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Winter prey selection of moose (*Alces alces*) by Scandinavian wolves (*Canis lupus*)

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Abstract

In ten wolf territories, prey selection of moose by wolves was studied in south-central Scandinavia during winters of 1997/98 to 2002/03. A total of 392 calf and adult moose were classified as either wolf killed or probably wolf killed. Carcasses were found predominantly by using VHF and GPS-positioning of wolves in combination with snow tracking.

Calves were selected for in the majority of the ten territories, however, individual territories showed great variation in the proportion (39-93%) of wolf killed calves. Calf proportions in wolf kills were not correlated to the proportions in the standing moose population, indicating different hunting strategies among wolf packs. The higher average calf proportion in wolf kills of this study (72%) compared to a number of North American studies (13-56%) is argued to be related to poor anti-predation behavior by Scandinavian female moose, rendering physically subordinate calves more susceptible to wolf predation.

Proportionally more calves, less 2-10 years and more ≥ 11 years moose were wolf killed as compared to human harvest. When separating for sex, less 2-10 year-olds and more ≥ 11 years female moose were wolf killed, whereas among males differences were not consistently significant, but proportionally more calves and fewer 2-10 years were wolf killed. Differences between wolf killed females and males were most probably related to wolves selecting for old females. It is suggested that senescence in old females make them more susceptible to wolf predation.

Among adults (≥ 1 years), proportionally less adult males were wolf killed (24%) compared to human harvest (59%). This may be explained by intensive harvest of adult males. When comparing wolf killed adult male proportion to estimates of the standing moose population, a difference was found to moose observations (37%), however, no significant difference was found compared to corrected moose observations (33%) and aerial counts (34%).

Key words: Wolf, moose, winter prey selection, age, sex, poor condition, anti-predation behavior, Scandinavia.

Introduction

According to the optimal foraging theory, strategies that maximize the net rate of energy intake should be adopted, i.e., benefits in term of the food item's energy value should be maximised in relation to costs associated with the foraging activities (Chapman and Reiss, 1999; Townsend et al. 2000; Krebs, 2001). Townsend et al. (2000) argued that predators with long handling time relative to search time (e.g. lions) would profit the most if specialising on prey easiest to catch (immature, lame and old), especially regarding the energy-demanding pursuit. However, observations in nature do not perfectly fit the theoretical predictions due to a number of constraints, but findings have been made in support for the generality of the optimal foraging theory (Chapman and Reiss, 1999; Townsend et al. 2000). In a lower Pleistocene paleocommunity, terrestrial carnivores (such as saber-toothed felids, *Homotherium latidens* and *Megantereon whitei*, and wild dogs, *Canis falconeri*) selected for juveniles, females and individuals with reduced locomotor capabilities in large ungulate prey species (Palmqvist et al. 1996).

Characteristics of predated individuals of a specific prey species may vary spatially, temporally, or between predator species, implying that prey vulnerability need not always follow a standard model (Husseman et al. 2003). The level of snow depth can influence which categories (calves and/or adults) of elk that are wolf killed (Huggard, 1993b). Peterson et al. (1984) concluded that in a number of North American studies, the average proportion of wolf killed moose calves was often correlated with snow depth. In addition, prey abundance may influence prey selection (Kunkel et al. 2004; for moose, see Weaver, 1994).

Following the great geographical range of wolves, different wolf populations inhabit areas with a wide variety of prey species, with probably all potential prey species being wolf killed sometime (Mech and Boitani, 2003). However, only one or two of the prey species available in a specific area usually make up most of the wolf's diet (studies reviewed in Mech, 1970). Predators with the majority of their diet consisting of one or two prey species are considered to be specialist predators (Krebs, 2001). Weaver (1994) argued that in high ungulate diversity areas wolves might be "expanding specialists" that specialize on vulnerable individuals of large prey, but generalize on smaller prey. Bergerud and Elliot (1998) stated that moose, because of their great biomass, is the prey species most important in maintaining wolf numbers in most multiple-ungulate systems.

In prey that represents a great challenge to wolves, selection for young and old individuals is usually more evident, with prime-aged animals often being underrepresented (cf. Hayes et al. 2000). Many studies of wolves' winter predation have found a positive selection, represented by *young-of-the-year* (Elk: Husseman et al. 2003; Bison: Smith et al. 2000; Moose: Mech et al. 1995) and *old animals* (Elk: Husseman et al. 2003, Huggard, 1993a; Moose: Peterson et al. 1984, Mech et al. 1995). Studying winter predation, Kunkel et al. (1999) found wolves and cougars to kill more elk calves and ≥ 10 year olds compared to hunters. Similarly, Fuller and Keith (1980) showed calves and ≥ 11 years moose to be overrepresented in wolf kills compared to randomly captured adults and aerial surveyed calves, whereas 2-5 years were killed less often. Notably, wolf killed moose were collected from late August to May.

Mech et al. (1995) found that wolves selected male caribou, but found no significant selection for either sex in wolf killed adult moose. Fuller and Keith (1980) reported wolves to select for adult male moose compared to males in the winter population. However, a review of studies of wolf

predation in eastern Europe by Okarma (1995) concluded that male moose was killed less than expected compared to the sex proportion in the population.

This study focuses on the prey selection of moose by wolves during winter in south-central Scandinavia, where moose represent more than 95% of the consumed biomass (Sand et al. 2004). Moose is also the game species that attracts most hunters, about 250 000 hunt moose annually in Sweden (Swedish Association for Hunting and Wildlife Management) and about 58 000 in Norway (Statistics Norway). Game-hunting on ungulates yields considerable socio-economic incomes on the Scandinavian Peninsula and from an economical viewpoint, moose is the most important game species in Sweden (Swedish Association for Hunting and Wildlife Management) and Norway (Solberg et al. 2003). On the other hand, economic loss due to moose browsing is considerable for forestry. Considering only pine browsing in Sweden alone, income loss amounts to 30-80 million SEK annually, with future (in 30-50 years) annual quality losses being estimated to 500-1 300 million SEK (Glöde et al. 2004). Also, there are other goals like minimising the number of moose collisions on the roads (5 000-10 000 annual moose-vehicle collisions in Sweden; Swedish Road Administration). With a re-colonizing wolf population, conflicting interests are faced with a new challenge. This calls for a better knowledge about the ecology of wolves.

What wolves eat is central to the conflicts between humans and wolves (Mech and Boitani, 2003). In this study, age and sex of moose killed by wolves in ten wolf territories have been analyzed in relation to estimates of the standing population structure and human harvest. Patterns of prey selection across and within individual wolf territories are presented.

Hypotheses:

1. Moose calves are positively selected by wolves compared to their presence in the standing moose population and compared with human harvest (cf. Okarma, 1995).
2. Yearlings and old moose (≥ 11 years) are positively selected by wolves compared to human harvest. Conversely, middle-aged moose (2-10 years) are selected against by wolves (cf. Fuller and Keith, 1980).
3. Wolf killed adult male moose (≥ 1 years) are younger than females (e.g. Mech et al. 1995).
4. Wolves select against adult male moose (≥ 1 years) compared to their presence in the standing adult moose population and compared with human harvest (cf. Okarma, 1995).
5. Selection of vulnerable moose individuals is less evident in Scandinavia when compared to other areas, following that Scandinavian moose are generally more naïve to predators, particularly wolves (cf. Berger et al. 2001).

Study area

This study was conducted in the south-central part of the Scandinavian Peninsula (Figure 1) during the winters (October-April) of 1997/98 to 2002/03. The study area is dominated by boreal forest, covering approximately 60-90%. Tree composition is mainly represented by coniferous tree species such as Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) with minor contribution of lodgepole pine (*Pinus contorta*). Birch (*Betula pendula*, *B. pubescens*) is the most common deciduous tree. In addition, aspen (*Populus tremula*), alders (*Alnus glutinosa*, *A. incana*) and willows (*Salix* spp.) are present in the area. (Nilsson, 1990).

The topography is variable, including lowland bogs to higher terrain of the Scandinavian mountain range, with altitudes between 0-700 m (Fredén, 1994). The average precipitation of 400-1000 mm is evenly distributed throughout the year. Snow cover exists for roughly 90-180 days, with

maximum average annual snow depths being approximately 30-90 cm. Average daily minimum temperatures ranges between 0°C to -15°C in winter (lowest temperatures in January-February), depending largely on latitude. (SMHI, Swedish Meteorological and Hydrological Institute, 1961-1990). The road network is relatively dense, with on average 0.71 km (0.55-0.86 km) of road/km² (Wildlife Damage Centre, Sweden).

Available prey species are moose, roe deer (*Capreolus capreolus*), beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*) and badger (*Meles meles*). The winter density of moose in nine of the studied wolf territories (no data available for the Koppang territory), using faecal pellet group counts and aerial surveys, ranges between 0.48/km² (4.8/1000ha) and 2.64/km² (26.4/1000ha), with an average of 1.11/km² (11.1/1000ha). Carnivores like brown bear (*Ursus arctos*), lynx (*Lynx lynx*) and red fox (*Vulpes vulpes*) are present. Scavengers are mainly red foxes and ravens (*Corvus corax*), but many other species has also been reported, primarily different birds (cf. Wikenros, 2001).

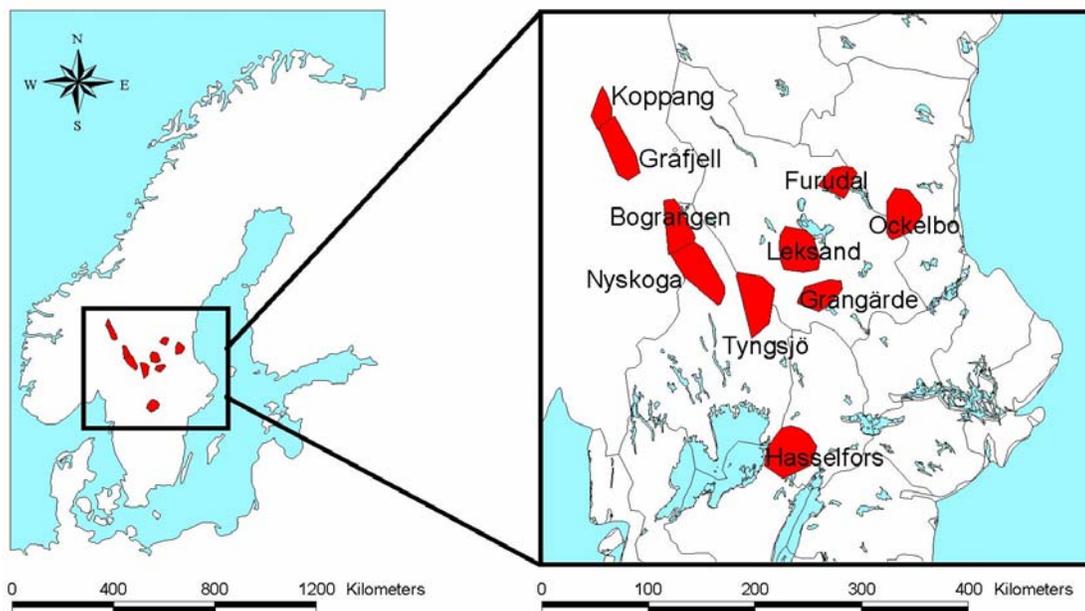


Figure 1. Study area on the Scandinavian Peninsula showing the ten territories studied (six in Sweden, two on the Swedish-Norwegian border and two in Norway). The centre of the study area is approximately at 67°N, 14°E.

