WWF RAPPORT

Illegal jakt
på stora rovdjur i Sverige

ILLEGAL JAKT – PÅ STORA ROVDJUR I SVERIGE

En omfattande illegal jakt av stora rovdjur pågår. Uppskattningsvis dödas varje år hundratals av de drygt 5 000 stora rovdjur som lever i Sverige. Den illegala jakten står ofta för en stor del av den årliga dödligheten.

Under de senaste tio åren har en mängd beslut och åtgärder genomförts av svenska myndigheter och politiker, åtgärder som borde ha minskat omfattningen av den illegala jakten på stora rovdjur. Jaktkvoterna har höjts och två licensjakter på varg har genomförts. Möjligheterna att freda tamdjur har ökat liksom regionalt medbestämmande via viltförvaltningsdelegationer. Andra exempel är att polis- och åklagarmyndigheterna prioriterat brott där stora rovdjur är inblandade och länsstyrelserna arbetar med att vara synliga i fält. Men frågan är om detta haft någon effekt på den illegala jakten på stora rovdjur?

Världsnaturfonden WWF har därför beställt fyra forskningsrapporter om stora rovdjur (björn, järv, lo och varg), som så långt det är möjligt beskriver hur omfattande den illegala jakten är i dag och eventuella trender över tiden. Rapporterna bygger på studier av rovdjur som varit försedda med sändare men även på resultat från undersökningar som gjorts kring dödsorsaken. Om forskarnas studieområden är representativa, så har inte den illegala jakten på lo, järv och björn minskat sedan 1990-talet trots högre jaktkvoter och otaliga beslut av både myndigheter och politiker. Glädjande har den illegala jakten på varg minskat med två tredjedelar och brytpunkten verkar ha skett runt år 2005. Orsaken till detta trendbrott går inte specifikt att säga. I sammanfattningen nedan har illegal jakt och sannolik illegal jakt slagits samman och benämns gemensamt som illegal jakt. Kriterier för detta redovisas i de olika rapporterna.

Björn (tidsperiod 1984-2010) - dagens population ca 3 300 djur
Den illegala jakten är statistiskt högre i norra studieområdet i jämförelse med det södra. Det finns ingen skillnad över tiden vilket pekar på att den illegala jakten inte verkar ha minskat jämfört med tidigare år. Varje år står den illegala jakten för en dödlighet hos vuxna honor med 0,1-0,6 procent i söder och 2,3–3,1 procent i norr. Den illegala jakten på björn har inte stoppat tillväxten eftersom björnpopulationen ökar, och i dag finns det ungefär 3 300 björnar i Sverige. Lokalt kan dock den illegala jakten påverka björnstammen. Det verkar inte finnas någon koppling mellan ökad jaktkvot och storleken på den illegala jakten för björn, trots stor ökning av jaktkvoten. I år får 293 björnar fällas.

Lodjur (tidsperiod 1994-2010) - dagens population ca 1 250 djur
Vuxna lodjur dör främst på grund av mänskliga aktiviteter (jakt, trafik och illegal jakt). I det nordliga området är illegal jakt den främsta dödsorsaken hos vuxna lodjur (79 % av dödsfallen), med illegal jakt var ungefär lika viktigt som naturliga dödsorsaker hos yngre lodjur (45 %). I det södra området är naturliga dödsorsaker samt jakt och trafik de främsta dödsorsakerna (62 % för dessa tillsammans) och var ungefär dubbelt så stor som illegal jakt och förmodad illegal jakt (29 %). Den illegala jakten var statistiskt signifikant högre i det nordliga området jämfört med det södra området. Den illegala jakten var inte signifikant olika mellan de två studieperioderna (1994-1999 jämfört med 2000-2010) i varken det nordliga eller det sydliga området. Om de båda studieområdena är representativa för renskötselområdet respektive söder om renskötselområdet, då är det beräknade antalet illegalt skjutna lodjur 77 per år i renskötselområdet och 22 per år söder om renskötselområdet.

Järv (tidsperiod 1993-2011) - dagens population ca 650 djur
Järvarna har studerats i Jokkmokks kommun i Norrbottens län. Illegal jakt var den viktigaste dödsorsaken bland vuxna järvar (60 %) och anmärkningsvärt är att för vuxna hanar så står den illegala jakten för hela 94 % (resterande 6 % var naturlig död). Den illegala jakten dödar årligen 10 % av den totala vuxna järvpopulationen. Noterbart är att dödlighet orsakad av illegal jakt var högre, mer än dubbelt så hög hos hanar (21 %) än hos honor (8 %). Nästan all illegal jakt på vuxna järvar skedde under snösäsongen (december-maj), med en tydlig topp i mars-maj. Den viktigaste dödsorsaken bland järvungar (0-1 år gamla) var inomartspredation. Nivån på illegal jakt verkar inte ha förändrats från perioden 1993-1999 till 2000-2011. Våra analyser visar att illegal jakt är en viktig del i järvars populationsdynamik i Sverige. Emellertid tyder inventerings-resultaten på att populationen i landet ökar och att illegala jakten inte är tillräckligt omfattande för att stoppa populationen från att växa som helhet. Den illegala jakten är det som främst påverkar den svenska populationens tillväxt.

Varg (tidsperiod 1998-2011) - dagens population ca 230 djur
Total årlig dödlighet i Skandinavien för hela studieperioden var 25,9 %. Illegalt dödande utgjorde 12,8 % och andra orsaker stod för 13,1 % av den totala dödligheten. Norge hade högre nivåer än Sverige, både för total dödlighet (Norge 35,6 %; Sverige 22,4 %) och för illegalt dödande (Norge 17,9 %; Sverige 11,1 %). Mellanårsvariationen var stor både för total dödlighet och för illegalt dödande, men i Sverige visade den senare en klart avta-gande tendens med tiden. Analyser visade att trendbrottet för minskningen av den illegala jakten för denna dödlighet med största sannolikhet inträffade före år 2005.

Mellan 1998-2005 minskade den totala dödligheten från 30,5 % till 16,8 %. Det illegala dödandet gick ned från 15,7 till 7,7 % mellan 2006 och 2011 i Skandinavien. Den illegala dödligheten uppvisade dock motsatta tidstrender i Norge och Sverige. Norge hade en icke-säkerställd ökning av denna typ av mortalitet efter 2005, medan Sverige hade en statistiskt säkerställd, minskning från 16,9 % till 2,5 %. Detta motsvarar en minskning av antalet illegalt dödade vargar per år med två tredjedelar, från 9-20 individer under perioden 1998-2005 till 3-7 individer under perioden 2006-2010.

Causes of mortality, especially illegal killing, among Swedish brown bears, 1984-2010

Report 2011-3 from the Scandinavian Brown Bear Research Project to World Wide Fund for Nature, WWF (Sweden)

(Photo: Djuro Huber)

Jon E. Swenson*, Andreas Zedrosser, Sven Brunberg & Peter Segerström
(*jon.swenson@umb.no)

Skandinaviska Björnprojektet

Abstract

We analyzed the fates of 305 brown bears that were radiomarked when they died or we lost contact with them during the period 1984-2010 in two study areas in southern and northern Sweden. The proportion of nonresearch deaths attributable to illegal killing was significantly higher in the north (44.8-58.6%) than in the south (4.1-26.9%). We found no area differences in the frequence of illegally killed bears due to sex, age, or study period ($\leq$1997 and $\geq$1998). We estimated annual rates of illegal mortality among adult females to be 0.1-0.6% in the south and 2.3-3.1% in the north. The documented and suspected illegal deaths showed no seasonal trend in the south, but were concentrated to spring and autumn in the north. Generally, illegal killing does not seem to be an important factor affecting population trends among brown bears in Sweden, but it may be important locally, and then it may affect the bears' life-history traits. It is important that managers attempt to identify areas of high illegal killing. Managers should also recognize that the level of illegal mortality appears to be stable, probably is not related to the level of legal hunting mortality, and that it probably is additive to legal hunting mortality.

Introduction

In human-dominated landscapes throughout the world, human-caused mortality is one of the major causes of mortality in large carnivore populations (Woodroffe & Ginsberg 1998). This is also the case for the four species of large carnivores in Scandinavia, brown bear (*Ursus arc*tos), wolverine (*Gulo gulo*), Eurasian lynx (*Lynx lynx*), and gray wolf (*Canis lupus*) (Andrén et al. 2006, Liberg et al. 2008, Bischof et al. 2009, Persson et al. 2009). At least in parts of Scandinavia, illegal killing is an important source of mortality for the populations of all of these species, (Swenson & Sandegren 1999, Andrén et al. 2006, Liberg et al. 2008, Bischof et al. 2009, Persson et al. 2009).

