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Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden

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The predation behaviour of six lynx *Lynx lynx* family groups, i.e. adult females with dependent kittens, was studied using radio-tracking and snow-tracking in the Sarek area of northern Sweden during winter 1995/96 and 1996/97. One hundred and six daily radio-locations were obtained, and 340 km of intervening tracks were followed in the snow. Forty-one scats were collected, and 57 hunting attempts, 37 of which were successful, were recorded. Semi-domestic reindeer *Rangifer tarandus* contributed over 90% to lynx ingested meat calculated from both scats and kills. Eighty-three percent of hunting attempts on reindeer, and 53% of attempts on small prey species, mainly *Lagopus* sp. and mountain hares *Lepus timidus*, were successful. Four incidents of multiple-killing of reindeer were documented. Reindeer were generally in poor body condition, with an average femur marrow fat content of 27%. Lynx spent an average of three nights at each reindeer kill-site. Reindeer were less completely consumed than small prey (61% vs 99%). The amount of meat eaten from a reindeer was proportional to the number of lynx-nights on the kill. An overall kill rate of one reindeer per five days was calculated. We concluded that reindeer are a very important food source for lynx in winter, which potentially could lead to problems in resolving the carnivore-livestock conflicts in the region.

Key words: carnivore-livestock conflicts, diet, Lynx lynx, predation, Rangifer tarandus, semi-domestic reindeer

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Large carnivore populations are now recovering over much of Europe due to changes in the management strategies emphasising conservation (Boitani 1995, Mech 1995, 1996, Nowell & Jackson 1996, Breitenmoser 1998). Large carnivores have large home ranges and occur at low densities; this limits the abilities of small national parks and protected areas, as found in Europe (IUCN 1994), to conserve these species. A successful conservation strategy will have to include multi-use landscapes with suitable habitats (Fritts & Carbyn 1995). The unfortunate result, however, is often conflict with human land-use activities. Foremost among these conflicts is depredation on domestic livestock (Mech 1995, Cozza, Fico, Battistini & Rogers 1996, Kaczensky 1996).

While depredation on domestic sheep is the most widespread conflict throughout Europe and North America (Cozza et al. 1996, Kaczensky 1996, Linnell, Smith, Odden, Kaczensky & Swenson 1996), predation on semi-domestic reindeer *Rangifer tarandus* can be important throughout Fennoscandia and parts of northern Russia (Kjelvik, Kvam & Nybakk 1998). Reindeer herding is very different from the raising of domestic sheep and cattle; it requires wide-ranging movements over large areas in an attempt to avoid over-grazing and trampling of the lichen pastures that are of vital importance to reindeer in winter. Reindeer herding is also closely tied to the culture of several northern ethnic groups (Nybakk & Ingerslev 1997).

The fact that large carnivores prey on semi-domestic reindeer is undisputed (Haglund 1966, Nieminen & Leppäluoto 1988, Bjärvall, Franzén, Nordkvist & Åhlman 1990), although there is much discussion about the proportion of losses due to large carnivore depredation (Kvam, Nybakk, Overskaug, Sørensen & Brøndbo 1995). The low-intensity herding system means that most carcasses of missing animals are never recovered. The standard approach to this problem in Fennoscandia has been to study the mortality of reindeer (Nieminen & Leppäluoto 1988), often using mortality sensing radio-collars which allow rapid recovery and examination of the carcass so that cause of death can be determined (Bjärvall et al. 1990, Kvam et al. 1995, Kjelvik et al. 1998). While such studies provide vital information on the extent of predation, a full understanding of depredation also requires studies of predator behaviour. This approach is of particular importance in Sweden as a compensation system which is not based on paying for losses, but on the number of carnivores present, has recently been introduced (Bergström, Attergaard, From & Mellqvist 1997). To set appropriate levels of compensation, estimates of the kill rates of individual carnivores are needed.

Although brown bears *Ursus arctos*, wolverines *Gulo gulo* and wolves *Canis lupus* are found in the reindeer husbandry areas of Fennoscandia, Eurasian lynx *Lynx lynx* are by far the most abundant large carnivore species (Swenson, Sandegren, Bjärvall, Söderberg, Wabakken & Franzén 1994, Bergström, Bø, Franzén, Henriksen, Nieminen, Overrein & Stensli 1996, Bergström et al. 1997, Landa, Tufto, Franzén, Bø, Lindén & Swenson 1998). In the last decade lynx foraging behaviour has been extensively studied in the forested ecosystems of central Europe (Breitenmoser & Haller 1993, Okarma, Jedrzejewski, Schmidt, Kowalczyk & Jedrzejewska 1997). However, data relevant to reindeer husbandry areas have either come from analyses of stomach contents (Sunde & Kvam 1997) or from analyses of snow-tracking data that are more than 30 years old (Haglund 1966), and therefore originate from a period in which reindeer herding practises and lynx population levels were different from what they are today.