Methods

Data collection

GPS-positioning, radio tracking, snow tracking of collared wolves along with observations of scavengers and/or information from local people were used in order to locate wolf killed moose. GPS-collars were programmed for 1-2 positions per hour, but receiving a GPS-fix sometimes failed (probably due to dense forest cover). GPS-positions were retrieved via remote downloading of data with a handheld receiver (RX-900), whereas positions from wolves with traditional radio collars were received through standard ground telemetry triangulation technique (Kenward, 1987). In the search for carcasses, priority was given to clusters of positions, as these were more likely to include a moose carcass. A cluster was defined as having at least two positions no more than 200 m apart.

Data concerning age, sex and cause of death were collected in the field. Age estimation was made in the field by looking at teeth development or skeletal attributes, separating between calves and adults (cf. Markgren, 1969). For adult moose, age determination was made in a laboratory by sectioning the first molar (M1) and counting annual cementum layers (Wolfe, 1969). Sex was determined in the field by looking for antlers or antler pedicels and sexual organs.

Moose carcasses were classified as wolf killed if at least one of the following three criteria was fulfilled;

- 1) Hunting tracks in the snow (cf. Hayes et al. 2000; Fuller and Keith, 1980); signs of chase and/or struggle related to wolf and moose tracks, preferably with moose blood and/or hair along the trail.
- 2) Fresh blood (cf. Hayes et al. 2000; Fuller and Keith, 1980), preferably column bleeding (massive, concentrated bleeding due to a ruptured large blood vessel). Wolves and bears are the only predators with potential to afflict such severe damage to moose in Scandinavia.
- 3) Bite marks; two penetrations surrounded by dark-reddish spots, indicating that the bite marks were done while the moose was alive. By measuring the distance between the centres of the two penetrations, the predator species may be identified. The distance between the centres of the two canines in the upper jaw of wolves is 40-55 mm, while bears have 30-70 mm (Landa, 1999).

With most bears hibernating throughout winter, carcasses found and classified with the aid of criterion 2 and criterion 3 most likely result from a wolf kill, especially if other signs of wolves can be established (tracks, scats, territory markings, radio tracked or GPS-positioned locations).

Carcasses classified as *probably* wolf killed had not fulfilled any of the three criteria mentioned above. A *probable* wolf kill included either wolf tracks, scats, territory markings, VHF or GPS-positioned locations that indicated wolf presence at the carcass. Signs of wolf activity at the site of the carcass also had to match with the estimated time of death.

Seven of the ten wolf territories examined have been subject to intensive studies (Appendix 1, Table I and II), meaning that collared wolves (always at least one alpha individual) have been radio tracked or followed by GPS-positioning in combination with snow tracking during intense periods. In the other three territories (extensive) (Appendix 1, Table I and II), moose carcass search was mainly done through snow tracking, with minor assistance from radio tracking or GPS-positioning. Consequently, these studies have relied more on the snow conditions, resulting in less continuity compared to the intensive studies.

Data on moose population estimates

Data on moose observations and harvest were collected from parishes representative of the ten wolf territories. A combination of the proportion of a parish that was located within the territory and the proportion of the territory covered by a parish were used as selection criteria. The proportion of a parish within a territory was used to weight moose observations and harvest data to the wolf territory in question. Also, a correction for harvest was made by simply taking the total number of moose observations minus the total number of harvested moose in order to get a better approximation on moose categories being available for predation by wolves in the following winter

(moose are observed and harvested mainly in autumn, overlapping little temporally with wolves' winter predation). The proportions of moose categories were assumed to be homogenous throughout the parish. For each territory, the three years best synchronised temporally with years subject to wolf studies were selected (combining several years dampen individual year's extreme values). As the Koppang territory was studied for six years, corresponding years were chosen.

In the five wolf territories subject to aerial surveys, areas of best overlap were chosen. Notably, harvested moose divided into age classes does not correspond to harvest data from parishes.

Statistical analyses

There was an inherent discrepancy in the data, concerning whether carcasses were collected in intensive or extensive study areas, with proportionally more calves found in intensive study areas ($P < 0.05$). Therefore, data from intensive studies were analyzed both separately and pooled with data from extensive studies, thereby accounting for any methodological confounding factors. Also, there was a tendency that the proportion of wolf killed calves was higher than those classified as *probably* wolf killed in all ten territories ($P = 0.09$). A difference in proportion of sex was also found between wolf killed and *probably* wolf killed adult (≥ 1 years) moose ($P < 0.01$), why only wolf killed moose were used in tests concerning proportion of sex. Also, only wolf killed moose in the seven intensive studies were considered in tests concerning age class distribution.

SPSS (2002) was used for logistic regressions and correlation tests (Hypotheses 1 and 4); chi-square tests have been analyzed with StatView (1992-98) (Hypotheses 2 and 5); while randomization tests used Excel (2002) with the PopTools extension (Hypothesis 3). Randomization tests were used to analyze differences between observed values in two groups in relation to observed values being randomly shuffled and rearranged into the two groups (1000 iterated randomizations). Randomization tests are especially suitable for data with an evident non-normal distribution where a considerable number of tied values are present (Manly, 1997). In all tests, the significance level 0.05 has been used.

Results

Age selection

In total, 392 moose carcasses were registered as either a calf or an adult and classified as either wolf killed or *probably* wolf killed, with 176 (45%) being both age and sex determined (Appendix 1, Table A-C). Henceforth, when considering tests of calves in relation to adults, wolf killed and *probably* wolf killed moose will be referred to as wolf kills. Number of wolf killed calves in relation to adults was higher in intensive studies (209:64 or 77% calves) compared to extensive studies (74:45 or 62% calves) ($\chi^2 = 8.5$, $df = 1$, $P < 0.01$).

The average proportion of calves (72%) in wolf killed moose is clearly higher than estimated proportions of calves in the winter population and in harvest (Figure 2a, Table 1, $P < 0.001$). Calves are about 6.4-8.1 times more likely to be wolf killed as compared to their occurrence in the winter population as estimated from moose observations, corrected moose observations and aerial counts, whereas calves are 4.3 times more likely to be wolf killed as compared to harvested.

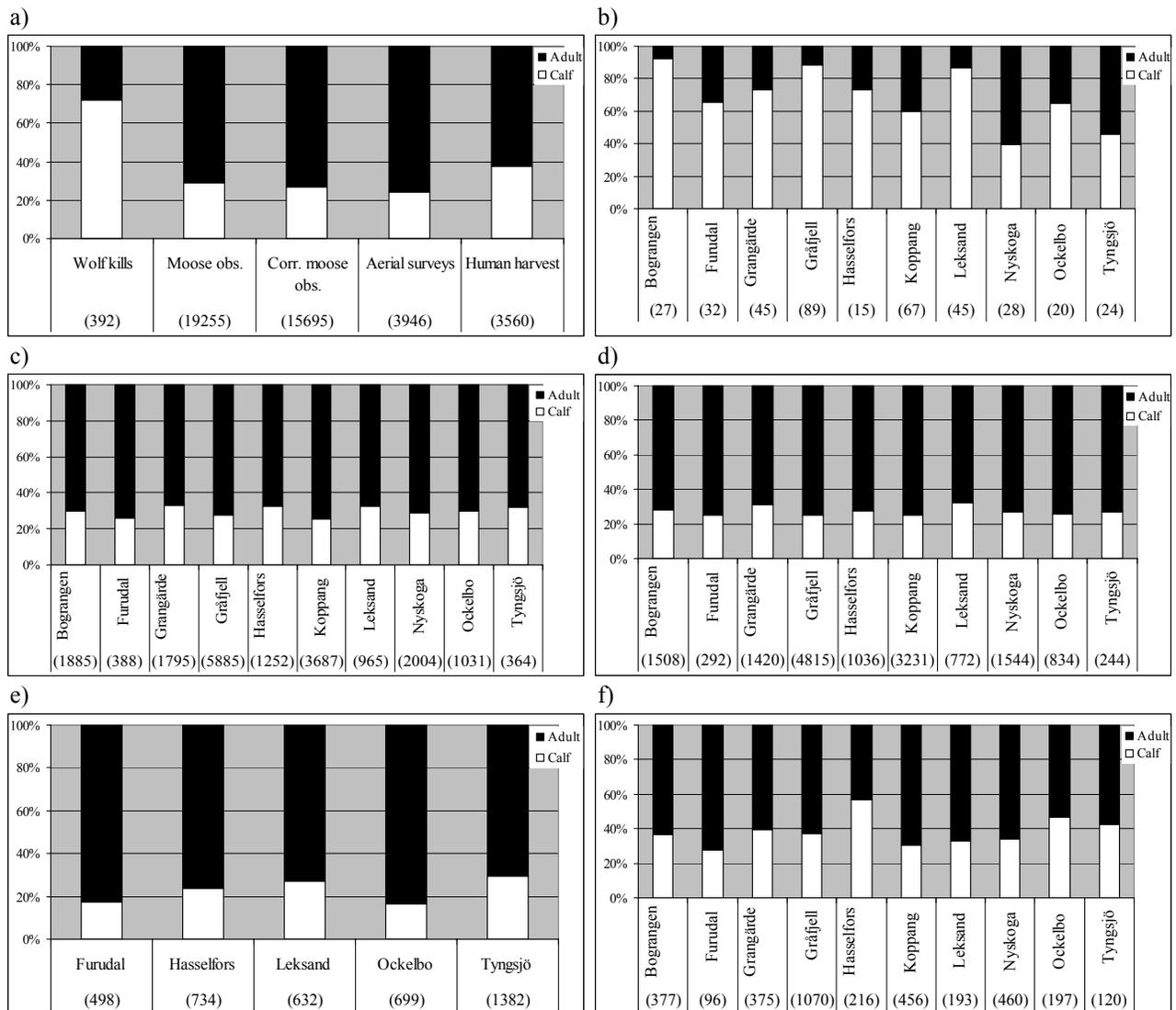


Figure 2. Average (a) and territory specific estimates of proportion of calves and adults in wolf kills (b), moose observations (c), corrected moose observations (d), aerial surveys (e), and human harvest (f). Number of moose are presented within paranthesis.