WWF-Sweden has requested an updated evaluation of the effect of illegal killing on the brown bear population in Sweden. The last evaluation of this was in 1998 (Swenson & Sandegren 1999). Swenson & Sandegren (1999) estimated the mortality due to illegal killing among radiomarked brown bears to be 2.8 times higher than the legal hunting mortality in their northern study area and 0.6 of the legal hunting mortality in the southern study area. During their study period, 1984-1998, the average legal harvest of brown bears in Sweden was 38.5 bears annually, compared with over 200 bears annually today.

In this updated study, we compare the proportion of illegally killed bears by study area, sex, age, and study period. The latter was to investigate whether the level of illegal killing changed over time and whether levels of illegal killing decreased as levels of legal killing increased, which often is expected (Andrén et al. 2006). Here, we also estimate the annual rate of illegal mortality specifically for adult females, which is the demographically most important segment of the population (Sæther et al. 1998). We conclude with an evaluation of the effects of illegal killing on the brown bear population in Sweden.

Study areas

This study was conducted in two areas in Sweden, separated by 600 km. The southern study area, hereafter named the south, was in Dalarna and Gävleborg counties in southcentral Sweden (61º N, 15º E). The rolling landscape in the south is covered with coniferous forest, dominated by Scots pine, *Pinus sylvestris*, or Norway spruce, *Picea abies*. The northern study area, hereafter named the north, was in Norrbotten County in northern Sweden (67º N, 18º E). The landscape is mountainous, with altitudes up to 2,000 m and a subalpine forest dominated by birch, *Betula pubescens*, and willows, *Salix* spp., below the timberline and a coniferous forest of Scots pine and Norway spruce below the subalpine forest. Bears are hunted in both areas, but the northern study area was partially within national parks, where bears were protected.

Methods

We based this study on the fates of radiomarked bears. We captured and immobilized brown bears from a helicopter according to the methods described in Arnemo et al. (1996, 2011). This protocol has been approved by the Swedish Animal Welfare Agency and the Norwegian Experimental Animal Ethics Committee. The bears received either VHF or GPS telemetry units (GPS in recent years) attached to a collar and some of them received an implanted VHF transmitter. We relocated bears with VHF collars from the air or ground at intervals varying from once a week (early in the study period in the south) to a few times a year (late in the study period in the north). We obtained locations of bears with GPS units about every 30 minutes and were received remotely, either via the GSM mobile telephone network (central Sweden) or via satellite (northern Sweden). The first bear was captured and collared in 1984 in the north and in 1985 in the south. The results reported here ended with denning in late autumn 2010. The study area in the south has remained relatively stable during the study period, but the study area in the north was originally confined to the protected national parks, then expanded also to include lower-lying areas adjacent to the protected areas, and now is only outside the protected areas. The reason for this is that all radiomarked bears that had their home ranges within the protected areas are now dead.

We attempted to determine the cause of death for all bears that died while carrying a functioning radio transmitter. This was generally quite easy, but in some cases the bear was located too late to judge the cause of death. This was especially the case in the north late in the study period, when bears were located only about three times a year. We sent the bears we found dead to Sweden's National Veterinary Institute for necropsy. We found few cases of bears that definitely had been killed illegally; in some cases we found illegally killed bears without their collar, but with the implanted transmitter still functioning, or found only the functioning collar that obviously had been handled by humans (see cover photograph). We accepted all bears reported to the authorities by hunters as killed legally to be so. That means that we did not include a bear that had been killed during the hunting season using illegal methods, and reported to the authorities as killed legally. Thus, this report deals with bears that have been killed illegal and not reported to the authorities. In Sweden, all hunters are required to report killed bears to the authorities the day of kill and the carcass must be inspected by an inspector appointed and trained by the wildlife management authorities.

It was more difficult to determine the fate of bears that we lost contact with. We know that people may remove or destroy the collars on bears that they kill illegally, but telemetry units may also malfunction or young bears may emigrate from the study area. We classified a bear we lost contact with as a "suspected illegal killing" if 1) it was a resident bear with an external and internal transmitter and both quit simultaneously, 2) it was a resident bear with a new transmitter that had not shown any signs of malfunction (abnormal or weak signals) and was in an area that we searched often and/or observed snowmobile or other human-made tracks in the same area at the time of disappearance, or 3) we received an anonymous call or message that a specific bear had been killed, when we had not made the loss public. We were restrictive in our judgement of cases of "suspected illegal killing", but we recognize that we could have included some bears that actually were still alive. However, the results of an earlier study suggested that this probability was very low (Swenson and Sandegren 1999). Thus, we included these cases in our calculation of the minimum proportion and rate of illegal killing. All other bears that we lost contact with were classified as "fate unknown".

We classified the documented causes of mortality into the following categories: killed by another bear, capture for research, management (including bears killed on the order of police or wildlife management authorities or by citizens in defense of life or property), legal hunting, traffic, illegal killing, and unknown (including bears that were found dead, but a cause of death could not be accertained). Disappearances were classified as “suspected illegal” for bears where contact was lost under circumstances that gave us a strong suspicion of illegal killing, see above, and “uncertain fate” for bears where contact was lost without specifically suspecting illegal killing. We calculated the minumum proportion of nonresearch deaths due to illegal killing as the proportion of documented and suspected illegal deaths among all deaths, excluding those caused by capture during research and disappearances with uncertain fate. We calculated the maximum proportion as the proportion of documented and suspected illegal deaths and those of uncertain fate among all deaths, excluding those caused by capture during research. We excluded deaths caused by research, because this mortality factor does not occur in the unmarked population of bears, for which we were generalizing our results.

We have recently used multistate capture-recapture models to estimate cause-specific mortality rates for yearlings, subadults (2-4 years old), and adults (≥5 years old) in our two study areas (Bischof et al. 2009). Causes of mortality were divided into legal hunting and other causes. This method allows the inclusion of mortalities that were not detected through radiotelemetry. Bischof et al. (2009) did not specifically report mortality rates due to other causes between areas or sexes, so we used area-specific rates for adult females presented in Bischof & Swenson (2009). Thus, to estimate the annual rate of illegal killing for adult females in each study area, we multiplied the nonhunting annual mortality rate reported by Bischof & Swenson (2009) by the minumum and maximum estimates of the proportion of this mortality that was due to illegal killing. Here we used proportions of nonhunting deaths due to illegal killing, which was different than the nonresearch deaths calculated above, to correspond with Bischof et al. (2009), who included research-caused deaths. The minimum estimate of illegal killing among nonhunting mortality was the proportion of documented and suspected illegal deaths among all deaths, excluding those caused by hunting and disappearances with uncertain fate. The maximum was the proportion of documented and suspected illegal deaths and those of uncertain fate among all deaths, excluding those caused by hunting.

We tested for differences in frequency data using χ^2 tests in SigmaStat, version 1.0. We used Yate’s correction for 2x2 contingency tables.

Results

We were able to record the death or disappearance of 305 bears while they were carrying functioning radiotransmitters; 198 in the south (Table 1) and 107 in the north (Table 2). The proportion of nonresearch deaths attributable to illegal killing varied between 4.1-26.9% in the south and 44.8-58.6% in the north (Table 3), based on the criteria described in the methods. The frequency of illegal killing (known and suspected) compared with other causes of death (research related deaths and uncertain fates) was highly significantly higher in the north (44.8%, N=67) than in the south (4.1%, N=147; χ^2_c= 51.6, df=1, p<0.0001).

The occurrence of documented and suspected illegally killed bears was evenly spread from April to August in the south (Fig. 1). In the north, however, there was a sharp peak in June and another peak in the autumn (September-November) (Fig. 1).

We know from earlier research that the mortality rate due to legal hunting has increased from 1984-1997 to 1998-2006 in the southern study area, due to increases in hunting quotas, but not in the northern study area, where hunting quotas remained stable (Bischof et al. 2009). To determine whether we could detect this change in our data, we compared the frequency of hunter-killed bears and bears that died due to all other causes of death (excluding capture for research and disappearance with uncertain fate) between these

Table 1. Causes of death of brown bears with functioning radio transmitters by age and sex category and period in the southern study area in Sweden, 1985-2010. “Management” included bears killed on the order of police or wildlife management authorities or by citizens in defense of life or property. “Unknown” included bears that were found dead, but a cause of death could not be accertained. “Suspected illegal” included bears where contact was lost under circumstances that gave us a strong suspicion of illegal killing. “Uncertain” included bears that where contact was lost without suspecting illegal killing. The total column includes 3 males of unknown age in the “uncertain fate” category from 1997 and before.