In this study we examine the foraging behaviour of radio-collared adult female lynx in a semi-domestic reindeer husbandry area in northern Sweden during winter. The central research objective was to determine the degree of lynx predation on the reindeer.

Study site

The 5,000 km^2 study area straddles the southeastern border of the Sarek National Park, around Kvikkjokk (67°00'N, 17°40'E) in the county of Norrbotten, northern Sweden. The landscape is composed of Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* boreal forest, sub-alpine birch *Betula* sp. forest and treeless alpine habitats along an altitudinal gradient ranging from 300 m to over 2,000 m a.s.l., with the tree-line lying at about 800 m. The climate is continental with warm summers and cold winters (the December average during the study was -10.5°C). Snow depths in winter regularly exceed 1 m.

Reproducing populations of lynx, brown bear and wolverine all occur in the study area. Moose *Alces alces* are the only wild ungulate occurring in significant numbers. All reindeer present within the study area are semi-domestic. Due to the absence of suitable wild ungulates for lynx to prey on, the only alternative prey apart from the semi-domestic reindeer are

small prey species, such as red foxes *Vulpes vulpes*, mountain hare *Lepus timidus*, capercaillie *Tetrao urogallus*, black grouse *T. tetrix*, hazel grouse *Bonasa bonasia*, willow grouse *Lagopus lagopus* and ptarmigan *L. mutus*.

Most of the study area was situated within the Jåkkåkaska (2,643 km^2) reindeer grazing area, although parts of the Sirkas (6,205 km^2) and Tuorpon (3,960 km^2) reindeer grazing areas were included on the north and south sides, respectively. Over-wintering herd sizes in these three areas were 3,700, 17,000, and 6,000 reindeer, respectively. Wintering herds were heavily skewed towards adult females, with the percentages of adult males, adult females and calves in the Jåkkåkaska area being 11, 65, and 24, respectively. Reindeer were herded to the higher, western portion of the area in summer, and to the lower, eastern section in winter. The study area spanned the transition area between the two seasonal ranges and a large portion of the herd was moved outside the study area in winter. However, in each year of the study, an unknown number of animals occurring in small dispersed groups, or as individuals, remained behind.

Material and methods

In this study we intensively followed family groups consisting of a radio-collared adult female lynx and her dependent kitten(s) <1 year old, during January - April. The lynx were radio-collared as part of a larger research project (Andrén, Ahlquist, Andersen, Kvam, Liberg, Lindén, Odden, Overskaug, Linnell & Segerström 1998). Four family groups were monitored in each of the winters of 1995/96 and 1996/97, belonging to six individual adult female lynx (i.e. two of the adult females were studied in both winters). We attempted to obtain sequential, daily radio-locations from a focal family group, and to follow their tracks in the snow between daily locations. However, problems intrinsic to field work in remote areas during winter, weather conditions and equipment failure, lead to sequences of irregular lengths. To avoid disturbing the lynx, suspected kill sites were only examined after the lynx had left the area.

Data collected during snow-tracking included scats and descriptions of hunting behaviour, regardless of success. Variables recorded for each event included: success or failure, attempted stalk or immediate attack, detection distance (distance between lynx and prey when the chase began), chase length (distance the prey was chased before contact or when the chase was abandoned), riding distance (distance that the lynx was carried by a reindeer before bringing it down), and the sinking depth of tracks in the snow from both the lynx and the prey. Horizontal distances were measured to the nearest metre using a tape measure, and sinking depth was measured to the nearest centimetre using a plastic ruler. Sex and age (calf/adult) was determined for each reindeer killed, and a femur was collected for analysis of marrow fat content using the modified Babcock method (Helrich 1990). The percentage of each reindeer consumed was estimated by eye, but only in cases when there was no evidence of scavengers.

Analysis of scats followed Sunde (1996), except in the four cases when a scat contained two prey types. For these the relative proportions of each prey were assumed to be equal. Factors correcting for differential digestibility of different prey species were use when calculating mass of prey ingested from scats (Sunde 1996). When calculating ingested mass from carcasses we used representative live weights for small prey species and winter slaughter weights of reindeer (18, 29 and 40 kg for a calf, adult female and adult male, respectively) because skin and guts of large ungulates are rarely eaten by lynx, whereas small prey are completely eaten.