Although the average proportion of calves among wolf killed moose was higher than estimated proportion of calves in the population, wolf kills showed great variation (39-93%) in different territories (Figure 2b). As a consequence, calf selection was non-consistent in all wolf territories. Wolves selected for calves more than expected from their availability, as estimated from moose observations and corrected moose observations, in eight out of ten (80%) territories (Table 2). Calf proportions in wolf kills were also significantly higher in four out of five (80%) territories when compared to calf proportions from aerial surveys. In addition, wolves killed calves proportionally more than harvest in six out of ten (60%) territories.

Among wolf territories, Bograngen had a significantly higher proportion of wolf killed calves as compared to Furudal, Koppang, Nyskoga, Ockelbo and the Tyngsjö territory ($P < 0.05$) and a tendency to have a higher proportion of wolf killed calves as compared to the Grangårde territory (Table 3, cf. Figure 2b).

Table 1. Logistic regression testing proportion of calves and adults in wolf kills against population estimates and harvest. Sample size for each estimate is presented within parenthesis. Wolf killed moose (N = 392) has been used as reference category.

	B	S.E.	Wald	df	P-value	Exp(B)
TOTAL TEST			474	4	<0.001	
Moose observations (19255)	1.86	0.11	267	1	<0.001	6.4
Corr. moose observations (15695)	1.96	0.11	295	1	<0.001	7.1
Aerial surveys (3946)	2.10	0.12	312	1	<0.001	8.1
Human harvest (3560)	1.46	0.12	154	1	<0.001	4.3
Constant	0.52	0.03	429	1	<0.001	1.69

Table 2. Logistic regression testing proportion of calves and adults in wolf kills against population estimates and harvest, with each territory being tested individually. The P-value for each pair-wise comparison is in bold if significant, with sample size presented within parenthesis. Wolf killed moose was used as reference category.

Territory	Moose observations		Corr. moose observations		Aerial surveys		Human harvest	
Bogringen (27)	<0.001	(1885)	<0.001	(1508)	-		<0.001	(377)
Furudal (32)	<0.001	(388)	<0.001	(292)	<0.001	(498)	<0.001	(96)
Grangärde (45)	<0.001	(1795)	<0.001	(1420)	-		<0.001	(375)
Gråfjell (89)	<0.001	(5885)	<0.001	(4815)	-		<0.001	(1070)
Hasselfors (15)	0.003	(1252)	<0.001	(1036)	<0.001	(734)	0.22	(216)
Koppang (67)	<0.001	(3687)	<0.001	(3231)	-		<0.001	(456)
Leksand (45)	<0.001	(965)	<0.001	(772)	<0.001	(632)	<0.001	(193)
Nyskoga (28)	0.23	(2004)	0.16	(1544)	-		0.58	(460)
Ockelbo (20)	0.002	(1031)	<0.001	(834)	<0.001	(699)	0.13	(197)
Tyngsjö (24)	0.18	(364)	0.06	(244)	0.09	(1382)	0.76	(120)

- No data available

Table 3. Logistic regression testing proportion of wolf killed calves and adults between wolf territories using the Bogringen (N = 27) territory as reference category for pairwise comparisons. Number of moose is presented within parenthesis.

	B	S.E.	Wald	df	P-value	Exp(B)
TOTAL TEST (392)			45	9	<0.001	
Furudal (32)	1.88	0.82	5.2	1	0.023	6.5
Grangärde (45)	1.51	0.81	3.5	1	0.061	4.5
Gråfjell (89)	0.46	0.81	0.3	1	0.570	1.6
Hasselfors (15)	1.51	0.94	2.6	1	0.107	4.5
Koppang (67)	2.13	0.78	7.6	1	0.006	8.4
Leksand (45)	0.65	0.86	0.6	1	0.445	1.9
Nyskoga (28)	2.96	0.83	12.7	1	<0.001	19.3
Ockelbo (20)	1.91	0.87	4.8	1	0.029	6.7
Tyngsjö (24)	2.69	0.84	10.2	1	0.001	14.8
Constant	-2.53	0.73	11.8	1	0.001	0.08

No significant correlation in calf proportion between wolf kills and the other four estimates was found (Table 4, cf. Figure Ia-d in Appendix 2). Also, no significant correlation was found between wolf killed calf proportion and number of wolves in different packs (Spearman's rho = -0.17, N = 13, P = 0.58, Figure II in Appendix 2).

Table 4. Spearman's rank correlation test comparing calf proportion between wolf kills and the other four estimates.

	Spearman's rho	N	P-value
Moose observations	0.25	10	0.48
Corr. moose observations	0.29	10	0.42
Aerial surveys	0	5	1
Human harvest	0.04	10	0.92

The proportion of calves in wolf killed moose of this study (72%) was significantly higher compared to two studies in North America; 36% in Mech et al. (1995) and 47% in Hayes et al. (2000) (Table 6).

Table 6. Logistic regression testing proportion of wolf killed calves and adults between this study and two North American studies. This study (N = 392) was used as reference category for pairwise comparisons.

	N	B	S.E.	Wald	df	P-value	Exp(B)
TOTAL TEST				56.9	2	<0.001	
Mech et al. (1995)	140	1.51	0.21	52.4	1	<0.001	4.5
Hayes et al. (2000)	49	1.08	0.31	12.2	1	<0.001	2.9
Constant		-0.09	0.12	0.6	1	<0.44	0.9

In areas with moose as primary prey, winter wolf packs (represented by at least two wolves) in Scandinavia and North America did not differ significantly in size (Table 7). For data on number of wolves in specific winters and territories of this study, see Table D in Appendix 3.

Table 7. Randomization test analyzing differences in winter wolf pack sizes (North American data were presented in Mech and Boitani, 2003).

		Mean	STD	N	P-value
Winter wolf pack sizes	North America	6.92	2.35	13	0.53
	Scandinavia	6.27	3.06	15	

Wolf killed moose in age classes

Among the four age classes of moose used in this study, calves represented the highest proportion in both wolf kills and human harvest (Figure 3a). Except for the Tyngsjö territory, the 2-10 years age class had the lowest proportion in wolf kills, whereas this age category was the second largest in harvested moose. In harvest, the proportion of yearlings and 2-10 years moose was at least twice that of wolf killed moose, while harvested ≥ 11 years moose were less than half the proportion of wolf killed moose.

When considering age class distribution for each sex, calves represented the highest proportion for both wolf killed and harvested males and females (Figure 3b). For wolf killed females, ≥ 11 year-olds was the second largest age group whereas yearlings were the second largest among wolf killed males. In fact, the high proportion of wolf killed ≥ 11 year-olds was represented by females only, with no males ≥ 11 years being wolf killed. In contrast, 2-10 year-olds was the second most abundant age group among harvested moose.

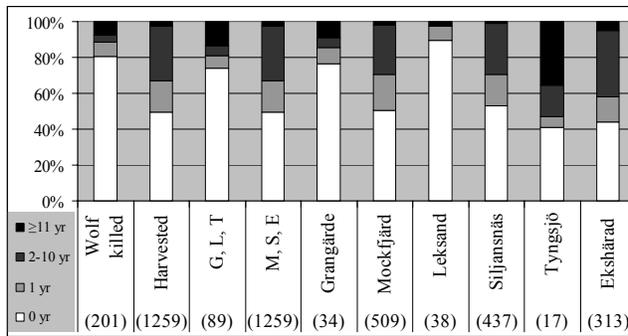


Figure 3a. Wolf killed and harvested moose grouped into four age classes. Wolf killed moose is represented by the seven territories subject to intensive study, while harvested moose is represented by three harvest areas (M, S, E). G, L, T corresponds to three wolf territories (Grangärde, Leksand, Tyngsjö) where intensive studies were carried out and M, S, E to their respective harvest areas (Mockfjärd, Siljansnäs, Ekshärad). Individual comparisons were made between Grangärde-Mockfjärd, Leksand-Siljansnäs and Tyngsjö-Ekshärad. Number of moose are presented within parenthesis.

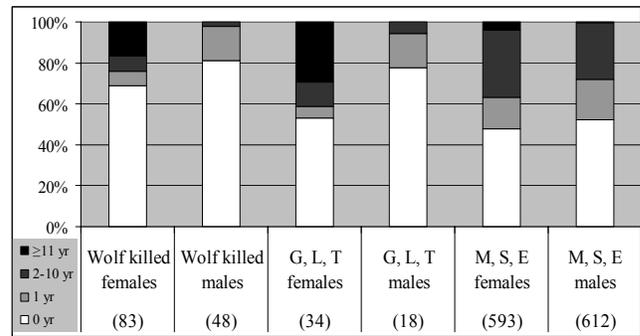


Figure 3b. Wolf killed and harvested moose grouped into four age classes for each sex. Wolf killed moose is represented by the seven territories subject to intensive study. G, L, T corresponds to three wolf territories (Grangärde, Leksand, Tyngsjö) where intensive studies were carried out and M, S, E to their respective harvest areas (Mockfjärd, Siljansnäs, Ekshärad). Number of moose are presented within parenthesis.

Except for males in the three wolf territories and their corresponding harvest areas, significant differences were found in age class distribution between wolf killed and harvested moose (Table 8). Differences were most likely attributed to the low proportion of wolf killed 2-10 year-olds, the higher proportion of wolf killed ≥ 11 year-old females and the generally higher proportion of calves in wolf kills (Figure 3a and 3b). The difference between wolf killed females and males was mostly due to the high proportion of old (≥ 11 years) female moose (cf. Figure 3b).