Cause of death	Males						Females						Total
	≤ 1997			≥1998			≤ 1997			≥1998			
	1 yr	2-4	≥5	1 yr	2-4	≥5	1 yr	2-4	≥5	1 yr	2-4	≥5	
Other bear	1	2					4			10	2	3	22
Capture		1	1		1			1	1				5
Management	1	2	2		3	1	1					2	12
Hunting		1	2		8	16	1		2	9	20	37	96
Traffic		1				1						1	3
Unknown				1	1						4	2	8
Illegal		1				1			1	1	1	1	6
Suspected illegal													0
Uncertain fate		2	2	1	7	4	2	1	2		16	6	46
Total	**2**	**10**	**7**	**2**	**20**	**23**	**8**	**2**	**6**	**20**	**43**	**52**	**198**

Table 2. Causes of death of brown bears with functioning radio transmitters by age and sex category and period in the northern study area in Sweden, 1984-2010. “Management” included bears killed on the order of police or wildlife management authorities or by citizens in defense of life or property. “Unknown” included bears that were found dead, but a cause of death could not be accertained. “Suspected illegal” included bears where contact was lost under circumstances that gave us a strong suspicion of illegal killing. “Uncertain” included bears that where contact was lost without suspecting illegal killing. The total column includes 1 male of unknown age in the “uncertain” category from 19987 and after.

Cause of death	Males						Females						Total
	≤ 1997			≥1998			≤ 1997			≥1998			
	1 yr	2-4	≥5	1 yr	2-4	≥5	1 yr	2-4	≥5	1 yr	2-4	≥5	
Other bear	1	2										2	5
Capture								1				2	3
Management					1						2	5	8
Hunting		2	1		3	2		2			2	4	16
Traffic													
Unknown	2	1			1	1	2	1		2		4	14
Illegal					1							1	2
Suspected illegal	1	3	3	1		3	1	1	4	1	5	5	28
Uncertain	1	6	1		6	3				1	2	10	31
Total	**5**	**14**	**5**	**1**	**12**	**9**	**3**	**5**	**4**	**4**	**11**	**33**	**107**

Table 3. Causes of death of brown bears with functioning radio transmitters in the southern and northern study areas in Sweden, 1984-2010, expressed in percent. This is a summary of Tables 1 and 2. The percentages shown in bold were used to estimate the minimum and maximum proportions of illegal killing among nonresearch deaths.

Cause of death	South			North		
	All	Without capture	Without uncertain fate, or capture	All	Without capture	Without uncertain or capture
Other bear	11.1	11.4	15.0	4.7	4.8	7.5
Capture	2.5			2.8		
Management	6.1	6.2	8.2	7.5	7.7	11.9
Hunting	48.5	49.7	65.3	15.1	15.4	23.9
Traffic	1.5	1.6	2.0	0	0	0
Unknown cause	4.0	4.1	5.4	13.1	13.5	20.9
Illegal	3.0	**3.1**	**4.1**	1.9	**1.9**	**3.0**
Suspected illegal	0	**0**	**0**	26.2	**26.9**	**41.8**
Uncertain fate	23.2	**23.8**		29.0	**29.8**	
Sample size	198	193	147	107	104	67

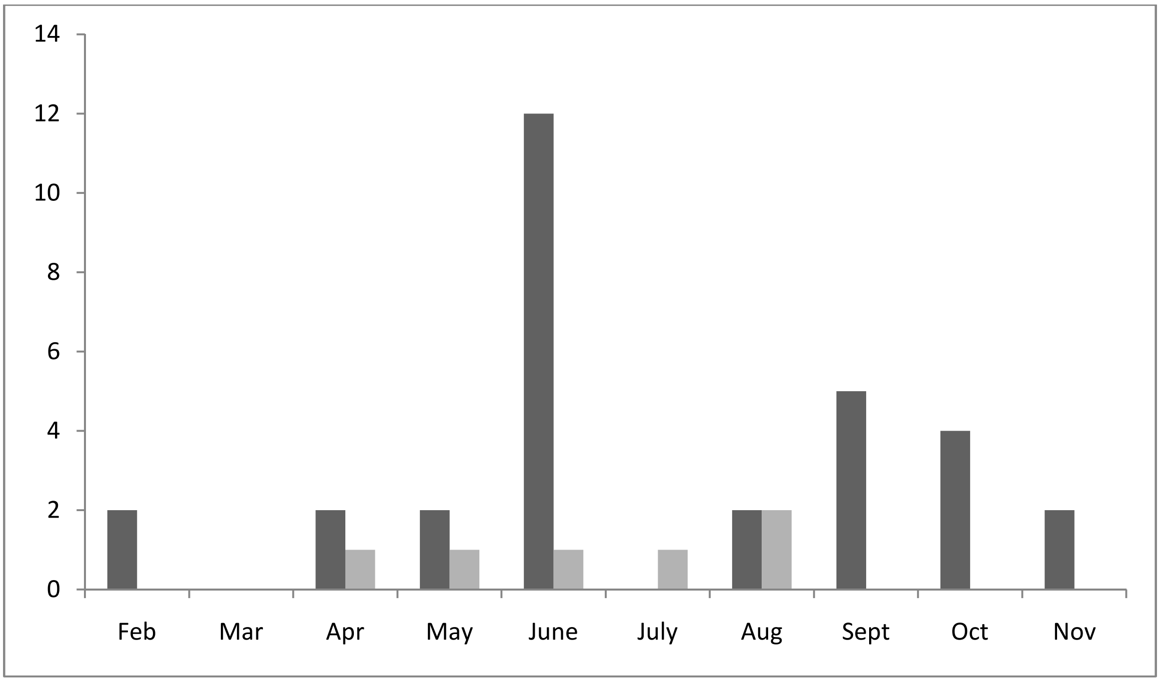


Fig. 1. Month that a brown bear was documented or suspected killed illegally in the northern (black) and southern (gray) study areas in Sweden and Norway. Especially for suspected illegal killing, the event may have occurred somewhat earlier than shown here.

two periods. As expected, based on the results of Bischof et al. (2009), we found a significant difference in the frequency of hunting deaths in the south between 1985-1997 (27%, N=22) and 1998-2010 (72%, N=125, χ^2_c= 14.6, df=1, p=0.0001). Also as expected, based on the results of Bischof et al. (2009), there was no significant difference in the frequency of hunting deaths in the north between 1984-1997 (18%, N=27) and 1998-2010 (14%, N=80, χ^2_c= 0.60, df=1, p=0.81).

We then compared the frequency of illegally killed bears (documented and suspected) with that of bears that died due to all other causes of death (excluding hunting, capture for research, and disappearance with uncertain fate) between the two periods. We found no significant difference in the frequency of illegal deaths in the north between 1984-1997 (59%, N=22) and 1998-2010 (49%, N=35, χ^2_c= 0.25, df=1, p=0.62). We found the same result in the south, comparing 1985-1997 (12%, N=16) with 1998-2010 (11%, N=35, Fisher's exact test, p=1.00). We therefore conclude that the rate of illegal killing has not changed between these two periods in either study area.

Based on the results of this test, we combined the data from both periods and compared the frequency of illegally killed bears (documented and suspected) with that of bears that died due to all other causes of death (excluding hunting, capture for research, and disappearance with uncertain fate) between the sexes. We found no differences between the proportion of illegally killed bears among males (57%, N=21) and females (50%, N=36) either in the north (χ^2_c= 0.060, df=1, p=0.81) or the south (males 11%, N=18; females (12%, N=33; Fisher's exact test, P=1.00). Therefore we combined the sexes to test for age differences. We did not find age differences in the frequency of illegally killed bears in either the north (yearlings, 36%, N=11; subadults, 56%, N=18; adults, 57%, N=28; χ^2= 1.46, df=2, p=0.48) or the south (yearlings, 5%, N=19; subadults, 12%, N=17; adults, 20%; χ^2= 1.75, df=2, p=0.42).

We multiplied estimates of the proportion of nonhunting deaths attributable to illegal killing (10.7-51.0% in the south and 50.0-67.1% in the north; Table 4) by the annual nonhunting mortality rates for adult females during 1998-2007 in the south (1.2%, 95% confidence intervals = 0.3-3.0%) and in the north (4.6%, 2.5-7.1%) reported in Bischof & Swenson (2009). From this, we estimated annual rates of illegal mortality among adult females to be 0.1-0.6% in the south and 2.3-3.1% in the north.

Table 4. Causes of death of brown bears with functioning radio transmitters in the southern and northern study areas in Sweden, 1984-2010, expressed in percent. This is a summary of Tables 1 and 2. The percentages shown in bold were used to estimate the minimum and maximum proportions of illegal killing among nonhunting deaths for calculation of the mortality rates due to illegal killing.