Statistical analysis was carried out using the SPSS for Windows computer package. Proportions were analysed using Fisher's exact test, differences in sinking depths between lynx and reindeer within a given chase were analysed using a Paired t-test, and the non-parametric Mann Whitney U-test and Kruskal Wallis ANOVA were used to compare all other variables. The relationship between reindeer consumption and the number of lynx-nights on a carcass was examined using a Spearman's correlation.

Results

During winter 1995/96 and 1996/97 a total of 106 (56 in 1995/96, 50 in 1996/97) daily radio-locations were obtained and 340 km (194 in 1995/96 and 146 in 1996/97) of lynx tracks were followed. Four family groups were followed during each winter, but as two adult females were followed in both winters a total of six adult females were studied. The number of lynx-days for which each group was followed varied from 9 to 21 within a given winter. In most periods the family group consisted of an adult female and one or

Table 1. Diet of eight lynx family groups as estimated from scats and kills found while snow-tracking (N = 41 scats and 37 kills) in winter 1995/96 and 1996/97. CF = correction factor after Sunde (1996), BM = % ingested body mass.

	Scats					Kills		
	N	Dry weight (g)	CF	Mass (g)	BM %	N	Meat weight (kg)	BM %
Rangifer tarandus	35	580.7	65	37746.8	93.1	19	318.4	91.9
Lepus timidus	6	47.8	18	908.6	2.2	5	15	4.3
Lagopus sp.	4	100.4	19	1907.6	4.7	12	6	1.8
Vulpes vulpes	0					1	7	2
Total	45	728.9		40563.0	100	37	346.4	100

two kittens. However, in some shorter periods the family groups were accompanied by other animals including an adult male and a yearling female as determined by radio-tracking.

Diet

In total, 41 scats and 37 kills were found (Table 1). Reindeer was the prey species of which remains most frequently occurred in scats (85%) and the most common among the kills (51%), as it contributed 93% of the mass to lynx diet during this study period (see Table 1).

Hunting success

In total, we identified 57 hunting attempts on reindeer, mountain hares, *Lagopus* sp., capercaillie and red fox. Of these, 65% were successful and resulted in a kill. Of the hunting attempts on reindeer, 83% (19 of 23) were successful, in contrast to 53% (18 of 34) successful attempts on small prey species (Fisher's exact test, P = 0.026). One factor that might explain the high success rate of lynx on reindeer is that reindeer always sank deeper into the snow than lynx (22.3 ± 5.4 cm vs 15.4 ± 2.7 cm; Paired t-test, t = 4.8, df = 8, P = 0.001) during chases.

No attacks were initiated from a spot with dense cover. In half the cases attacks were initiated without any stalking, whereas in the other half at least some attempt was made to stalk in the final approach (Table 2). We did not observe any attacks from ambush sites. Although small sample sizes precluded statistical analyses of the hunting parameters for all prey groups apart from *Lagopus* sp. (Mann-Whitney U-test: chase length: U = 32, P = 0.9; detection distance: U = 19.5, P = 0.3), there were very few differences between those for successful and unsuccessful hunts (see Table 2). In general, lynx appeared to be able to stalk close to all prey before being detected, i.e. the maximum value was 40 m. Chases on reindeer varied greatly; in two cases contact was made with reindeer with a chase of under 10 m, while in two other cases contact was not made for 65 and 94 m, respectively. In most cases where reindeer were killed, the lynx was carried by the reindeer for up to 80 m before the reindeer fell. All reindeer were killed with bites to the throat. In four cases we observed multiple kills where two reindeer were killed within 150 m of each other. In two of these cases the carcasses were found within 10 m of each other indicating that they were killed in the same attack.

Characteristics of reindeer kills

Of the 18 reindeer which could be aged and sexed, 10 (56%) were females ≥1.5 years old. Four males

Table 2. Characteristics of successful and unsuccessful predation attempts on three prey species by lynx interpreted from snow-tracking data. Means, ranges and sample sizes are presented for detection distances and chase lengths, whereas the frequencies are given for the type of approach used.