Table 8. Chi-square tests analysing differences in age class distribution (0, 1, 2-10, ≥ 11 years) between wolf killed and harvested moose at different levels of scales. Also, differences between wolf killed and harvested moose in age class distribution for each sex are presented, as well as differences between sexes among wolf killed moose. Df = 3.

Age class test ^a	χ^2 -value	P-value	Age class + sex test ^a	χ^2 -value	P-value
Wolf kills in 7 territories (N=201)			Wolf killed females in 7 territories (N=83)		
vs.	103.7	<0.0001	vs.	46.9	<0.0001
Moose harvest areas M,S,E (N=1259)			Females in moose harvest areas M,S,E (N=593)		
Wolf kills in study areas G,L,T (N=89)			Wolf killed males in 7 territories (N=48)		
vs.	59.2	<0.0001	vs.	18.7	0.0003
Moose harvest areas M,S,E (N=1259)			Males in moose harvest areas M,S,E (N=612)		
Wolf kills in study area G (N=34)			Wolf killed females in study areas G,L,T (N=34)		
vs.	19.2	0.0003	vs.	44.7	<0.0001
Moose harvest area M (N=509)			Females in moose harvest areas M,S,E (N=593)		
Wolf kills in study area L (N=38)			Wolf killed males in study areas G,L,T (N=18)		
vs.	21.8	<0.0001	vs.	5.5	0.14
Moose harvest area S (N=437)			Males in moose harvest areas M,S,E (N=612)		
Wolf kills in study area T (N=17)			Wolf killed females in 7 territories (N=83)		
vs.	31.9	<0.0001	vs.	12.8	0.005
Moose harvest area E (N=313)			Wolf killed males in 7 territories (N=48)		
			Wolf killed females in study areas G,L,T (N=34)		
			vs.	8.4	0.04
			Wolf killed males in study areas G,L,T (N=18)		

^a Wolf kills in the seven territories are represented by all study areas subject to intensive studies.

Wolf kills in study areas G,L,T are represented by the Grangärde, Leksand and Tyngsjö territories, respectively.

Their corresponding moose harvest areas M,S,E are represented by Mockfjärd, Siljansnäs and Ekshärad, respectively.

When conducting an age test in wolf killed adult moose (≥ 1 years) without separating for age classes, male moose was younger than females (Table 9, $P = 0.002$). With wolf killed females being older than harvested females ($P < 0.001$), and with no difference in age of wolf killed males and harvested males ($P = 0.22$), wolf killed females being older than wolf killed males is probably related to wolves' selection for old female moose.

Table 9. Randomization tests analyzing age of adult (≥ 1 years) moose being wolf killed or harvested.

		Mean age	STD	N	P-value
Age of adult moose (≥ 1 years)	Wolf killed females	9.9	6.1	26	0.002
	Wolf killed males	1.6	1.7	9	
	Wolf killed females	9.9	6.1	26	<0.001
	Harvested females	3.9	3.6	309	
	Wolf killed males	1.6	1.7	9	0.22
	Harvested males	2.3	1.7	293	
	Harvested females	3.9	3.6	309	<0.001
	Harvested males	2.3	1.7	293	

Comparison with other studies

No difference was found between wolf killed and harvested moose in another Scandinavian study (Olson et al. 1997) (Chi-square test, $\chi^2 = 1.2$, $df = 3$, $P = 0.75$, cf. Figure 4a). However, wolf kills in Olson et al. (1997) differed from wolf kills in this study (Chi-square test, $\chi^2 = 30.8$, $df = 3$, $P < 0.001$). Wolves of this study killed a relatively higher proportion of calves and a lower proportion of 2-10 year-old moose compared to the findings by Olsson et al. (1997) (Figure 4a).

I also compared the proportion of moose from the three oldest age classes in this study (1, 2-10, ≥ 11 years) with data from several studies in North America and Olson et al.'s study (1997). Original data (*Isle Royale*, *Other studies*, *Kenai Peninsula*: Peterson et al. 1984; *Yukon*: Hayes et al. 2000) have been recalculated to facilitate comparison with this study. Data showed that wolves from this study killed the highest proportion of yearlings and the lowest proportion of 2-10 year-old moose (Figure 4b), which explained the significant differences to the *Isle Royale* study and to a number of different studies conducted in North America (*Other studies*). However, compared to the *Kenai Peninsula* study in Alaska, more yearlings and fewer ≥ 11 year-olds were wolf killed in this study, whereas fewer 2-10 years and more ≥ 11 years were killed compared to the study by Olson et al. (1997). Notably, no significant difference could be found between this study and the *Yukon* study in Canada. (Table 10).

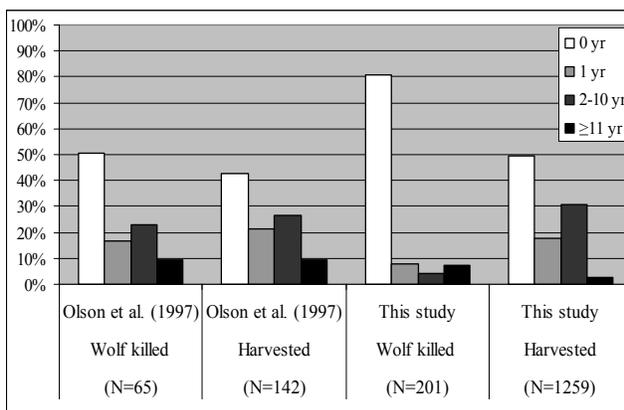


Figure 4a. Age class distribution of wolf killed and harvested moose in two studies in Scandinavia.

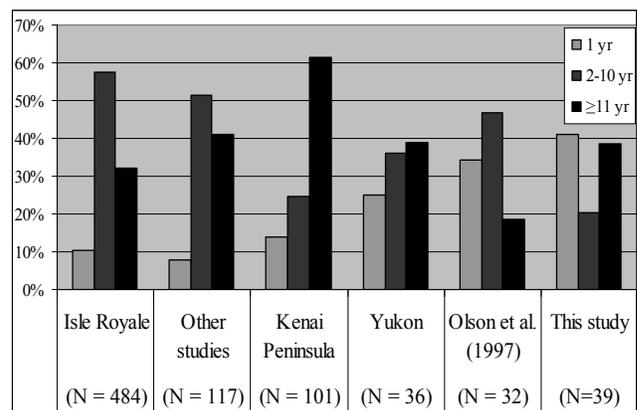


Figure 4b. International comparison of age class distribution in adult wolf killed moose.

Table 10. Age class distribution of wolf killed adult moose (1, 2-10, ≥ 11 years) in this study compared to three North American studies (*Isle Royale*, *Kenai Peninsula* and *Yukon*), a combination of several North American studies (*Other studies*) and one Scandinavian study (*Olson et al. 1997*).

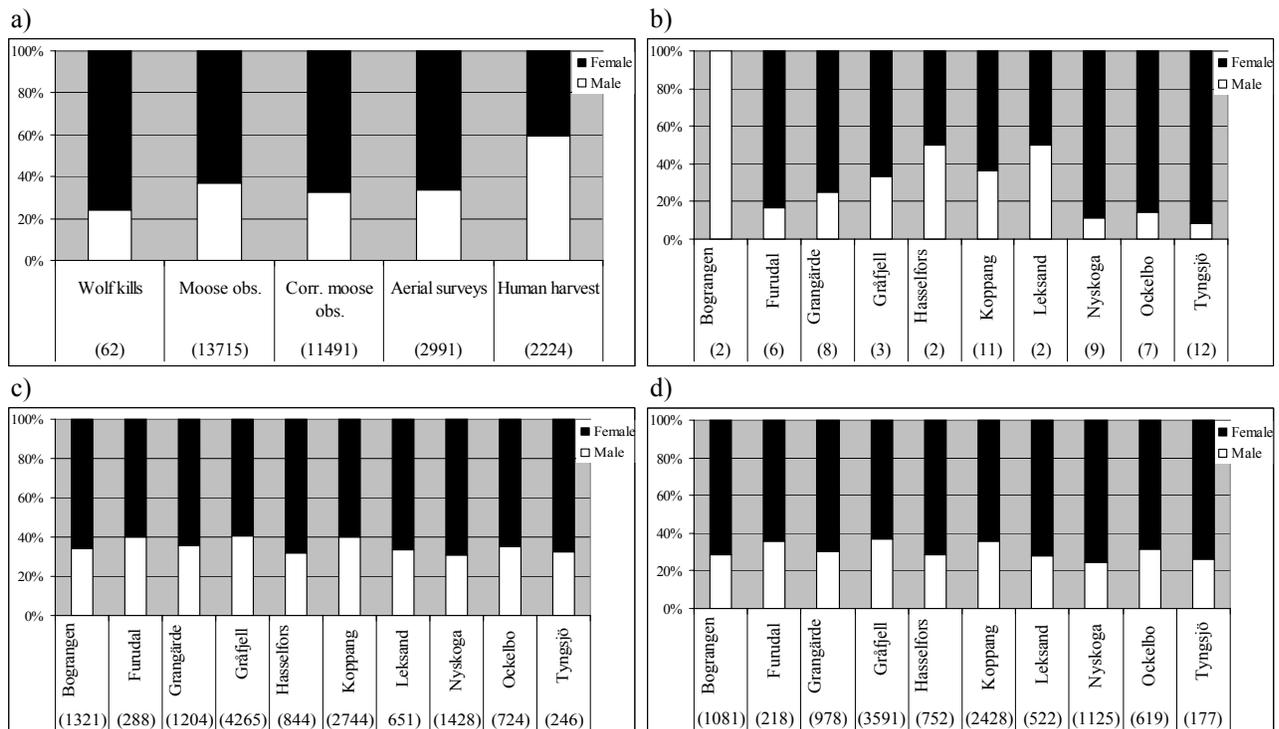
	χ^2 -value	df	P-value
Isle Royale ^a (N=484)	36.4	2	<0.0001
Other studies ^a (N=117)	26.7	2	<0.0001
Kenai Peninsula ^a (N=101)	12.6	2	0.002
Yukon ^b (N=36)	3.1	2	0.22
Olson et al. (1997) (N=32)	6.3	2	0.04

^aOriginal data presented in Peterson et al. (1984)

^bOriginal data presented in Hayes et al. (2000)

Selection of sex

The average proportion of adult male moose (≥ 1 years) in wolf kills (24%) was lower than other estimates of the standing moose population and harvest (Figure 5a). However, although significant differences were found in the total test, only moose observations and human harvest differed significantly from the wolf kills within the pairwise comparisons (Table 11). In addition, the adult male proportion was higher in human harvest as compared to the three estimates of male proportion in the standing moose population (Table 12, $P < 0.001$, cf. Figure 5a), indicating an intensive harvest pressure on adult male moose.



