde territory decreased slightly in size during the winter of 2000–2001 and boundaries changed as compared to the previous winter. Ballard *et al*. (1987) explained shifts in territory boundaries in increasing wolf populations as a result of adjustments to other packs, changes in pack members, or changes in prey density. The loss of the adult female was probably the reason why the adult male in the Grangärde pack changed territory size. According to snow- and radio-tracking, the adult male and the pups in the Grangärde pack were solitary most of the time during winter of 2000–2001, while the adult pair was in company in 87% of locations during the previous winter. In North America adult pairs and their pups are together in 80–100% of the locations during winter (Peterson *et al*. 1984, Ballard *et al*. 1987). Vila *et al*. (1995) measured activity on females with pups in Spain, and found that the female and her young abandoned rendezvous sites

and started to move with other pack members in November and continued doing so until May. Ballard *et al*. (1997) found pack members to be divided into subgroups for hunting. This was not the case in the Grangärde pack, as the radio-collared pups did not kill ungulates alone, until the end of March 2001. The solitary behaviour in the Grangärde pack during winter of 2000–2001 may have been a consequence of the loss of the adult female in the previous autumn.

The spatial separation of pack members did not seem to have a direct effect on pup survival, because pups in the Grangärde pack, when not in company with the adult male, managed by revisits and scavenging. Messier and Crête (1985) found that some wolf packs compensate lower kill rates by scavenging. Removal of an adult female during winter, while considering future control of the Swedish wolf population, will probably not have a detrimental effect of pup survival. Consequences of a removal of an adult male or the breeding pair in a pack, need to be further investigated since the adult male probably is responsible for the major part of the killing of prey (Ballard *et al*. 1997).

Conclusions

1. Kill rate doubled when pack size doubled, but kill rate in terms of number of days between kills per wolf remained the same.
2. Increased hunting experience by the male the second year of the study in combination with naïve prey and high moose density may have contributed to the high kill rate on ungulates.
3. The low consumption by wolves at first feeding occasion during both winters was probably a consequence of prey being easy to kill.
4. Nutritional condition of wolf-killed moose did not differ from the average condition of moose in the population.
5. Moose being more difficult to kill by wolves if not taken within a shorter distance, as compared to roe deer, may explain why successful chasing distances on roe deer were longer than on moose.
6. The pups' incapability of killing ungulates by themselves until the end of their first winter resulted in a longer handling time at first feeding occasion by the pups as compared to the adult male.
7. Scavenging and revisits at previously wolf-killed ungulates were important food sources for the wolves.
8. The increased spatial separation between pack members the winter after the recruitment of pups, as compared to the adult pair, was probably a result of the loss of the adult female during autumn.
9. The loss of the adult female during autumn after the breeding did not seem to have a direct detrimental effect on pup survival in this pack.

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Appendix 1. Found ungulate carcasses that were utilized by wolves in the Grangärde territory during winter of 2000–2001.

ID no.	Species	Found by[a]	Cause of death[b]	Age	Sex	Date of death	No. of wolves present at the killing	Proportion consumed at first feeding (%)	Handling time (days)	
									9804	0101 0102
1	moose	C	3	0	–	–	–	–	–	–
2	moose	A	1	0	F	12/18/00	2–4	25	0.46	–
3	moose	A	1	0	–	12/27/00	2–4	95	2.55	–
4	moose	B	1	0	M	01/02/01	1	10	0.60	–
5	moose	B	3	–	–	–	–	–	–	–
6	moose	A	1	0	M	01/07/01	3	75	–	–
7	moose	B	3	0	–	–	–	–	–	–
8	moose	C	2	0	–	–	–	–	–	–
9	moose	C	3	0	–	–	–	–	–	–
10	moose	A	1	0	M	01/13/01	2–3	25	0.98	–
11	moose	A	1	1	–	01/16/01	–	95	1.02	–
12	moose	A	1	16	F	01/23/01	3–4	70	0.85	–
13	roe deer	A	1	4	M	01/24/01	3	25	0.20	–
14	moose	B	3	–	–	–	–	–	–	–
15	moose	B	3	–	–	–	–	–	–	–
16	moose	B	3	–	–	–	–	–	–	–
17	moose	B	1	16	F	01/29/01	2–4	25	2.64	–
18	moose	A	1	12	F	02/01/01	3–4	60	3.78	–
19	moose	A	1	0	–	02/06/01	–	95	–	–
20	moose	B	1	0	F	02/08/01	1	10	0.48	–
21	moose	B	1	0	M	02/12/01	1	15	1.18	–
22	moose	C	1	0	F	02/15/01	–	55	0.40	–
23	moose	B	3	–	–	–	–	–	–	–
24	moose	A	3	3	M	–	–	–	–	–
25	moose	A	1	0	–	02/24/01	2–3	100	0.99	4.97
26	moose	C	1	1	F	02/27/01	2	10	0.50	0.50
27	moose	A	1	0	–	02/28/01	2	95	0.50	6.55
28	roe deer	A	1	1	–	03/03/01	3	100	1.50	1.50
29	moose	A	1	1	M	03/06/01	2–3	10	0.98	0.98
30	moose	A	1	0	–	03/07/01	2	85	–	–
31	moose	A	3	0	–	–	–	–	–	–
32	moose	C	2	–	–	–	–	–	–	–
33	moose	C	1	1	M	03/11/01	2	15	1.41	1.41
34	moose	A	1	0	–	03/14/01	2	100	1.02	6.00
35	roe deer	B	1	2	F	03/15/01	1	90	–	–
36	roe deer	A	1	–	–	03/20/01	–	100	–	–
37	roe deer	A	1	–	–	03/20/01	1	100	–	–
38	roe deer	C	1	5	M	03/22/01	1	45	–	–
39	moose	B	1	0	M	03/24/01	1	5	0.34	–
40	roe deer	B	3	–	–	–	–	–	–	–
41	moose	B	2	17	F	–	–	–	–	–
42	roe deer	B	1	–	–	03/25/01	2	100	–	1.18
43	roe deer	A	1	–	–	03/29/01	–	100	–	–