Cause of death	South			North		
	All	Without hunting	Without uncertain fate, or hunting	All	Without hunting	Without uncertain fate, or hunting
Other bear	11.1	21.6	39.3	4.7	5.5	8.3
Capture	2.5	4.9	8.9	2.8	3.3	5.0
Management	6.1	11.8	21.4	7.5	8.8	13.3
Hunting	48.5			15.1		
Traffic	1.5	2.9	5.4	0	0	0
Unknown cause	4.0	7.8	14.3	13.1	15.4	23.3
Illegal	3.0	**5.9**	**10.7**	1.9	**2.2**	**3.3**
Suspected illegal	0	**0**	**0**	26.2	**30.8**	**46.7**
Uncertain fate	23.2	**45.1**		29.0	**34.1**	
Sample size	198	102	56	107	91	60

Discussion

We did not find any statistically significant differences in frequency of illegally killed bears compared to other causes of mortality based on age class, sex, or study period. There was, however, a highly significant difference between study areas. We estimated that the proportion of nonresearch deaths attributable to illegal killing was between 4.1-26.9% in the south and 44.8-58.6% in the north. We calculated the rate of illegal killing for adult females to assess its impact on the population (Sæther et al. 1998). The estimated annual rate of illegal mortality among adult females was minimal in the south, 0.1-0.6%, but much higher in the north, 2.3-3.1%. These results were supported by findings of Bischof et al. (2009) that the recapture probability of newly dead bears without functioning transmitters was higher in the south than in the north and that their second-best model showed that the mortality rate due to factors other than legal hunting was slightly lower in the south. In an analysis of causes of brown bear mortality in Scandinavia from 1984-1998, Swenson and Sandegren (1999) found that the annual rate of illegal mortality was 4-5 times higher in the north than in the south. This difference is still evident. Andrén et al. (2006) found the highest illegal mortality among radiomarked Eurasian lynx in four study areas in Scandinavia to be in the same northern study area. Similarly, Persson et al. (2009) found a substantial rate of illegal mortality among wolverines in this same area. There seems to be no question that the illegal killing of large carnivores is high in this specific area, but it is difficult for us to determine how widespread the phenomenon is for bears.

There was also a difference in the seasonal pattern of illegal deaths between the south and north. Whereas there was no obvious pattern in the south, there was a sharp peak in June in the north. The June peak includes bears that we could not relocate in June and we suspected had been killed illegally. Some of these may have been killed in May. Especially May is an important period of bear predation on reindeer calves and most suspected illegally killed bears were last located on reindeer calving grounds. The peak in the autumn corresponds with the hunting season.

Although the rate of illegal killing was higher in the north, it did not seem to occur at a level that was causing a general population decline. Bischof & Swenson (2009) reported that the population in the southern study area could sustain an annual female hunting mortality of 11.2% (95% CI: 8.2% - 13.5%), compared with 12.7% (95% CI: 10.4% - 14.5%) in the northern study area, when accounting for nonhunting mortality. The present harvest rate is far below that in the northern study area, but not in the south (Bischof & Swenson 2009). In addition, the brown bear population in Sweden as a whole has been growing at an average instantaneous rate of 0.045 during 1998-2007 (Kindberg et al. 2011) and densities of brown bears are increasing in many areas with formerly lower densities, both in the north and south (Kindberg 2010). Only two Swedish counties have not shown significant rates of growth in this period; Dalarna, where our southern study area is located, and Västerbotten, which is in northern Sweden, but south of our study area (Kindberg et al. 2011). Thus, we conclude that illegal killing is generally not a limiting factor for the brown bear population in Sweden, but that it can be an important factor locally, such as in the northern study area.

Bischof et al. (2009) did not report area-specific rates of nonhunting mortality for adult males, because their models indicated that there was no significant difference. Nevertheless, earlier studies have suggested a reduced occurrence of adult males in the northern study area, presumably due to a higher rate of illegal killing there, compared with the southern study area (Swenson et al. 2001). This appears to have had life-history effects on the population, with higher rates of sexually selected infanticide in the south (Swenson et al. 2001) and a higher reproductive success among younger males in the north than in the south (Zedrosser et al. 2007). Presumably due to the lack of older males in the north, estrous females there selected the larger young males for mating, whereas in the south, they chose older males (Bellemain et al. 2006). Thus, illegal killing may impact the life-history traits and not just the size or trends of a brown bear population.

We did not find a difference in the frequency of illegally killed bears and other nonresearch and nonhunting mortality causes when comparing the periods <u><</u>1997 and <u>></u>1998 in either study area. A comparison of the frequency of hunter-killed bears did show a difference between periods for the south, but not for the north, similar to what Bischof et al. (2009) found in a more sophisticated analysis based primarily on the same data. We conclude that the rate of illegal killing has not changed over the study period and that it was not related to the mortality rate due to legal hunting. Andrén et al. (2006) also found that there was not a simple inverse relationship between rate of legal harvest and poaching for Eurasian lynx in Scandinavia, although this relationship commonly is expected. However, we do not know if future changes in the way management deals with bears that depredate reindeer will affect the rate of illegal killing.

Bischof et al. (2009) concluded that hunting mortality was additive to other forms of mortality in Scandinavian brown bears. The apparent lack of relationship between harvest rate and illegal killing suggests that this might also hold for illegal killing. Thus, when managers set hunting quotas, they must be aware that illegal killing may come in addition to the legal mortality. This may be especially important in areas where managers suspect the rate of illegal mortality to be high.

We found strong evidence of a spatial difference in rates of illegal killing of brown bears within Sweden. The rate of illegal killing was high in our northern study area, but the bear population is increasing and expanding in many areas in northern Sweden. It is therefore important to identify the areas where illegal killing is common. This is probably not easy to do. However, one possible method to evaluate this would be to examine the changes in distribution of hunter-killed females over time. Given that the population has been increasing generally, one might suspect a higher rate of illegal killing in areas where the occurrence of hunter-killed females has declined over time, unless other reasonable factors could explain it. One could compare changes in the distribution of hunter-killed females between mountainous and forested areas within the reindeer raising area, for example. Another possible method might be to use mark-capture-recapture techniques, based on the individually-identified bears in the sca-based population estimates, to estimate total mortality rates in areas where two scat surveys have been conducted. Such data are now available for Västerbotten and Norway, and may soon be available from other Swedish counties.

It is very difficult to document illegal killing, primarily because it is illegal. We believe that our minimum and maximum estimates have bracketed the true values of the proportion and rate of illegal killing. Nevertheless, there are several sources of bias beyond documenting the deaths. For example, the fact that people know that animals are radiomarked in an area may reduce illegal mortality, to avoid being caught or alerting the authorities of this activity. However, it may also increase illegal mortality, if the poachers have access to equipment that helps them locate radioed animals. They might destroy the transmitter(s) after killing the animal, or report it as legally killed, if killed during the hunting season. In the latter case, they would not be included in our estimates. Our study area has remained quite stable during the study period in the south. In the north, however, the distribution of radiomarked animals has moved from the protected areas to now almost completely outside them, due partially to documented and suspected illegal killing within the protected areas. Thus, we did not estimate illegal killing within the same areas during the two time periods, which also could be a source of bias.

Literature Cited

Anderson, A. L. 2001. Use of GIS to study brown bear, *Ursus arctos*, distribution in relation to habitat and traditional reindeer (*Rangifer tarandus*) herding in Scandinavia. Master of Science thesis, University of Stirling, UK.

Andrén, H., J. D. C. Linnell, O. Liberg, R. Andersen, A. Danell, J. Karlsson, J. Odden, P. F. Moa, P. Ahlqvist, T. Kvam, R. Franzén, and P. Segerström. 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation 131:23-32.

Arnemo, J. M., P. Ahlqvist, R. Andersen, F. Berntsen, G. Ericsson, J. Odden, S. Brunberg, P. Segerström, and J. E. Swenson. 2006. Risk of capture-related mortality in large free-ranging mammals: experiences from Scandinavia. Wildlife Biology 12:109-113.

Arnemo, J. M., A. Evans & Å. Fahlman, (editors), Ahlqvist, P., Andrén, H., Brunberg, S., Liberg, O., Linnell, J. D. C., Odden, J., Persson, J., Sand, H., Segerström, P., Sköld, K., Strømseth, T. H., Støen, O.-G., Swenson, J. E & Wabakken, P. 2011. Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Report to the Directorate for Nature Management, Trondheim, Norway.

Bellemain, E., A. Zedrosser, S. Manel, L. P. Waits, and J. E. Swenson. 2006. The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide. Proceedings of the Royal Society London, Series B. 273 283 – 291.

Bischof, R. and J. E. Swenson. 2009. Preliminary predictions of the effect of increasing hunting quotas on brown bear population growth in Sweden. Report No. 2009-3 from the Scandinavian Brown Bear Research Project.