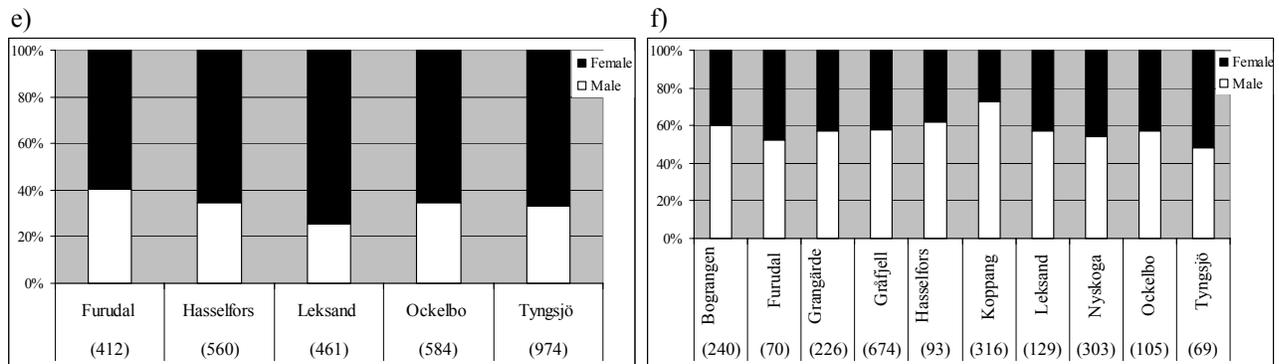


Figure 5. Average (a) and territory specific estimates of adult (≥ 1 years) moose sex proportion in wolf kills (b), moose observations (c), corrected moose observations (d), aerial surveys (e), and human harvest (f). Number of moose are presented within paranthesis.

Table 11. Logistic regression testing differences between estimates in respect to adult moose sex proportion in all territories. Number of moose for each estimate is presented within parenthesis. Wolf killed moose ($N = 62$) has been used as reference category.

	B	S.E.	Wald	df	P-value	Exp(B)
TOTAL TEST			554	4	<0.001	
Moose observations (13715)	0.61	0.30	4.3	1	0.039	1.85
Corrected moose obs. (11491)	0.42	0.30	2.0	1	0.155	1.53
Aerial surveys (2991)	0.46	0.30	2.3	1	0.126	1.58
Human harvest (2224)	1.52	0.30	25.8	1	<0.001	4.58
Constant	-0.54	0.06	79.0	1	<0.001	0.58

Table 12. Logistic regression testing number of adult males in relation to female moose (≥ 1 years). Number of moose for each estimate is presented within parenthesis. Harvested moose ($N = 2224$) has been used as reference category.

	B	S.E.	Wald	df	P-value	Exp(B)
TOTAL TEST			554	4	<0.001	
Wolf kills (62)	-1.52	0.30	26	1	<0.001	0.22
Moose observations (13715)	-0.91	0.05	380	1	<0.001	0.40
Corrected moose obs. (11491)	-1.10	0.05	535	1	<0.001	0.33
Aerial surveys (2991)	-1.06	0.06	336	1	<0.001	0.35
Constant	-0.54	0.06	79	1	<0.001	0.58

Discussion

Age selection

Selection for moose calves by wolves in winter has been reported in many studies (e.g. Peterson et al. 1984; Mech et al. 1995; review in Okarma, 1995). In this study, the proportion of wolf killed calves pooled over all territories was significantly higher than estimates of calf proportion in the standing moose population and harvest. However, at the level of individual wolf territories, eight out of ten territories showed a higher wolf killed calf proportion when compared to the local moose population. The large variation in proportion of wolf killed calves among territories (39-93%) was not attributed to a corresponding variation of calf proportion in the local moose population,

represented by moose observations (26-33%), corrected moose observations (25-32%) and aerial surveys (16-30%). Thus, my results imply that Scandinavian wolves select moose calves irrespective of the availability in the moose population, which suggest different hunting strategies among packs. In Scandinavia, Sand et al. (in press) found a positive correlation between hunting success on moose and the age (and suggestively experience) of alpha males. Also, alpha females increased hunting success with age, but only up to a point, with relatively old females showing a lowered hunting success. This indicates that wolves generally become more efficient hunters through their lifetime and that differences among packs in this study may depend on age/experience of individual wolves. It is argued that individual wolves more skilled in separating vulnerable prey individuals would most certainly have an evolutionary advantage due to less likelihood of hunting related injury, especially when hunting large and potentially lethal prey like moose (cf. Temple, 1987; cf. Wirsing et al. 2002). Adult moose have a good chance in succeeding with fighting off predators. In 92 direct confrontations with grizzly bears and wolves, adult moose survived 88-92% of the time (White et al. 2001). Calves, however, are physically subordinate to adults and much less likely to survive a wolf attack, especially without adequate maternal protection (Mech, 1970; Haber, 1977; Peterson et al. 1984). Therefore, wolves may find calves an optimal forage item with regard to available biomass per kill and the risk of hunting related injury (cf. Persson and Sand, 1998).

Alternatively, calves could be more easily killed due to poor condition. With moose calves growing rapidly in summer, Peterson et al. (1984) argued that less energy was left for building fat reserves, thus explaining why wolf killed moose calves showed bone marrow fat depletion in December, while adults exhibited depletion of fat reserves after February. In addition, Mech et al. (1995) found lower fat content in moose calves than in adults. Wikenros (2001) found wolf killed moose calves to generally exhibit a lower marrow fat content than wolf killed adults in a territory included in this study (Grangårde), however, the difference was non-significant. In the same study, no selection for moose calves or adults low in mandible fat content was concluded when comparing wolf kills with harvest. In addition, Olson et al. (1997) found no indication of either wolf killed or harvested moose being in poor condition (represented by disease or malformation) in a territory located in south-central Scandinavia.

Noteworthy, the cause of death of two calves found in the Hasselfors territory in late winter could not be determined. One calf looked malnourished and exhibited signs of jawbone necrosis. In Scandinavia, Cederlund et al. (1991) found snow depth to be significantly associated with loss of body mass in harvested moose calves. Also, small calves lost a larger proportion and more kilograms of their body mass than large calves. However, the high harvest pressure in Scandinavia results in a generally good food situation for moose, with malnourished moose being relatively uncommon (Sand et al. 2004).

The higher average proportion of wolf killed calves in Scandinavia (72%) as compared to a number of North American studies (13-56%) (Peterson et al. 1984) is striking and I argue that this may be explained by different anti-predation behavior in Scandinavian compared to North American female moose. In a North American study, Haber (1977) found females to usually stay right behind their offspring, attempting to avoid being separated from the calves. Similar observations were made on Isle Royale (Michigan, USA), with female moose nearly always having the calf in front while escaping something, with no more than 1-2 body lengths separating them (Vucetich, pers. comm.). Wolves and moose have coexisted for more than 50 years on Isle Royale and the isolated and confined nature of the island calls for a strong interaction between predator and prey. In addition, moose is the only large prey available to Isle Royale wolves (Mech and Boitani, 2003), probably resulting in most moose, if not all, encountering wolves quite frequently (for female-calf pairs, see

Mech et al. 1998). The Scandinavian situation is quite different; only a small wolf population was present in the northern part of Scandinavia by the mid 1960's, with no more than ten animals in Sweden (Haglund, 1968). Until the early 1990's, the Scandinavian wolf population never exceeded ten animals (Wabakken et al. 2001). Consequently, virtually all Scandinavian moose should be relatively inexperienced with wolves. Notably, in 135 occasions of marking newborn moose calves on the wildlife research area of Grimsö in Sweden, no evident protective behavior from the female could be discerned (Grängstedt, pers. comm.). Stephens and Peterson (1984) concluded that co-evolution of wolves and moose has resulted in subtle patterns of habitat selection which confer a survival advantage that seems especially clear for moose calves, the age group most vulnerable to wolves. This aspect of the anti-predation behavior could also explain why fewer North American calves succumb to wolf predation, considering that areas subject to wolf predation studies in North America probably involves moose that have lived more or less constantly with wolves throughout a longer time period.

Knowing how Scandinavian females act when encountering wolves is essential for understanding the prey selection by wolves. The use of domestic dogs when hunting moose is extensive on the Scandinavian Peninsula. Most of these dogs have a wolf-like appearance and are trained to put the moose at bay. How this influences the anti-predation behavior in moose is an issue that needs further investigation. However, with approximately 20-30% of harvested moose being shot when put at bay by the hunting dog, flight rather than fight is probably beneficial in Scandinavian moose's anti-predatory behavior (Sand, pers. comm.). In large prey like moose, a greater chance of survival is evident for individuals facing the wolves as opposed to trying to escape (Mech, 1970). In 38 wolf-moose encounters, Peterson et al. (1984) observed wolves to chase every moose that ran, while moose that stood their ground or initially ran but stopped to fight off the pursuing wolves were left alone (cf. Fuller and Keith, 1980). In addition, while studying wolf-bison interactions, Smith et al. (2000) found that if the bison did not run, wolves quickly lost interest.

If defending calves less aggressively means that females are reducing their own mortality risk, trade-off between calf-protection and self-protection should be directed towards the latter in areas of high calf recruitment, as each calf is less important, especially to young females facing many more years of reproduction. Thus, the high wolf killed calf proportion might be related to a high calf recruitment in Scandinavian moose. (see Pianka, 1974 for discussion on the relationship between predator avoidance and prey's reproductive value). Alternatively, if twin calf proportion is high in Scandinavia, the difficulty of protecting two calves rather than one (cf. Mech et al. 1998) could partly explain the high wolf killed calf proportion in Scandinavia.

A selection for calves can not be attributed to an overestimation of calves due to sampling bias. More to the contrary, intermittent sampling of wolf locations is expected to result in finding the largest prey, as more food will occupy wolves longer (Mech et al. 1995). The fact that intensive study periods resulted in proportionally more wolf killed calves than those sampled during more extensive work in this study could be due to intermittent sampling being more evident in extensive studies (see Methods). Recovering carcasses in North America has been done during intensive periods. However, the North American search method differs from this study through relying heavily on flight observations and not ground search. Whether these two methods are equally good in discovering wolf killed calf and adult moose is unknown.