[a]A) Radio-tracking
B) Snow-tracking
C) Due to information from local people

[b]1) Wolf-killed prey
2) Possibly wolf-killed prey
3) Other carcasses

Appendix 2. Bone marrow fat content of wolf-killed moose found in the Grangärde territory in winters of 1999–2000 and 2000–2001, in reference material from Grimsö Wildlife Research Area consisting of moose harvested by hunters in autumns of 1999–2000, and in one moose that died from natural causes in spring 2001.

ID	Age	Bone marrow fat content (%)						
no.		Femur	Tibia	Metatarsus	Humerus	Radius	Metacarpal	Mandible
2	0	–	–	–	–	25	–	53
3	0	–	–	–	–	–	39	49
4	0	–	35	–	–	–	–	55
6	0	–	–	–	–	69	–	65
10	0	–	–	45	–	–	–	52
11	1	–	61	–	–	–	–	47
12	16	–	–	–	–	85	80	72
17	16	–	–	–	–	86	–	75
18	12	–	85	–	–	–	87	77
19	0	–	50	–	–	–	–	58
20	0	44	47	–	–	–	–	51
21	0	22	24	–	–	–	–	–
22	0	–	22	–	–	–	–	–
25	0	–	–	–	–	27	–	48
26	1	–	89	–	–	–	–	72
27	0	–	–	–	–	–	–	50
29	1	–	82	–	–	–	–	65
30	0	–	–	–	–	24	–	50
33	1	–	72	–	–	–	–	59
34	0	–	10	–	17	–	–	–
39	0	–	–	–	–	–	23	52
1[a]	0	63	–	–	–	–	–	–
4[a]	0	30	–	–	–	–	–	71
6[a]	0	–	–	–	–	–	28	69
9[a]	0	38	–	–	–	–	–	61
12[a]	0	–	–	58	–	–	–	72
17[a]	0	–	–	–	63	–	–	59
19[a]	0	–	–	–	35	–	–	–
21[a]	0	–	–	–	–	–	48	67
23[a]	7	–	–	–	–	–	91	78
24[a]	0	28	–	–	–	–	–	64
25[a]	7	–	–	50	–	–	–	–
26[a]	0	–	–	–	45	–	–	–
51–99	0	–	–	–	45	56	–	56
49–99	0	50	56	74	49	68	49	55
01–00	0	36	40	35	36	41	38	58
50–99	0	39	34	40	37	39	34	52
51–99	0	41	54	21	–	–	94	55
44–99	0	41	53	–	40	53	45	61
46–99	0	–	–	40	–	–	43	62
03–00	0	60	74	49	61	69	45	64
48–00	0	56	56	49	56	60	47	52
49–00	0	34	43	42	36	39	58	51
43–99	1	62	74	69	64	72	–	66
45–99	1	76	85	84	78	77	85	69
46–00	1	84	89	85	86	87	89	66
48–99	2	65	62	69	65	60	66	67
47–00	11	89	89	86	90	90	90	82
[b]	12	6	7	7	–	–	–	7

[a]Wolf-killed moose during winter of 1999–2000 (Palm 2001).
[b]Assumed to have died from natural causes in spring 2001.


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