Bischof, R., J. E. Swenson, N. G. Yoccoz, A. Mysterud, and O. Gimenez. 2009. The magnitude and demographic selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. Journal of Animal Ecology 78:656-665.

Kindberg, J. 2010. Monitoring and management of the Swedish brown bear (*Ursus arctos*) population. PhD thesis, Swedish University of agricultural Sciences, Umeå.

Kindberg, J., J. E. Swenson, G. Ericsson, E. Bellemain, C. Miquel, and P. Taberlet. 2011. Estimating population size and trends of the Swedish brown bear (*Ursus arctos*) population**.** Wildlife Biology: in press.

Liberg, O., H. Sand, H. C. Pedersen & P. Wabakken. 2008. Dödlighet och illegal jakt i den skandinaviska vargstammen. Viltskadecenter Rapport nr 1 / 2008.

Persson, J., G. Ericsson, and P. Segerström. 2009. Human caused mortality in the endangered Scandinavian wolverine population. Biological Conservation 142:325-331.

Swenson, J. & F. Sandegren. 1999. Misänkt illegal björnjakt i Sverige. Pages 201-206 in Bilagor till Sammanhållen rovdjurspolitik; Slutbetänkande av Rovdjursutredningen. Statens offentliga utredningar 1999:146. Stockholm, Sweden.

Swenson, J. E., F. Sandegren, S. Brunberg, and P. Segerström. 2001. Factors associated with loss of brown bear cubs in Sweden. Ursus 12: 69-80.

Sæther, B. E., S. Engen, J. E. Swenson, Ø. Bakke, and F. Sandegren. 1998. Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: the effects of uncertain parameter estimates. Oikos 83:403-416.

Woodroffe, R. and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126-2128.

Zedrosser, A., E. Bellemain, P. Taberlet, and J. E. Swenson. 2007. Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age heterozygosity and population density. Journal of Animal Ecology 76:368-375.

Mortality and poaching of lynx in Sweden

Dödlighet och illegal jakt på lodjur i Sverige

Henrik Andrén, Gustaf Samelius, Peter Segerström, Kent Sköld, Geir-Rune Rauset and Jens Persson

Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences (SLU), SE - 730 91 Riddarhyttan, Sweden.

Corresponding author:
Henrik Andrén
Tel: 0581-69 73 02
E-mail: henrik.andren@slu.se

A report to World Wide Fund for Nature, (Sweden)

Mortality and poaching of lynx in Sweden

Henrik Andrén, Gustaf Samelius, Peter Segerström, Kent Sköld, Geir-Rune Rauset and Jens Persson

Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences (SLU), SE - 730 91 Riddarhyttan, Sweden.

The views in this report are the authors, and may not necessary be the ones of WWF.

ABSTRACT

We described causes of mortality and survival rate for 216 radio-marked Eurasian lynx (*Lynx lynx*) followed for 621 radio-years in two different study areas in Sweden. The northern study area was located in the county of Norrbotten around Kvikkjokk and the southern study area was located mainly within northern Örebro county. The main causes of mortality in adult Eurasian lynx in both study areas were anthropogenic, with starvation, intraspecific killing and disease having only a minor role. In the northern study area poaching and assumed poaching were the main cause of mortality in adult lynx (79 % of the mortality events), whereas poaching (including assumed poaching) and natural causes were equally important in subadults (45 %). In the southern study area natural causes, hunting and traffic were the main causes of mortality (62 % for these factors combined) and accounted for about twice the mortality caused by poaching and assumed poaching (29 %). The poaching rate (including assumed poaching) was significantly higher ($p<0.001$) in the northern study area (11.1 % ± 2.2 % SE) than in the southern study area (3.4 % ± 1.5 % SE). The estimated poaching rates were not significantly different between the two periods (1994-1999 versus 2000-2010) in neither the northern ($p=0.94$) nor the southern ($p=0.15$) study area. The estimated growth rates based on demographic data were not significantly different ($p=0.30$) from the observed change in the lynx population in either study area. Thus, the estimated rates of mortality (including assumed poaching) were probably not overestimated. If the two study areas are representative for the reindeer husbandry area and the area south of the reindeer husbandry area in Sweden, respectively, then the estimated number of lynx poached in the reindeer husbandry area would be around 77 lynx (± 16 lynx SE) per year and around 22 lynx (± 10 lynx SE) per year south of the reindeer husbandry area. To conclude, poaching is an important cause of mortality in lynx in Sweden, especially in the northern study area, and the poaching rate does not seem to have changed between two periods (1994-1999 versus 2000-2010).

Dödlighet och illegal jakt på lodjur i Sverige

Henrik Andrén, Gustaf Samelius, Peter Segerström, Kent Sköld, Geir-Rune Rauset och Jens Persson

Grimsö forskningsstation, Institutionen för ekologi, Sveriges Lantbruksuniversitet (SLU), 730 91 Riddarhyttan.

SVENSK SAMMANFATTNING

Den här studien beskriver dödsorsaker och överlevnad hos 216 radiomärkta lodjur (*Lynx lynx*) som har följts under 621 radio-år i två olika studieområden i Sverige. Det nordliga studieområdet ligger Norrbottens län i Kvikkjokk fjällen. Medan det sydliga studieområdet främst ligger i norra Örebro län. Dödsorsakerna hos vuxna lodjur var främst av mänsklig orsak (jakt, trafik och illegal jakt). I det nordliga området var illegal jakt (inklusive förmodad illegal jakt) den främsta dödsorsaken hos vuxna lodjur (79 % av dödsfallen), med illegal jakt (inklusive förmodad illegal jakt) var ungefär lika viktigt som naturliga dödsorsaker hos yngre lodjur (45 %). I det södra området var naturliga dödsorsaker, jakt och trafik de främsta dödsorsakerna (62 % för dessa tillsammans) och var ungefär dubbelt så stor som illegal jakt och förmodad illegal jakt (29 %). Den illegala jakten (inklusive förmodad illegal jakt) var signifikant högre ($p<0.001$) i det nordliga området (11.1 % ± 2.2 % SE) jämfört med det södra området (3.4 % ± 1.5 % SE). Den illegala jakten var inte signifikant olika mellan de två studieperioderna (1994-1999 jämfört med 2000-2010) i varken det nordliga ($p=0.94$) eller det sydliga området ($p=0.15$). Den beräknade tillväxttakten baserat på demografisk data (reproduktion och överlevnad) var inte signifikant skild från de observerade populationsförändringarna i respektive område ($p=0.30$). Därför är de beräknade mortalitetsvärdena antagligen inte överskattade. Om de båda studieområdena är representativa för renskötselområdet respektive söder om renskötselområdet, då är det beräknade antalet illegalt skjutna lodjur 77 (± 16 SE) per år i renskötselområdet och 22 (± 10 SE) per år söder om renskötselområdet. Sammanfattningsvis är illegal jakt på lodjur en viktig dödsorsak hos lodjur i Sverige, speciellt i det nordliga studieområdet, och den illegala jakten verkar inte har förändrats mellan studieperioderna (1994-1999 jämfört med 2000-2010).

1. INTRODUCTION

Reintegrating large carnivore populations into our modern landscapes is always a difficult task, largely because of the problem with predation on domestic animals and the competition between hunters and large carnivores for common prey (Swenson and Andrén, 2005). In Scandinavia, Eurasian lynx (*Lynx lynx*) occur mainly outside protected areas in the surrounding matrix of multi-use landscapes (Andrén et al. 2010, Linnell et al. 2010) where the potential for diverse conflicts is high. Furthermore, most protected areas in Sweden and Norway are smaller than the home ranges of large carnivores, which mean that the majority of large carnivores occur outside protected areas (Linnell et al. 2001).

Today, lynx are found in most of Sweden (Andrén et al 2010) and in most of Norway except in the southwestern parts (Linnell et al. 2010). In both Sweden and Norway, lynx are found within the Sami reindeer husbandry area, as well as in areas with sheep herding. In the reindeer husbandry area semi-domestic reindeer (*Rangifer tarandus*) are the main prey for lynx (Pedersen et al. 1999, Sunde et al. 2000, Mattisson 2011). In areas outside the reindeer husbandry area roe deer (*Capreolus capreolus*) are the main prey (Nilsen et al. 2009), but sheep (*Ovis aries*) are also preyed upon in these areas (Odden et al. 2002).