In this study, one cannot totally ignore the effect of chance in the quite small sample sizes that each territory represents (15-89 moose). The tendency for the calf proportion among wolf killed moose to

be higher than for probably wolf killed moose in this study indicates an underestimation of the true proportion of wolf killed calves. This also suggests scavenging events to erroneously have been classified into probable wolf kills, potentially having compromising effects, especially in territories with small sample sizes. Also, conducting multiple statistical tests (e.g. Table 2) increase the risk of both type 1 errors (to find differences when there are none) and type 2 errors (not detecting differences when they in fact exist) (1 in 20 tests are on average erroneous when using 0.05 as significance level).

Wolf killed moose in age classes

Similar to findings by Hayes et al. (2000), proportionally more calves, less middle-aged moose (2-10 years) and more old moose (≥ 11 years) were wolf killed compared to human harvest in this study. However, the Tyngsjö territory contrasts with a relatively low proportion of calves and exceptionally high proportion of ≥ 11 years moose being wolf killed. This variation was not attributed to corresponding differences in the local moose population (assuming that harvest is representative of the age structure in the local moose population). Except for Grangärde (100% and 70% in the two studied years; Perjons, pers. comm.), the degree of overlap between the wolf territory and the respective harvest area is not fully evaluated, thus, age distribution of the local moose population in the wolf territory might differ from that of the harvest area.

Proportionally less than half the 1 year-old and 2-10 year-old female moose were wolf killed compared to harvested females, whereas more than four times the proportion of ≥ 11 years females were wolf killed. In males, the 2-10 years age class was also underrepresented for in wolf kills compared to harvest whereas calves were overrepresented. With wolf killed male moose proportions being similar in the seven and the three territories, smaller wolf killed sample size ($N = 18$) is argued to explain the non-significant results found when comparing the three wolf territories with their respective harvest areas.

Young (calves and yearlings) wolf killed male moose make up 98% and 95% in the seven and the three territories of intensive studies, respectively. This, together with ≥ 11 years moose being represented by females only are argued to explain the difference between wolf killed females and males. Also, when performing a test without moose being sorted into age classes, adult wolf killed males (≥ 1 years) were significantly younger than females. In contrast, Hayes et al. (2000) found no difference in age between wolf killed female and male moose (≥ 2 years). With harvested male moose (≥ 1 years) being younger than harvested females in this study, results are likely to depend on inherent differences in the standing moose population. Also, with wolf killed females (≥ 1 years) being older than harvested females, and with no difference found between wolf killed and harvested males, the difference is likely related to wolves' selection for older females, whereas males is being wolf killed more in correspondence to male age structure in the standing moose population. However, using age classes highlight that male moose older than 1 year are not likely to be killed by wolves. This could be attributed to yearlings being less experienced and physically subordinate relative to older adults (White et al. 2001). Mech et al. (1995) argued that the explanation for wolf killed adult male moose being younger than females was related to males being subject to arthritis in earlier years than females, rendering males more susceptible to predation. With wolf killed adult males of this study being predominantly yearlings and with no debilitating factors found in Scandinavia (Olson et al. 1997), this argument is probably not true for this study.

The selection against middle-aged (2-10 years) moose in this study is probably due to most animals being in their prime and consequently a dangerous opponent to wolves (cf. Persson and Sand, 1998). It is suggested that wolves select for old (≥ 11 years) female moose due to senescence, i.e. older

moose is more susceptible to wolf predation because aging is taking its toll (cf. Ericsson and Wallin, 2001). The deterioration in general fitness in old animals is indicated by the noticeable decrease in fertility and fecundity in ≥ 11 years female moose in Scandinavia (Sand, 1996; Solberg et al. 2000). Alternatively, 2-10 years female moose might be relaxed from wolf predation due to offspring association, following that calves are most likely to be targeted by wolves. Conversely, ≥ 11 years female moose being less fertile should involve more instances of solitude, probably resulting in increased attention by wolves, especially with senescence playing a more significant role.

As relatively old male moose (≥ 11 years) were rare (only 0.3%) in harvested male moose, they are probably uncommon in nature as well. Thus, wolves probably seldom encounter them, which more or less preclude wolves from selecting old male moose. The low proportion of old males is attributed to the intensive adult male harvest. Therefore, selection patterns in this study are expected to differ from areas where moose are unharvested by man or where harvest of adult male moose is less intensive.

Comparison with other studies

Olson et al. (1997) found no difference in age class distribution (0-2, 3-11 and ≥ 12 years) between wolf kills and human harvest. Also, when applying Olson et al.'s (1997) data to the age class classification of this study (0, 1, 2-10 and ≥ 11 years), no difference between wolf kills and human harvest was found. With differences being found between wolf killed and harvested moose of this study, and given that harvested age class distribution was similar in the two studies, it is argued that wolves of this study exhibit a stronger selection, with proportionally more calves and less middle-aged moose (2-10 years) being wolf killed in this study. Even though Olson et al.'s (1997) study was conducted over several years, it was done in a single wolf territory, increasing potential risk of territory specific effects of prey selection. Also, 20% of the wolf kills were not made in winter.

Noteworthy, this study exhibited the highest proportion of wolf killed yearlings and the lowest proportion of 2-10 years moose when compared to a number of other studies. However, relating patterns of moose selection by wolves to the local context (e.g. age of local moose population) are essential if any relevant comparison between different wolf areas is to be made. For example, if Scandinavian moose generally are younger than North American moose, with proportionally more yearlings, this could be the sole explanation to wolf killed yearlings being the highest in this study. The results may also be confounded partly by debilitating factors in North American moose, for example, Mech et al. (1995) reported that more than a third of the wolf kills had mandibular necrosis, and a third or more exhibited arthritis in their lumbosacral or coxofemoral joints. Peterson et al. (1984) suggested a later physical degeneration (at least in females) to explain the delayed susceptibility to wolf predation in Kenai moose as compared to Isle Royale moose. If Kenai moose is an exception to the rule, middle-aged moose in North America might be more exposed to wolf predation due to an earlier physical degeneration compared to Scandinavian moose. Noteworthy, Peterson et al. (1984) classified old moose as being ≥ 13 years and middle-aged as 7-12 years.

Selection of sex

In Europe, a review by Okarma (1995) found wolves to select against adult male moose. This is supported in this study when comparing wolf killed sex proportion with proportion of harvested adult moose (≥ 1 years). However, this is most probably due to intensive harvest of adult males, aiming at having a skewed sex proportion in favour of adult females in the living population and hence a more productive moose population (Solberg et al. 2003). In a Swedish moose population, Ericsson (1999) concluded that the mortality rate during hunt was 3.4 times higher for adult male moose as compared to females. The higher adult male proportion in harvested moose as compared to

the three estimates of the standing moose population structure confirms an intensive male harvest in this study. In Peterson et al. (1984), three males and 69 females were wolf killed in the adult moose population; all of the males were yearlings. However, this skewed sex ratio was merely a reflection of the low proportion of males in the adult moose population (11%) due to the intensive male harvest. In Olson et al.'s (1997) study on the Scandinavian Peninsula, wolves killed significantly more female moose (76%) than hunters (53%), and among wolf-predated moose, no male was older than two years. This is in close agreement with this study, indicating a consistent selection pattern of adult male moose by Scandinavian wolves.

In this study, the proportion of wolf killed adult male moose was lower compared to moose observations, but not when compared to corrected moose observations or aerial surveys. Also, when the number of observed moose was adjusted to the number of wolf killed moose, no difference in proportion of sex in adult moose was found, indicating large sample size in moose observations to be responsible of a statistical difference that might be biologically irrelevant. In extant ungulates (ranging in size from dik dik antelopes to moose and rhinos), Berger and Gompper (1999) found differences between live and killed adult sex proportions neither being correlated to female or male body mass nor sexual dimorphism. However, males were generally killed proportionally more often compared to their abundance. This contrast with findings of this study when considering all ten territories, with wolf killed adult male sex proportion being lower (24%) than the estimates of live adult male moose proportion (33-37%).

The wolves of the Denali National Park (Alaska, USA) have been shown to scavenge considerably on adult male moose (Mech et al. 1995; Haber, 1977). If some scavenged carcasses were classified as being probably wolf killed, this might explain the difference in sex proportion between wolf killed and probably wolf killed adult male moose in this study. However, with a young and healthy male moose population in Scandinavia, few moose and even fewer males probably die of natural causes (Stubsjoen et al. 2000; Ericsson and Wallin, 2001). Instead, the intensive adult male harvest in this study should result in a higher, relative to females, incidence of hunting related injuries in male moose. Thus, predation and scavenging by wolves on adult male moose might in this case be increased due to harvest.

Effects of wolf predation on the Scandinavian moose population

Moose densities are generally higher in Scandinavia than in North America (cf. Solberg et al. 2003), resulting in predation effects probably being less severe in most cases in Scandinavia. Also, with wolves selecting for calves and less productive females (≥ 11 years) in this study, the high productive rate of Scandinavian moose (Solberg et al. 2003; Sand et al. 2004) should not decrease due to wolf predation, more to the contrary (see reasoning in Crawley, 1992). A selective harvest of low-reproductive females in a Swedish moose population resulted in a 2.5 times higher potential population growth rate compared to a random harvest of adult females (Ericsson, 1999). Keeping a high-density female-biased moose population should be the primary goal in wolf territories (Nilsen et al. 2005).

In Scandinavia, Palm (2001) estimated 4% to 15% of the winter moose population to be removed by wolves in three wolf packs (included in this study), with higher values being explained by relatively small territory size and high kill rate. Olson et al. (1997) concluded a pack of five wolves to annually kill less than 10% of a Scandinavian moose population. Even though every wolf-moose interaction should be treated case-by-case, this implies that Scandinavian wolves generally will not kill in excess of 15% of the moose population. However, with wolf predation being

significant and mainly additive, Nilsen et al. (2005) showed that a moose population in south-eastern Norway would decline if harvest was not reduced.