		Detection distance (m)			Chase length (m)			Approach	
Prey	Success	Mean	Range	N	Mean	Range	N	Direct	Stalk
Rangifer tarandus	Yes	8	0-12	4	44	6-87	5	4	1
	No	19	6-40	4	44	12-70	4	4	0
Lepus timidus	Yes	12	0-1	2	12	3-20	2	1	1
	No	7	20-35	2	28	20-35	2	0	3
Lagopus sp.	Yes	6	0-1	6	9	2-20	6	2	4
	No	10	3-18	10	9	2-20	11	4	6

(22%) ≥1.5 years old and four calves (22%) made up the remainder. Although there was some variation, the animals killed appeared to be in poor body condition as indicated by femur bone marrow fat content (mean for 15 animals: 27% ± 24 (SD)). Mean (± SD) bone marrow fat content for calves (N = 4), adult females (N = 5), adult males (N = 4) and uncategorised animals (N = 2) was 27% ± 31, 36% ± 25, 22% ± 25 and 15% ± 19, respectively. The femur bone marrow fat content did not differ significantly between the three categories calves, adult females and adult males (Kruskal-Wallis: $\chi^2 = 2.008$, df = 3, P = 0.554).

Kill consumption, time on kill and kill rates

Examination of 18 reindeer provided estimates of the proportion consumed by the lynx. A significantly smaller proportion of the meat on reindeer carcasses (61% ± 23.7 (SD), range: 5-90%, N = 18) was utilised as compared to the small prey kills (98.8% ± 2.1 (SD), range: 95-100%, N = 17) (Mann-Whitney U-test, U = 0, N = 35, P < 0.001). There was also much greater variation in the consumption of reindeer. Of four reindeer at least 90% was consumed while less than 20% of three other reindeer had been eaten. The lowest consumption was found in two of the cases of multiple killing; however, there was no overall difference in the consumption rates of single or multiple kills (Mann-Whitney U-test: U = 27.5, N = 18, P = 0.274). Small prey were always consumed in a single meal. Reindeer, however, potentially provided food for a whole family group for several nights. Lynx spent an average of 3 ± 1 nights on a reindeer kill site (counting multiple kills as a single site or event), with a range of 1-5 nights.

The amount of meat eaten per reindeer carcass per lynx-night was calculated using the known number of lynx on each kill, the number of nights spent on the kill site, the percentage use of the kill, and the mean slaughter weight of the appropriate class of reindeer. A significant positive correlation was found between kilograms of meat removed and number of lynx-nights spent at the carcass ($r_s = 0.7$, N = 14, P = 0.004). On average 2.5 kg ± 1 of reindeer was consumed per lynx per night.

When feeding on a reindeer, lynx generally (in 9 of 15 cases) spent the days in lairs within 250 m of the carcass. When not in the immediate vicinity of the carcass, they were an average of 1.9 km (N = 6, range: 0.7-3.2 km) away. Lynx family groups moved a long distance each day (up to 12 km in a straight line between locations), although this distance was significantly shorter when feeding on a reindeer kill (0.71 km ± 0.67) than when not feeding on a reindeer (4.63 km ± 3.2; U = 156, N = 97, P < 0.001).

In addition to the 19 reindeer found by snow-tracking, there were two more incidents where radio-collared lynx spent three or four nights within an area of < 3 km². Because of poor tracking conditions no carcass could be found, however, the behaviour was typical of a lynx feeding on a reindeer so we assumed

Table 3. Individual sequences of intensive tracking of eight lynx family groups during winter 1995/96 and 1996/97. In each sequence the kills made on separate days are separated by a dash. L = *Lagopus* sp., R = reindeer, H = hare, F = red fox. The asterisk marks assumed reindeer kills.

Lynx no	Starting date	No of nights	Kill sequence	Number of		
				Reindeer killed	Small prey killed[3]	Reindeer killed/night
9402	05/02/96	9	L - R	1	1	0.11
9514	14/02/96	8	R - RS	2	1	0.25
9511	25/02/96	4		0	0	0
9403[1]	12/03/96	10	L - LL - LLLH	0	7	0
9514	21/03/96	13	R - R - LR	3	1	0.23
9511	09/04/96	7	R - LLH	1	3	0.14
9511	19/04/96	3	LH - H	0	3	0
9514	27/04/96	3		0	0	0
9514	08/01/97	11	R* - R	2	0	0.18
9622[2]	20/01/97	17	RR - R -R - R - RR	7	0	0.41
9511	05/02/97	12	RR - H - R*	3	1	0.25
9628	21/04/97	9	RR - F	2	1	0.22
Total		106		19 + 2*	18	0.20 ± 0.13