The rate of increase of large carnivore populations is most sensitive to changes in adult mortality (Sæther et al. 1998, 2005, 2010). Hunting mortality on large carnivores is often additive to other mortality (Swenson et al. 1997, Krebs et al. 2004, Linnell et al. 2010). Thus, from a conservation and management point of view it is very important to identify the primary causes of mortality. Furthermore, poaching has often been shown to be a major mortality factor in large carnivore populations (Andrén et al. 2006, Persson et al. 2009), and can potentially prevent the recovery of species with low or moderate rates of increase, especially for species that occur at low densities.

We have previously estimated the poaching rate of lynx (Andrén et al. 2006). Therefore, the aims with this report were to update the knowledge about poaching of lynx and to test whether the poaching has changed over the years.

2. STUDY AREAS

The study is based on radio-marked lynx from two different study areas in Sweden. The northern study area (Sarek; 8000 km^2) is located in the county of Norrbotten around Kvikkjokk (67°00’ N, 17°40’ E). Part of the area is within Sarek National Park (2600 km^2) and the Laponia World Heritage Site. The study area ranges from coniferous forest (Norway spruce, *Picea abies* and Scots pine, *Pinus sylvestis*) in the eastern parts (about 300 m. a.s.l.), through mountain birch forest (*Betula* sp.) and mountain meadows to high alpine areas with peaks around 2000 m a.s.l. and glaciers. The tree line is at about 800 m a.s.l. The area is located within the Sami reindeer husbandry area and includes the reindeer management units: mainly Tuorpon, Jåhkågasska and Sirges, but also parts of Luokto-Mávas and Sörkaitum. In addition to lynx, the study area also has reproducing populations of wolverines (*Gulo gulo*) and brown bear (*Ursus arctos*) that are also studied. Reindeer is the main prey for lynx in the area. Data on lynx survival for this study has been collected from 1994 to 2010.

The southern study area is about 8000 km^2 and is located around Grimsö wildlife research station (59°30' N, 15°30' E) in the Bergslagen region, mainly in Örebro county but also Västmanland, Värmland and Dalarna counties. The area is dominated by coniferous forest (Norway spruce and Scots pine) that is intensively managed for timber and pulp. The study area ranges from 30 to 500 m a.s.l. The proportion of agricultural land is higher in the southern parts (about 20 %) and decreases towards the northern parts (< 1 % of the area). In addition to lynx, the study area also has reproducing population of wolves (*Canis lupus*) that is also studied. Roe deer is the main prey for lynx in the area. Some lynx dispersed southwards and established in southernmost Sweden. In 2002, we also started to capture lynx in southernmost Sweden. We pooled the individuals from the Bergslagen region and southernmost Sweden in the survival analyses, as the sample size was too small for southernmost Sweden. Data on lynx survival for this study has been collected from 1996 to 2010.

3. METHODS

3.1. Capturing and types of collars

This study is based on radio-collared lynx. Young lynx were generally captured in February, when they were still together with their radio-marked mothers. Adult lynx were captured during autumn, winter and spring. Recaptures of radio-marked lynx were performed year round to replace old transmitters. Lynx were live-captured using a variety of methods, including darting from helicopter, unbaited walk-through box-traps, foot-snares placed at fresh kills, or treed with the use of dogs. The lynx were immobilised with a mixture of ketamine (5 mg/kg) and medetomidine (0.2 mg/kg) and equipped with either a radio-collar and/or an implanted transmitter. In late May – early June we intensively radio-tracked lynx females to confirm reproduction. We marked and counted the number of kittens found in the lair. The capturing and marking of lynx follow a pre-established protocol (Arnemo et al. 2011) that has been examined by the Swedish Animal Ethics Committee and fulfils the ethical requirements for research on wild animals.

We used two types of radio-transmitters in this study; from the beginning of the study to 2002 we only used VHF-collars, from 2002 we use both VHF- and GPS-collars. The lynx with VHF-collars were generally radio-tracked at least twice a month, usually more often. Most of the transmitters had a mortality function, which enhanced our chances of determining the fate of the lynx. Some lynx were marked with an implanted VHF-transmitter in addition to the GPS-collar to allow for long-term monitoring, as the battery-life of the VHF-implants are considerable greater than the battery-life of GPS-collars. In GPS/GSM-collars there was a mortality function that sent an SMS if the collar had not moved during 4 hours.

3.2. Determining cause of mortality in radio-marked lynx

The lynx carcasses, if found, were carefully examined in the field and then sent to the Swedish National Veterinary Institute for examination of the cause of mortality. Cause of mortality was classified as natural (e.g. starvation, sarcoptic mange, wounds from violent interaction with other lynx), traffic (i.e. lynx carcass found very close to a road showing violent death or direct report of car accident), harvest (i.e. lynx being shot during the legal hunting season), poaching (see below), assumed poaching (see below), or unknown cause of mortality (i.e. lynx confirmed dead but the cause of mortality could not be determined).

Poaching is generally very difficult to quantify. However, it was sometimes easy to conclude that the lynx was illegally shot, as when the lynx carcass was found with a gunshot wound or when the radio-transmitter was found smashed or had been cut off the lynx and thrown/hidden in a location where lynx do not naturally occur (e.g. in a river). We also considered that the lynx was illegally shot if the individual had two separate transmitters, i.e. one radio-collar and one implanted radio-transmitter, and both of the transmitters failed at the same time and we had been radio-tracking the area carefully after the disappearance.

However, lost contact with the radio-transmitter can result from several reasons, 1 – the lynx has been poached and the transmitter has been destroyed, 2 – the lynx has dispersed and we have lost contact with the individual, 3 – the transmitter has failed. Therefore, we used several criteria to separate between assumed poaching and unknown disappearance (such as rapid long distance dispersal or transmitter failure). We assume poaching if a resident adult lynx suddenly disappeared and we had been radio-tracking the area carefully from the air immediately after the disappearance. Furthermore, there had to be no signs of technical problems with the radio-transmitter (e.g. strange or weak signals) before the disappearance, and that at least half of the expected lifetime of the radio-transmitter was still available. Young lynx that had not established their own home range and were in the phase of dispersal were classified as assumed poaching if the disappearing lynx had a new radio-transmitter, we had followed parts of the dispersal phase, i.e. we had a dispersal direction, and we had been radio-tracking the area carefully from the air immediately after the disappearance. Otherwise, the lynx was classified as unknown fate.

3.3 Methods for estimating survival

Survival rates of radio-marked lynx were calculated using the staggered entry design, which is a modified Kaplan-Meier estimate (Pollock et al. 1989, R-development core team 2010, R library *survival*). We estimated survival for two age classes (subadults and adults), for the two study areas. The subadult age class included lynx from 6 months of age to the age of 2 years, and adults were lynx older than 2 years. We did not include lynx younger than 6 months in our analyses because of very limited data for this age category. We estimated two survival rates. The first rate included all mortality and the second rate excluded poaching and assumed poaching. The effect of poaching and assumed poaching on survival rate was estimated using competing risk models and cumulative proportional hazard (R library *cmprsk)*.

4. RESULTS

4.1. Cause of mortality in radio-marked individuals.

In the northern study area we followed 99 individuals for 326 radio-years. We determined the cause of mortality for 39 of these individuals (including assumed poaching). We lost contact with an additional 47 individuals for which we were not able to determine the cause of disappearance. The main cause of mortality for adult in the northern study area was poaching and assumed poaching (79 %). The second most important cause of mortality was natural causes adults (18 %; Table 1 and Figure 1). For subadults poaching (45 %) and natural causes (45 %) were equally important (Table 1 and Figure 1).

Table 1. Cause of mortality in radio-marked lynx in the two study areas in Sweden in 1994 to 2010.

Area	Age (years)	Natural	Traffic	Hunting	Poaching	Assumed poaching	Unknown cause of mortality	Unknown fate
North	0.5-2	5	0	0	0	5	1	28
	> 2	5	0	1	5	17	0	19
South	0.5-2	2	6	2	5	1	1	14
	> 2	7	3	8	4	3	3	42
Total	All	19	9	11	14	26	5	103

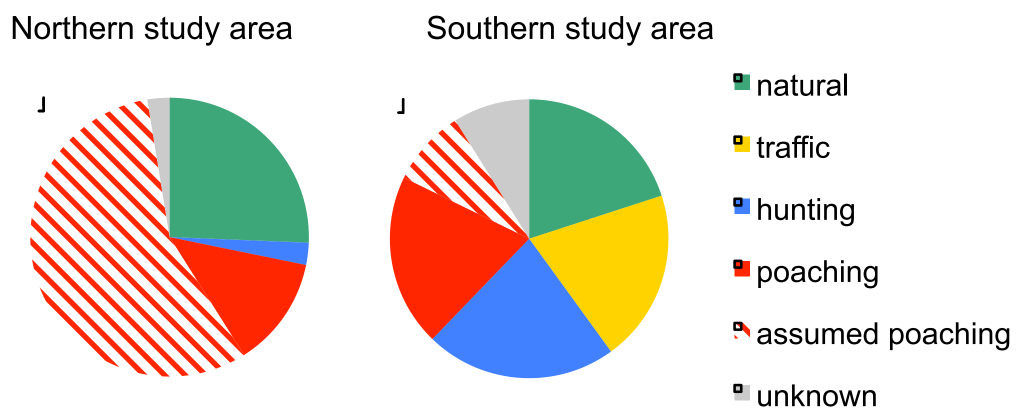


Figure 1. Causes of mortality in lynx in the northern study area (left, n=39) and in the southern study area (right, n=45) in 1994 to 2010.