Future prospects

As the test for individual wolf territories of this study show, one can not expect calves to be selected to a significant degree in all territories. It is, however, quite likely that calves will be selected in most territories. Following varying winter conditions in time and space for moose in Fennoscandia (Cederlund et al. 1991) there will most definitely also be between-year and within-year variation in wolf predation patterns within and between territories. Also, hunting skills of individual wolves is likely to affect predation patterns. Anti-predation behavior has been shown to transpire within a single generation in moose (Berger et al. 2001). Therefore, the proportion of wolf killed calves in Scandinavia could decrease within a foreseeable future, due to female moose adopting a more effective anti-predation behavior. This might result in other vulnerable individuals like yearlings (cf. White et al. 2001) and old female moose being targeted by wolves.

Olson et al. (1997) and Palm (2001) argued that small-scale reductions in harvest quotas might be necessary to avoid decrease in moose density in the long-term. If future increase in wolf numbers results in higher wolf densities due to decreasing wolf territories (cf. Fritts and Mech, 1981), wolf predation is expected to affect harvest to a greater extent in the future (cf. Olson et al. 1997).

Conclusions

- 1.** Selection for calves was significant in eight out of ten territories when compared to calf proportion in the standing moose population. Calf proportions in wolf kills varied largely among territories (39-93%) and were not significantly correlated to the availability of calves in the local moose population. The general selection of calves by wolves is believed to be related primarily to calves being more susceptible to wolf predation due to physical limitations, with poor maternal protection by Scandinavian female moose exacerbating the chances of a calf to survive a wolf encounter.
- 2.** Wolves kill proportionally less middle-aged moose (2-10 years) of both sexes and more old (≥ 11 years) females than harvest. Senescence in old female moose probably explains the susceptibility to wolf predation in this age class.
- 3.** Among wolf killed adult (≥ 1 years) moose, males were significantly younger than females.
- 4.** Proportionally less adult males (≥ 1 years) were wolf killed (24%) compared to human harvest (59%), with intensive adult male harvest explaining most of this significant difference.
- 5.** The predicted less evident selection of moose in this study could not be confirmed. The relatively strong selection for calves (72%) when compared to North America (13-56%) is argued to be attributed to Scandinavian female moose having an inexperienced anti-predation behavior, which are most detrimental to the relatively defenceless calves. In addition, this study exhibited the highest proportion of yearlings and the lowest proportion of 2-10 years moose.

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References

- Berger, J. and Gompper, M.E. 1999. Sex ratios in extant ungulates: Products of contemporary predation or past life histories? *Journal of Mammalogy*, **80**(4): 1084-1113.
- Berger, J., Swenson, J.E. and Persson, I-L. 2001. Recolonizing carnivores and naïve prey: Conservation lessons from Pleistocene extinctions. *Science*, **291**: 1036-1039.
- Bergerud, A.T. and Elliot, J.P. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. *Canadian Journal of Zoology*, **76**: 1551-1569.
- Cederlund, G.N., Sand, H.K.G. and Pehrson, Å. 1991. Body mass dynamics of moose calves in relation to winter severity. *Journal of Wildlife Management*, **55**(4): 675-681.
- Chapman, J.L. and Reiss, M.J. 1999. *Ecology: principles and applications*, second edition. Cambridge University Press. 330 pp.

- Crawley, M.J. 1992. Natural enemies: the population biology of predators, parasites and diseases. Blackwell Scientific Publications, Oxford. p. 127.
- Ericsson, G. 1999. Demographic and life history consequences of harvest in a Swedish moose population. Doctoral thesis. Swedish University of Agricultural Sciences.
- Ericsson, G. and Wallin, K. 2001. Age-specific moose (*Alces alces*) mortality in a predator-free environment: evidence for senescence in females. *Ecoscience*, **8**(2): 157-163.
- Excel. 2002. Copyright © Microsoft Corporation 1985-2001.
- Fredén, C. 1994. Sveriges Nationalatlas – Berg och Jord. Bokförlaget Bra Böcker, Höganäs. 208 pp.
- Fritts, S.H. and Mech, L.D. 1981. Ecology of a wolf population in Minnesota. *Wildlife Monographs*, **80**: 1-79
- Fuller, T.K. and Keith, L.B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *Journal of Wildlife Management*, **44**(3): 583-602.
- Glöde, D., Bergström, R. and Pettersson, F. 2004. Intäktsförluster p.g.a. älgetning av tall i Sverige – Arbetsrapport från Skogforsk, nr. 570.
- Grängstedt, P., pers. comm. Field Technician, Grimsö Wildlife Research Station, S-730 91 Riddarhyttan, Sweden.
- Haber, G.C. Socio-dynamics of wolves and prey in a subarctic system. Doctoral thesis. University of British Columbia, Vancouver. 786 pp.
- Haglund, B. 1968. De stora rovdjurens vintervanor II. *Viltrevy* **5**: 213-361. Almqvist & Wiksell Boktryckeri AB, Uppsala
- Hayes, R.D., Baer, A.M., Wotschikowsky, U. and Harestad, A.S. 2000. Kill rate by wolves on moose in the Yukon. *Canadian Journal of Zoology*, **78**: 49-59.
- Huggard, D.J. 1993a. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition of elk. *Canadian Journal of Zoology*, **71**: 140-147.
- Huggard, D.J. 1993b. Effect of snow depth on predation and scavenging by gray wolves. *Journal of Wildlife Management*, **57**(2): 382-388.
- Hussemann, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R. and Quigley, H. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos*, **101**: 591-601.
- Kenward, R. 1987. *Wildlife radio tagging: equipment, field techniques and data analysis*. Academic Press, Inc., Orlando. 222 pp.
- Krebs, C.J. 2001. *Ecology: the experimental analysis of distribution and abundance*, Fifth edition. Benjamin Cummings, an imprint of Addison Wesley Longman, Inc., San Francisco. 695 pp.
- Kunkel, K.E., Ruth, T.K., Pletscher, D.H. and Hornocker, M.G. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. *Journal of Wildlife Management*, **63**(3): 901-910.
- Kunkel, K.E., Pletscher, D.H., Boyd, D.K., Ream, R.R. and Fairchild, M.W. 2004. Factors correlated with foraging behavior of wolves in and near Glacier National Park, Montana. *Journal of Wildlife Management*, **68**(1): 167-178.
- Landa, A. 1999. Spår och tecken, ett häfte till hjälp vid artbestämning av stora rovdjur, pp. 1-20. Norsk institutt for naturforskning (NINA), Trondheim.
- Manly, B.F.J. 1997. *Randomization, bootstrap and Monte Carlo methods in biology*, second edition. Chapman & Hall/CRC. 399 pp.
- Markgren, G. 1969. Reproduction of moose in Sweden. *Viltrevy* **6**: 127-299.
- Mech, L.D. 1970. *The Wolf: the ecology and behavior of an endangered species*. Doubleday/Natural History Press, Garden City, N.Y. 384 pp.
- Mech, L.D., Meier, T.J., Burch, J.W. and Adams, L.G. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. *In Ecology and conservation of wolves in a changing world*.

- Edited by* Carbyn, L.N., Fritts, S.H. and Seip, D.R. Canadian Circumpolar Institute, University of Alberta, Edmonton. pp. 231-243.
- Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W. and Dale, B.W. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis. pp. 101-120.
- Mech, L.D. and Boitani, L. 2003. Wolves: behavior, ecology, and conservation. The University of Chicago Press. 448 pp.
- Nilsen, E.B., Pettersen, T., Gundersen, H., Milner, J.M., Mysterud, A., Solberg, E.J., Andreassen, H.P. and Stenseth, N.C. 2005. Moose harvesting strategies in the presence of wolves. *Journal of Applied Ecology*, **42**: 389-399.
- Nilsson, N-E. 1990. Sveriges Nationalatlas – Skogen. Bokförlaget Bra Böcker, Höganäs. 144 pp.
- Okarma, H. 1995. The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta Theriologica*, **40**(4): 335-386.
- Olsson, O., Wirtberg, J., Andersson, M. and Wirtberg, I. 1997. Wolf *Canis Lupus* predation on moose *Alces alces* and roe deer *Capreolus capreolus* in south-central Scandinavia. *Wildlife Biology*, **3**: 13-25.
- Palm, D. 2001. Prey selection, kill and consumption rates of Moose by Wolves in central Sweden – comparison to moose population and human harvest. Examensarbete, Swedish University of Agricultural Sciences, Grimsö Wildlife Research Station.
- Palmqvist, P., Martinez-Navarro, B. and Arribas, A. 1996. Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity. *Paleobiology*, **22**(4): 514-534.
- Perjons, J., pers. comm. Swedish Association for Hunting and Wildlife Management, Krontallsvägen 10, 791 55 Falun.
- Persson, J. and Sand, H. 1998. Vargen - Viltet, Ekologin och Människan. Svenska Jägareförbundet. Almqvist & Wiksell Tryckeri, Uppsala. 128 pp.
- Peterson, R.O., Woolington, J.D. and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs*, **88**: 1-52.
- Pianka, E.R. 1974. Evolutionary ecology. Harper & Row, Publishers, Inc., New York. p. 165.
- Sand, H. 1996. Life history strategies in moose (*Alces alces*): geographical and temporal variation in body growth and reproduction. Doctoral thesis. Swedish University of Agricultural Sciences, Uppsala.
- Sand, H., Liberg, O., Ahlqvist, P. and Wabakken, P. 2004. Vilken inverkan har vargen på älgstammen? *In Skogsvilt III – Vilt och landskap i förändring*. Edited by Jansson, G., Seiler, C. and Andréén, H. Grimsö Wildlife Research Station, Sweden. pp. 66-72.
- Sand, H., Wikenros, C., Wabakken, P. and Liberg, O. In press. 2006. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proceedings of the Royal Society B*, **273**(1592): 1421-1427.
- Sand, H., pers. comm. Researcher, Grimsö Wildlife Research Station, S-730 91 Riddarhyttan, Sweden.
- Smith, D.W., Mech, L.D., Meagher, M., Clark, W.E., Jaffe, R., Phillips, M.K. and Mack, J.A. 2000. Wolf-bison interactions in Yellowstone National Park. *Journal of Mammalogy*, **81**(4): 1128-1135.
- Solberg, E.J., Loison, A., Sæther, B-E. and Strand, O. 2000. Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildlife Biology*, **6**: 41-52.
- Solberg, E.J., Sand, H., Linnell, J.D.C., Brainerd, S.M., Andersen, R., Odden, J., Brøseth, H., Swenson, J., Strand, O. and Wabakken, P. 2003. Utredninger i forbindelse med ny rovviltmelding. Store rovdyrs innvirkning på hjorteviltet i Norge: Økologiske prosesser og konsekvenser for jaktuttak og jaktutøvelse. Norsk institutt for naturforskning (NINA) Fagrapport 63. 75 pp.
- SPSS for Windows. 2002. SPSS Inc. Copyright © 1989-2002, release 11.5.1.
- StatView for Windows. SAS Institute Inc. Copyright © 1992-1998, version 5.0.1.