[1] The family group was accompanied by an adult male lynx during the study period.
[2] The family group was accompanied by the female's female yearling from a previous litter for the latter part of the study period.
[3] Some small prey kills may have remained undetected in areas with bad tracking conditions; therefore no kill rate was calculated for small prey.

that a reindeer had been killed (following Okarma et al. 1997). These assumed kills were used in the calculations of kill rate only, resulting in an estimate of one reindeer killed every five days (Table 3). We did not calculate a similar value for small prey because some kills were probably missed in areas with poor snow conditions. Winter conditions, both in terms of climate and of reindeer being gathered on their winter grazing areas, lasted from approximately 1 December until 30 April, or 151 days. Assuming that the kill rate on reindeer is constant (1 reindeer/5 days) during this period each family group should be expected to kill 30.2 reindeer each winter.

Discussion

The main result of this study has been the documentation of the importance of semi-domestic reindeer in the winter diet of lynx family groups in the study area. The finding that reindeer contributed over 90% of the mass in lynx winter diet concurs with other studies of lynx predation in western Europe, which have repeatedly documented the importance of ungulates in lynx diet (Jedrzejewski, Schmidt, Milkowski, Jedrzejewska & Okarma 1993). For example, other studies have found that ungulates made up 89% of the biomass and 87% of the kills during winter in central and southern Norway, respectively (Dunker 1988, Kvam, Sunde & Overskaug 1998). Similar results have also been obtained from Poland and Switzerland, where ungulates (mainly roe deer *Capreolus capreolus*) always made up more than 80% of kills contributing to winter diet (Breitenmoser & Haller 1993, Jedrzejewski et al. 1993, Okarma et al. 1997, Aanes, Linnell, Perzanowski, Karlsen & Odden 1998). The only exceptions to this pattern come from the eastern parts of the lynx range in Russia, where small prey, especially hares, dominate (Jedrzejewski et al. 1993). Although 50% of kills found in our study were from small prey species, the larger amount of meat available from a reindeer carcass results in a disproportionate importance of reindeer in the diet. This result may underestimate the importance of small prey species to individual lynx, during some periods. For example, lynx appeared to have survived only on small prey during four of the tracking sequences. Given the unpredictable distribution of reindeer (both in space and time), the ability of lynx to survive on small prey for extended periods of time may be of greater importance than this study has found.

Reindeer not only provided more meat than small prey, but attacks on reindeer were also more successful, with a total of 83% of chases resulting in a kill, as compared to 53% for small prey. This concurs with earlier studies that have found a higher hunting success for lynx on ungulates than on small prey (Haglund 1966). The high success rate of lynx when chasing reindeer can at least partially be explained by the greater sinking depth of reindeer in the snow. Although we have no direct measures of how deep hares sink in the snow, it is likely to be no deeper than lynx. The fact that half of the attacks were launched without any stalking also indicates the ease with which lynx were able to kill reindeer. Even when lynx stalked the reindeer, very little cover was available, and the lynx were generally able to approach to within 10-20 m before beginning the chase. It should be born in mind that these estimates of hunting success are maximum estimates, because it is not possible to register hunting attempts that ended before the chase began, as would occur if the potential prey detected the lynx before it could approach close enough to launch an attack. This hunting success is very high compared to that of other felids, for example leopards *Panthera pardus* which only achieved a 38% hunting success (for all prey species) in a study in Namibia (Stander, Haden, Kaqece & Ghau 1997). Although we studied lynx family groups, which on some occasions also included an adult male and a yearling female, there was little evidence of cooperative hunting (Haglund 1966, Dunker 1988). In fact on one occasion when at least two members of a family group attacked a small reindeer herd at the same time, two reindeer were killed simultaneously, implying that each lynx chased different reindeer.

A reindeer provided potential food for many days, but they were not used as completely as small prey items which were consumed in a single meal. On average, a lynx family spent three nights feeding on a reindeer carcass, and consumed 60% of the available meat. It is unclear why the carcasses were not used completely, and why there was so much variation in consumption. However, similar results have also been found in Norway, with some reindeer carcasses being utilised completely, and others hardly touched (Kvam et al. 1998). These consumption rates are lower than those found for wild ungulate prey in central Europe (Breitenmoser & Haller 1993, Okarma et al. 1997), and may therefore be associated with the availability of easily killed reindeer. The estimated consumption rate of 2.5 kg per lynx-night is very

close to previous estimates for female lynx with kittens from Poland (1.6-2.2 kg per lynx-night; Okarma et al. 1997).