In the southern study area we followed 117 individuals for 295 radio-years. We determined the cause of mortality for 45 of these individuals (including assumed poaching). We lost contact with an additional 56 individuals for which we were not able to determine the cause of disappearance. In the southern study area natural causes, hunting and traffic caused the majority of mortality (62 % for these factors combined) with poaching and assumed poaching accounting for 35 % of the cause of mortality in subadults and 25 % in adults (Table 1 and Figure 1).

In the northern study area the number of poached lynx was higher in later winter/early spring, as well as in autumn (Figure 2). In the southern study area there was no clear seasonal differences in number of poached lynx, but the number of dead lynx was higher in February and March, because of legal hunting (Figure 2).

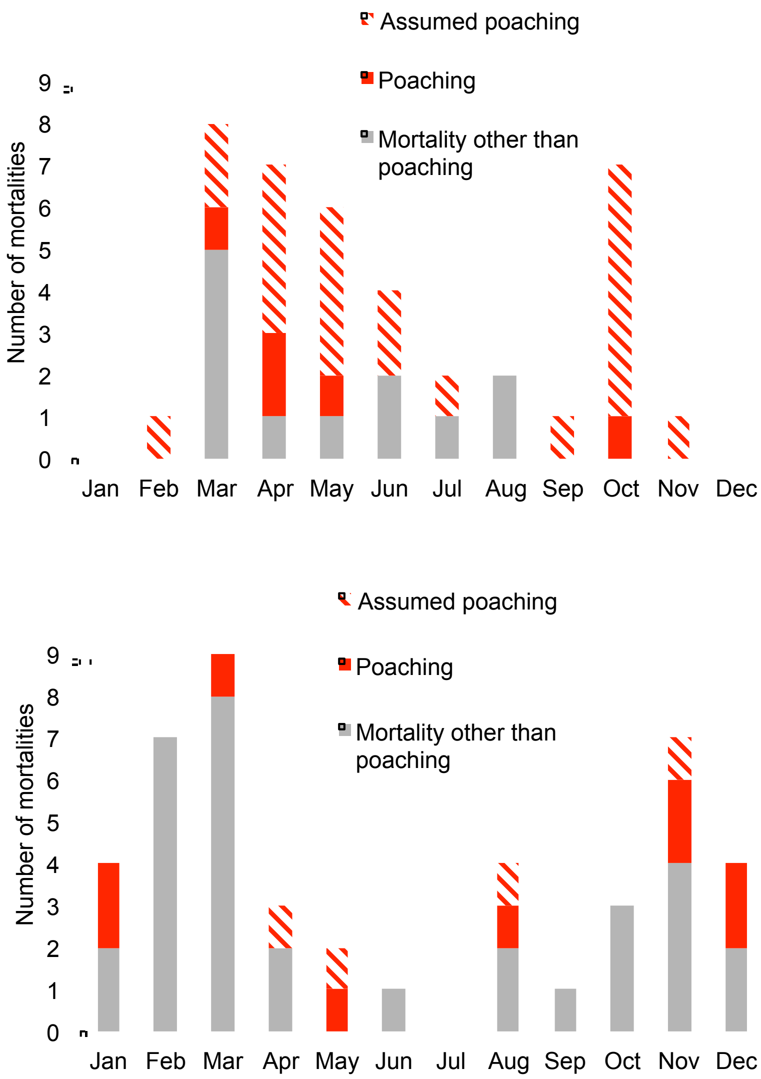


Figure 2. Number of mortalities of radio-marked lynx in relation to the month of the year in the northern study area (upper graph) and in the southern study area (lower graph) in 1994 to 2010.

4.2. Annual survival for radio-marked individuals

The mean annual survival for subadults was lower than for adults in both study areas (Table 2), whereas there was no significant difference in overall survival between the two study areas (χ^2=1.2, df=1, p=0.28, Table 2).

The estimated poaching (including assumed poaching) was significantly higher in the northern study area when compared to the southern study area (competing risk regression, p<0.001). However, the estimated poaching was not significantly different between the two periods (1994-1999 versus 2000-2010) in neither the northern (competing risk regression, p=0.94) nor the southern study area (competing risk regression, p=0.15). The average annual poaching rate (including assumed poaching) was 11.1 % (± 2.2 % SE) in the northern study area and 3.4 % (± 1.5 % SE) in the southern study area. The effect of miss-classification of one individual as assumed poached or unknown fate changed the poaching rate by approximately 0.3 %-units.

Table 2. Mean annual survival (±SE) for lynx, separated on two age classes in the two study areas in Sweden in 1994 to 2010.

Area	Age (years)	N (individuals)	N (radio-years)	Annual survival, all mortality (mean ± SE)	Annual survival, excluding poaching and assumed poaching (mean ± SE)
North	0.5 – 2	64	114	0.807 ±0.056	0.854 ± 0.054
	> 2	56	212	0.821 ± 0.031	0.962 ± 0.015
South	0.5 – 2	64	100	0.688 ± 0.058	0.758 ± 0.054
	> 2	78	195	0.793 ± 0.034	0.839 ± 0.032

5. DISCUSSION

The main cause of mortality of lynx in both study areas in Sweden was anthropogenic (hunting, traffic and poaching; Figure 1), with starvation, intraspecific killing and disease only having a minor role. Poaching (including assumed poaching) was quite substantial in the northern area (average annual rate 11.1 %), whereas it was lower in the southern area (average annual rate 3.4 %). However, it is always difficult to estimate poaching. For example, we have verified poaching in both study areas (5 cases in the north and 9 cases in the south), but the overall poaching rate is highly influenced by the number of assumed poaching (22 cases in the north and 4 cases in the south). The estimated poaching rate changes with about 0.3 %-units when one individual was wrongly classified as either assumed poached or unknown fate. Moreover, there were several lynx (47 cases in the north and 56 cases in the south) that disappeared and for which we do not know whether they died, performed long-distance dispersal or the transmitters failed. Thus, most of the lynx that disappeared were not classified as assumed poached. Individuals in the dispersing age group (from 7-8 months of age to almost 2 years old) can be very difficult to follow with radio-transmitters because they might disappear because of long-distance dispersal. Young inexperienced and dispersing individuals are often subjected to higher mortalities than residents (Blankenship et al. 2006). Therefore, one might underestimate the mortality rate in subadults. In the northern study area disappearance from unknown causes was common in subadults. Whereas, in the southern area dispersal of subadults has been one aim of the study so we therefore have fewer lynx that have disappeared from unknown causes.

The poaching rate was significantly higher in the northern study area than in the southern study area. The lynx conflict differs in the two study areas. In the northern study area the conflict is mainly with the reindeer herding industry loosing reindeer to lynx and resulting in a reduction in the harvest of reindeer. In the southern study area, the conflict mainly considers competition with hunters for the same prey, i.e. the roe deer. Thus, an explanation for the difference between the north and south could be a stronger economical incentive for poaching in the northern study area than in the southern study area. However, poaching of large carnivores has several other causes, such as a conflict between “the rulers and the ruled” or between urban and rural areas (Pyka et al. 2007)

We could not detect any change in poaching rate between the two periods (1994-1999 and 2000-2010). During the same period the Swedish EPA has issued hunting quotas on lynx that have lowered the lynx numbers within the reindeer husbandry area. The main reduction of lynx has occurred in Jämtland county. Within Norrbotten county, where our study area is located, neither the growth of the lynx population (mean growth rate in Norrbotten county, $\lambda = 1.0 \pm 0.07$ SE; Andrén et al. 2010) nor the management practices have changed during the study period (harvest rate less than 2 % of the estimated lynx population, until 2010 when it increased to 10 %; Andrén et al. 2010). In the southern study area the lynx population has gone through an increase and then a decrease. The legal hunting quotas have been fairly low during the study period (less than 6 % of the lynx population until 2009 when it increased to 9 %; Andrén et al 2010). Thus, there have not been any major changes in lynx management policy during the last years. Therefore, we cannot evaluate, for example, if there is a relationship between legal harvest and poaching.