- Stephens, P.W. and Peterson, R.O. 1984. Wolf-avoidance strategies of moose. *Holarctic Ecology*, **7**(2): 239-244.
- Stubsjoen, T., Sæther, B-E., Solberg, E.J., Helm, M. and Rolandsen, C.M. 2000. Moose (*Alces alces*) survival in three populations in northern Norway. *Canadian Journal of Zoology*, **78**(10): 1822-1830.
- Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? *Ecology*, **68**(3): 669-674.
- Townsend, C.R., Harper, J.L. and Begon, M. 2000. *Essentials of Ecology*. Blackwell Science, Inc., London.
- Vucetich, J.A., pers. comm. School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI, 49931, USA.
- Wabakken, P., Sand, H., Liberg, O. and Bjärvall, A. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. *Canadian Journal of Zoology*, **79**: 710-725.
- Weaver, J.L. 1994. Ecology of wolf predation amidst high ungulate diversity in Jasper National Park, Alberta. Doctoral thesis. University of Montana, Missoula. 183 pp.
- White, K.S., Testa, J.W. and Berger, J. 2001. Behavioral and ecologic effects of differential predation pressure on moose in Alaska. *Journal of Mammalogy*, **82**(2): 422-429.
- Wikenros, C. 2001. Wolf winter predation on moose and roe deer in relation to pack size. Examensarbete, Swedish University of Agricultural Sciences, Grimsö Wildlife Research Station.
- Wirsing, A.J., Steury, T.D. and Murray, D.L. 2002. Relationship between body condition and vulnerability to predation in red squirrels and snowshoe hares. *Journal of Mammalogy*, **83**(3): 707-715.
- Wolfe, M.L. 1969. Age determination in moose from cementum layers of molar teeth. *Journal of Wildlife Management*, **33**: 428-431.

Appendix 1

A. Age of calves and adults being positively or probably wolf killed was determined in a laboratory or estimated in the field. The ten wolf territories have been separated into intensive and extensive studies.

Territory	Wolf killed moose					Probably wolf killed moose				
	Age determination		Age estimation			Age determination		Age estimation		
	Calf	Adult	Calf	Adult	Unknown	Calf	Adult	Calf	Adult	Unknown
Bogragen	20	2	3	0	0	1	0	1	0	0
Grangärde	25	8	1	0	0	7	3	0	1	3
Gråfjell	44	4	14	1	1	6	3	15	2	5
Hasselfors	5	2	0	0	0	6	2	0	0	1
Leksand	22	4	12	2	1	3	0	2	0	1
Nyskoga	8	9	1	1	0	1	6	1	1	0
Tyngsjö	5	10	2	2	0	3	1	1	0	0
Total (intensive)	129	39	33	6	2	27	15	20	4	10
Furudal	5	4	14	3	1	0	2	2	2	0
Koppang	0	0	20	13	2	0	0	20	14	2
Ockelbo	2	5	8	2	0	0	0	3	0	0
Total (extensive)	7	9	42	18	3	0	2	25	16	2

B. Number of adult females and males (≥ 1 years) in the ten wolf territories separated into intensive and extensive studies. Moose were either positively or probably wolf killed.

Territory	Wolf killed moose			Probably wolf killed moose		
	Adult			Adult		
	Cow	Bull	Unknown	Cow	Bull	Unknown
Bogragen	0	2	0	0	0	0
Grangärde	6	2	0	2	1	1
Gråfjell	2	1	2	3	0	2
Hasselfors	1	1	0	2	0	0
Leksand	1	1	4	0	0	0
Nyskoga	8	1	1	3	4	0
Tyngsjö	11	1	0	1	0	0
Total (intensive)	29	9	7	11	5	3
Furudal	5	1	1	2	2	0
Koppang	7	4	2	1	9	4
Ockelbo	6	1	0	0	0	0
Total (extensive)	18	6	3	3	11	4

C. Number of wolf killed and probably wolf killed moose being aged (to a specific year) and/or sex determined in intensive and extensive studies (the Koppang territory excluded).

	Wolf killed moose				Probably wolf killed moose			
	Calf	Adult	Unknown	Total	Calf	Adult	Unknown	Total
Age + sex	96	35	-	131	14	14	-	28
Age	66	4	-	70	33	1	-	34
Sex	-	3	0	3	-	2	1	3
Unknown	-	3	2	5	-	2	9	11
Total (intensive)	162	45	2	209	47	19	10	76
Age + sex	7	8	-	15	0	2	-	2
Age	22	1	-	23	5	0	-	5
Sex	-	5	0	5	-	2	0	2
Unknown	-	0	1	1	-	0	0	0
Total (extensive)	29	14	1	44	5	4	0	9

Appendix 2

No significant correlation in calf proportion between wolf kills and the other four estimates was found (cf. Figure Ia-d). Also, no significant correlation was found between wolf killed calf proportion and number of wolves in different packs (cf. Figure II).

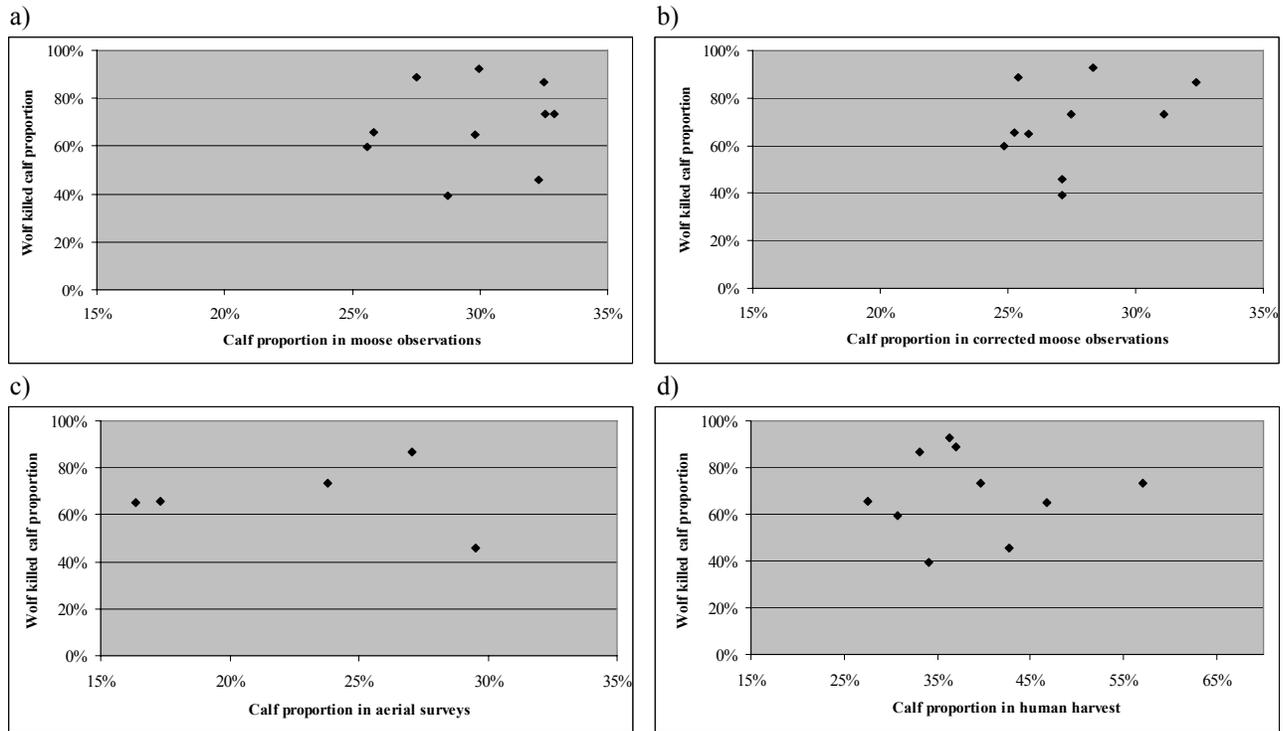


Figure I. Wolf killed calf proportion were compared to the proportion of calves in moose observations (a), corrected moose observations (b), aerial surveys (c) and human harvest (d). No significant correlation was found in any of the four correlations. Sample sizes with less than ten wolf killed moose were excluded from the correlation tests.

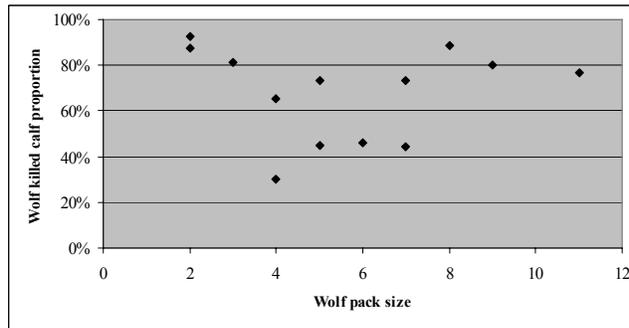


Figure II. Comparison between wolf killed calf proportion and wolf pack size.

Appendix 3

Number of wolves in specific winters and territories subject to this study is presented in Table D.

D. The ten territories and their number of wolves in specific winters of this study.

Intensive studies			Extensive studies		
Territory	Winter	No. of wolves	Territory	Winter	No. of wolves
Bogringen	2002/03	2	Furudal	2000/01	-
Grangärde	1999/00	2	Furudal	2001/02	9
Grangärde	2000/01	4	Furudal	2002/03	-
Gråfjell	2000/01	2	Koppang	1997/98	5
Gråfjell	2001/02	2	Koppang	1998/99	7
Gråfjell	2002/03	6	Koppang	1999/00	11
Hasselfors	2002/03	5	Koppang	2000/01	11
Leksand	1998/99	8	Koppang	2001/02	-
Leksand	1999/00	3	Koppang	2002/03	-
Leksand	2000/01	1	Ockelbo	2000/01	-
Nyskoga	2000/01	4	Ockelbo	2001/02	10
Nyskoga	2001/02	7			
Tyngsjö	2001/02	6			

- No data available

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