In one incident in our study, the lynx abandoned a carcass when a wolverine began to feed on it, but wolverines could be excluded as a factor from the other cases as the kill sites were checked for wolverine tracks daily. Clearly, the observed pattern of carcass use by lynx leads to a large number of partially consumed reindeer carcasses available for wolverines (Landa, Strand, Swenson & Skogland 1997) and other scavengers. The extent to which wolverines depend on lynx to provide food is a topic deserving of further work. Red foxes have also been reported among lynx prey items in other studies in Norway and Switzerland (review in Linnell, Odden, Pedersen & Andersen 1998). The finding that they were eaten implies that the fox must be regarded as a prey species, a finding which is not consistent among all cases of intra-guild predation (Palomares & Caro 1999).

The lynx hunting behaviour reported here is consistent with that of most members of the genus *Lynx* (Dunker 1988, Murray, Boutin, O'Donoghue & Nams 1995), in that attacks were only launched at relatively close quarters, the maximum being 40 m. Reindeer were pursued further than small prey, with some chases as long as 87 m. However, in contrast to Canadian lynx *Lynx canadensis* which seem to require cover (Murray et al. 1995), none of the attacks in our study were launched from dense cover or concealment. During the study, deep snow covered most vegetation that could conceal a lynx. The impression we got from the snow tracking was that the lynx moved along in straight paths, and simply approached and chased whatever prey species they encountered. Even though all reindeer were brought down with throat bites, the large size of the prey with respect to the lynx lead to the reindeer carrying the lynx on its back for considerable distances, up to 80 m. Although no injuries to lynx were documented during our study, such behaviour must carry considerable potential risks (Ross, Jalkotzy & Daquist 1995).

Although the sample is relatively small, and we do not know the exact age/sex structure of the reindeer population in the study area, there were surprisingly few calves and a large number of adult males among the reindeer killed. In order for this predation to have been a random sample from the population, there would have to have been a very biased sex structure among the reindeer in the study area compared to the total herd. The subjective impression that we acquired from our own observations of reindeer herds in the study area did not support this conclusion. Other predation studies have shown that calves and adult females generally dominate among reindeer killed by lynx, and that calves have a greater risk of being killed relative to their occurrence (Bjärvall et al. 1990, Kjelvik et al. 1998). Adult males generally have a body weight ranging within 60-100 kg, which means that they are 4-8 times heavier than a female lynx. One possible reason why lynx were able to regularly kill adult males, and demonstrate a high success rate on all reindeer hunts, could be that the reindeer killed were in poor condition. Average femur bone marrow fat levels were very low for all classes of reindeer killed, when compared to other studies of semi-domestic reindeer. Studies in central Norway and northern Sweden found bone marrow fat levels averaging >50% among reindeer killed by lynx (Bjärvall et al. 1990, Kjelvik et al. 1998). Unfortunately, we had no comparative data to determine if the results are due to lynx selecting reindeer in poorer than average condition, or to a general poor condition among reindeer in the study area. The fact that most attacks on reindeer were both short and successful indicates that lynx were not selecting reindeer based on condition, therefore the latter option seems most likely.

The kill rate of one reindeer every five days was identical to values obtained for lynx predation on wild ungulates from central Europe (Breitenmoser & Haller 1993, Okarma et al. 1997), although the absence of a reindeer density estimate for the study area makes direct comparison difficult. Sweden has introduced a compensation system where an extra subsidy is paid to reindeer management areas that can document the presence of lynx, instead of paying compensation for reindeer that have been killed. Therefore, estimates of kill rates may be an important tool which can be used to set the subsidy at the right level. Currently, the management areas are being paid the equivalent value of 200 reindeer for the presence of one lynx family group. This is intended to cover the losses of reindeer due to predation by that family group and the other solitary lynx in the area. From our data, we have estimated that an average family group will kill in the order of 30 reindeer during the winter. However, until kill rates are available for solitary lynx during winter, and for all age and sex classes in summer, it is hard to evaluate the appropriate level of compensation.

Conflicts between lynx, other large carnivores, and livestock are common throughout Europe (Aanes,

Swenson & Linnell 1996, Kaczensky 1996, Breitenmoser 1998). Livestock are rarely the main prey of large carnivores (e.g. Breitenmoser & Haller 1993, Jedrzejewski et al. 1993, Meriggi & Lovari 1996, Okarma et al. 1997) suggesting that large carnivores and livestock can coexist if suitable husbandry methods can be used to reduce depredation (Linnell et al. 1996). However, using this strategy in the Sarek region poses two problems. First, because the reindeer are only semi-domestic and use lynx habitat throughout the year, there are few options to change husbandry practices. Second, it appears that in the Sarek area lynx subsist mainly on reindeer. However, the incomplete consumption of kills implies that a 30% reduction in predation would not affect the amount of meat available to lynx, assuming that lynx responded by fully consuming their kills. Beyond this point, a reduction in the availability or accessibility of reindeer could have negative consequences for lynx (Pulliainen, Lindgren & Tunkkari 1995) in the absence of alternative wild ungulate prey. The implication is that a management strategy must be based on the acceptance that either losses of semi-domestic reindeer will continue, or lynx densities need to be reduced within the reindeer husbandry areas.

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References

Aanes, R., Linnell, J.D.C., Perzanowski, K., Karlsen, J. & Odden, J. 1998: Roe deer as prey. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); The European roe deer: the biology of success. Scandinavian University Press, Oslo, pp. 139-160.

Aanes, R., Swenson, J.E. & Linnell, J.D.C. 1996: Rovvilt og sauenæring i Norge. I. Tap av sau til rovvilt: en presentasjon av tapets omfang basert på brukeropplysninger. (In Norwegian with English summary: Carnivores and sheep-farming in Norway. I. Losses of sheep to carnivores: a presentation of the extent of losses based on information provided by farmers). - Norwegian Institute for Nature Research Oppdragsmelding 434: 1-32.

Andrén. H., Ahlquist, P., Andersen, R., Kvam, T., Liberg, O., Lindén, M., Odden, J., Overskaug, K., Linnell, J.D.C. & Segerström, P. 1998: The Scandinavian lynx projects: Annual report 1997. - Norwegian Institute for Nature Research Oppdragsmelding 518: 1-11.

Bergström, M.R., Attergaard, H., From, J. & Mellqvist, H. 1997: Järv, lodjur och varg i renskötselområdet: resultat från 1997 års inventering. - Länsstyrelsen Västerbottens län Meddelande 8: 1-8. (In Swedish).

Bergström, M.R., Bø, T., Franzén, R., Henriksen, G., Nieminen, M., Overrein, Ø. & Stensli, O.M. 1996: Store rovdyr. Samordning av forvaltningstiltak på Nordkalotten. (In Norwegian with English summary: Large carnivores. Standardisation of management measures in Nordkalotten). - Nordkalottkommitéens Rapportserie 42: 1-45.

Bjärvall, A., Franzèn, R., Nordkvist, M. & Åhlman, G. 1990: Renar och rovdjur. Rovdjurens effekter på rennäringen. - Naturvårdsverket förlag, Solna, 296 pp. (In Swedish).

Boitani, L. 1995: Ecological and cultural diversities in the evolution of wolf human relationships. - In: Carbyn, L.N., Fritts, S.H. & Seip, D.R. (Eds.); Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Alberta, Canada, pp. 3-12.

Breitenmoser, U. 1998: Large predators in the Alps: the fall and rise of man's competitors. - Biological Conservation 83: 279-289.

Breitenmoser, U. & Haller, H. 1993: Patterns of predation by reintroduced European lynx in the Swiss Alps. - Journal of Wildlife Management 57: 135-144.

Cozza, K., Fico, R., Battistini, M.L. & Rogers, E. 1996: The damage-conservation interface illustrated by predation on domestic livestock in central Italy. - Biological Conservation 78: 329-336.

Dunker, H. 1988: Winter studies on the lynx (Lynx lynx) in southeastern Norway from 1960-1982. - Meddelelser fra Norsk Viltforskning 3: 1-56.

Fritts, S.H. & Carbyn, L.N. 1995: Population viability, nature reserves, and the outlook for gray wolf conservation in North America. - Restoration Ecology 3: 26-38.

Haglund, B. 1966: Winter habits of the lynx (Lynx lynx L.) and wolverine (Gulo gulo L.) as revealed by tracking in the snow. - Viltrevy 4: 1-311.

Helrich, K. 1990: Official methods of analysis of the association of official analytical chemists. 15th edition. - AOAC Inc., Arlington, Virginia, 427 pp.

IUCN 1994: 1993 United Nations world list of national parks and protected areas. - IUCN Publications, Cambridge, 313 pp.

Jedrzejewski, W., Schmidt, K., Milkowski, L., Jedrzejewska, B. & Okarma, H. 1993: Foraging by lynx and its role in ungulate mortality: the local (Bialowieza Forest) and the Palaearctic viewpoints. - Acta Theriologica 38: 385-403.

Kaczensky, P. 1996: Livestock-carnivore conflicts in Europe. - Munich Wildlife Society, Munich, 106 pp.

Kjelvik, O., Kvam, T. & Nybakk, K. 1998: Dødelighet hos tamrein i et rovdyrområde. - Reindriftsnytt 1998: 35-42. (In Norwegian).

Kvam, T., Nybakk, K., Overskaug, K., Sørensen, O.J. & Brøndbo, K. 1995: Gaupa tar mye mer rein enn antatt. - Reindriftsnytt 1995: 40-43. (In Norwegian).

Kvam, T., Sunde, P. & Overskaug, K. 1998: Matvaner hos gaupe i Nord-Trøndelag. - In: Kvam, T. & Jonson, B. (Eds.); Store rovdyrs økologi i Norge: Sluttrapport. Norwegian Institute for Nature Research Temahefte 8: 94-104. (In Norwegian).

Landa, A., Strand, O., Swenson, J.E. & Skogland, T. 1997: Wolverines and their prey in southern Norway. - Canadian Journal of Zoology 75: 1292-1299.

Landa, A., Tufto, J., Franzén, R., Bø, T., Lindén, M. & Swenson, J.E. 1998: Active wolverine dens as a minimum population estimator in Scandinavia. - Wildlife Biology 4: 159-168

Linnell, J.D.C., Smith, M.E., Odden, J., Kaczensky, P. & Swenson, J.E. 1996: Strategies for the reduction of carnivore - livestock conflicts: a review. - Norwegian Institute for Nature Research Oppdragsmelding 443: 1-115.

Linnell, J. D. C., Odden, J., Pedersen, V. & Andersen, R. 1998: Records of intra-guild predation by Eurasian lynx, Lynx lynx. - Canadian Field Naturalist 112: 707-708.

Mech, L.D. 1995: The challenge and opportunity of recovering wolf populations. - Conservation Biology 9: 270-278.

Mech, L.D. 1996: A new era for carnivore conservation. - Wildlife Society Bulletin 24: 397-401.

Meriggi, A. & Lovari, S. 1996: A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock. - Journal of Applied Ecology 33: 1561-1571.

Murray, D.L., Boutin, S., O'Donoghue, M. & Nams, V.O. 1995: Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. - Animal Behaviour 50: 1203-1210.

Nieminen, M. & Leppäluoto, J. 1988: Predation in the reindeer husbandry area in Finland during 1976-1986. - Rangifer 8: 25-34.

Nowell, K. & Jackson, P. 1996: Wild cats: status survey and action plan. - IUCN Publications, Gland, Switzerland, 382 pp.

Nybakk, K. & Ingerslev, T. 1997: Samisk kultur, norsk politik og store rovdyr. - Naturens Verden 1997/2: 41-51. (In Norwegian).

Okarma, H., Jedrzejewski, W., Schmidt, K., Kowalczyk, R. & Jedrzejewska, B. 1997: Predation of Eurasian lynx on roe deer Capreolus capreolus and red deer Cervus elaphus in Bialowieza Primeval Forest, Poland. - Acta Theriologica 42: 203-224.

Palomares, F. & Caro, T.M. 1999: Interspecific killing among mammalian carnivores. - American Naturalist 153: 492-508.

Pulliainen, E., Lindgren, E. & Tunkkari, P.S. 1995: Influence of food availability and reproductive status on the diet and body condition of the European lynx in Finland. - Acta Theriologica 40: 181-196.

Ross, P.I., Jalkotzy, M.G. & Daquist, P.Y. 1995: Fatal trauma sustained by cougars, Felis concolor, while attacking prey in southern Alberta. - Canadian Field-Naturalist 109: 261-263.

Stander, P.E., Haden, P.J., Kaqece & Ghau 1997: The ecology of asociality in Namibian leopards. - Journal of Zoology (London) 242: 242.

Sunde, P. 1996: Foraging patterns of the European lynx (Lynx lynx) in Norway. - MSc thesis, University of Copenhagen, Copenhagen, Denmark, 66 pp.

Sunde, P. & Kvam, T. 1997: Diet patterns of Eurasian lynx Lynx lynx: what causes sexually determined prey size segregation ? - Acta Theriologica 42: 189-201.

Swenson, J.E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P. & Franzén, R. 1994: Size, trend, distribution and conservation of the brown bear Ursus arctos population in Sweden. - Biological Conservation 70: 9-17.