We estimated the poaching rate in two study areas in Sweden and an important question that arises is whether these areas are representative for other parts of Sweden. The northern study area is largely located within the mountain range, whereas most of the lynx in the reindeer husbandry area are found within the boreal forest (Andrén et al. 2010). Thus, from a landscape perspective the northern study area is not representative for the entire reindeer husbandry area. Poaching in the northern study area was higher in later winter/early spring, probably because the snow conditions make it possible to cover large areas with snowmobiles. This might result in a higher poaching rate in the mountain range with good snow cover late into the spring. On the other hand, the rugged slopes in the mountains might be areas where lynx can escape poaching and rugged slopes are also preferred habitat for lynx (Mattisson 2011). The research activities in the area might decrease the poaching risk. Thus, it is difficult to determine whether the poaching rate in the northern study area is higher or lower than in other parts of the reindeer husbandry area.

The southern study area is completely dominated by boreal forest with small and scattered patches of agricultural land that is typical for south-central Sweden. Thus, the southern study area is a fairly good representation of the landscape where most lynx south of the reindeer husbandry area are found. On the other hand, the attitudes towards lynx vary quite a lot among different municipalities in Sweden (Ericsson and Sandström 2005). The poaching rate might therefore vary among areas because of different attitudes towards them and not because of ecological factors, like lynx density, roe deer density or landscape composition. Thus, it is difficult to evaluate whether the southern study area was representative for other areas in south-central Sweden, especially for poaching, as it is very hard to study.

Andrén et al. (2006) estimated the annual growth rate of the lynx population in the northern study area to be 7% ($\lambda = 1.07 \pm 0.071$ SE) based on demographic data. However, this growth rate was not significantly different from stable population growth (i.e. $\lambda = 1$; p=0.34). In another study, Andrén et al. (2010) estimated the mean growth rate of lynx population for the entire Norrbotten County to be 0% ($\lambda = 1.0 \pm 0.07$ SE) between 1998 and 2010.

The estimated annual growth rate for the southern study area in 1996 to 2002 was 19% ($\lambda = 1.19 \pm 0.097$ SE, significantly higher than 1, p = 0.05), based on demographic data (Andrén et al. 2006). The lynx population in the southern study area has first increased (1994 to 2001) and then decreased (2002 to 2010). During the period that overlaps the period when the demographical data was collected (1996-2002), the lynx population in south-central Sweden had an annual increase of 11% ($\lambda = 1.11 \pm 0.03$ SE; Andrén et al. 2010).

As the growth rates based on demographic data were slightly higher than the observed population growth rates (but not significantly different, p=0.30) in both study areas, the estimated rates of mortality (including assumed poaching) were probably not overestimated; if anything mortality might be underestimated.

If the two study areas are representative for the reindeer husbandry area and the area south of the reindeer husbandry area in Sweden, respectively, then the estimated number of lynx poached in the reindeer husbandry area would be around 77 lynx (± 16 lynx SE) per year and around 22 lynx (± 10 lynx SE) per year south of the reindeer husbandry area. It was not possible to estimate a specific effect of poaching in southernmost Sweden, because of few radio-marked individuals in this area. Specifically, we have no confirmed cases of poaching and only one case of assumed poaching from this area, and cannot make an independent estimate of poaching on a small sample size that small. However, it is important to remember that during the colonisation phase of southernmost Sweden, poaching of the few females present in the area can be very efficient in preventing the establishment of a population.

To conclude, poaching is an important cause of mortality in lynx in Sweden, especially in the northern study area, and the poaching rate does not seem to have changed between two periods (1994-1999 versus 2000-2010).

6. Acknowledgements. WWF (Sweden) has funded this report. The research project was funded by The Swedish Environmental Protection Agency, the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas), WWF (Sweden), the Swedish Association for Hunting and Wildlife Management, the private foundations “Olle och Signhild Engkvists Stiftelser” and “Marie-Claire Cronstedts Stiftelse” and the county administration in Norrbotten.

7. References

Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, Y., Franzén, F. and Segerström, P. 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. – Biological Conservation 131: 23-32.

Andrén, H., Svensson, L., Liberg, O., Hensel, H., Hobbs, N.T. och Chapron, G. 2010. Den svenska lodjurspopulationen 2009-2010 samt prognos för 2011-2012. – Inventeringsrapport från Viltskadecenter 2010-4, Grimsö forskningsstation, SLU. 29 sidor. ISBN 978-91-86331-21-4

Arnemo, J.M, Evans, A. and Fahlman, Å. (editors). Ahlqvist, P. Andrén, H., Brunberg, S., Liberg, O., Linnell, J.D.C., Odden, J., Persson, J., Sand, H., Segerström, P., Sköld, K., Strømseth, T.H., Støen, O.-G., Swenson, J.E. and Wabakken, P. (Contributors). 2011. Biomedical Protocols for Free-ranging Brown Bears, Wolves, Wolverines and Lynx. - NINA, Norway, 14 pages (available on www.nina.no).

Blankenship, T.L., Haines, A.M., Tewes, M.E. and Silvy, N.J. 2006. Comparing survival and cause-specific mortality between resident and transient bobcats. – Wildlife Biology 12: 297-303.

Ericsson, G. och Sandström, C. 2005. Delrapport om svenskars inställning till rovdjurspolitik och –förvaltning. - FjällMistra-rapport nr. 10, 56 sidor.

Krebs, J., Lofroth, E., Copeland, J., Banci, V., Golden, H., Magoun, A., Mulders, R., and Shults, B. 2004. Synthesis of survival rates and causes of mortality in North American wolverine. - Journal of Wildlife Management 68: 493 – 502.

Linnell, J.D.C., Andersen, R., Kvam, T., Andrén, H., Liberg, O., Odden, J. and Moa, P.F. 2001. Home range size and choice of management strategy for lynx in Scandinavia. - Environmental Management 27: 869-880.

Linnell, J. D. C., Brøseth, H., Odden, J. and Nilsen, E.B. 2010. Sustainably harvesting a large carnivore? Development of Eurasian lynx populations in Norway during 160 years of shifting policy. - Environmental Management 45: 1142.

Nilsen, E.B., Linnell, J.D.C., Odden, J. and Andersen, R. 2009. Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. – Journal of Animal Ecology 78: 741-751.

Mattisson, J. 2011. Interaction between Eurasian lynx and wolverines in the reindeer husbandry area. - Doctoral thesis No. 2011:10, Faculty of Natural Resources and Agricultural Sciences, Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden, pp. 1-50

Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T. and Andersen, R. 2002. Lynx depredation on domestic sheep in Norway. - Journal of Wildlife Management 66: 98-105.

Pedersen, V., Linnell, J.D.C., Andersen, R., Andrén, H., Segerström, P. and Lindén, M. 1999. Winter lynx predation on semi-domestic reindeer in northern Sweden. - Wildlife Biology 5: 203-212.

Persson, J., Ericsson, G. and Segerström, P. 2009. Human caused mortality in the endangered Scandinavian wolverine population. – Biological Conservation 142: 325-331.

Pollock, K.H., Winterstein, S.R., Bunck, C.M. and Curtis, P.D. 1989. Survival analysis in telemetry studies: the staggered entry design. - Journal of Wildlife Management 53: 7-15.

Pyka, M., Nyqvist, A., Monstad, T., Hagstedt, J. och Korsell, L. 2007. Illegal jakt på stora rovdjur. Konflikt i laglöst land? – Brottsförebyggande rådet (BRÅ). Rapport 2007:22. 224 sidor.

R-Development-Core-Team. 2010. R: A language and environment for statistical computing. - R Foundation for statistical computing, Vienna.

Sæther, B.-E., Engen, S., Swenson, J.E., Bakke, Ø. and Sandegren, F. 1998. Assessing the viability of Scandinavian brown bear, *Ursus arctos* populations: the effect of uncertain parameter estimates. - Oikos 83: 403 – 416.

Sæther, B.-E., Engen, S., Persson, J., Brøseth, H., Landa, A. and Willebrand, T. 2005. Management strategies for the Scandinavian wolverine population: practical application of stochastic models in population viability analysis. – Journal of Wildlife Management 69: 1001-1014.

Sæther, B.-E., Engen, S., Odden, J., Linnell, J.D.C., Grøtan, V. and Andrén, H. 2010. Sustainable harvest strategies for age-structured Eurasian lynx populations: the use of reproductive value. - Biological Conservation 143: 1970-1979.

Sunde, P., Kvam, T., Bolstad, J.P. and Bronndal, M. 2000. Foraging of lynxes in a human-exploited boreal alpine environment. - Ecography 23: 291-298.

Swenson, J.E. and Andrén, H. 2005. A tale of two countries: large carnivore depredations and compensation schemes in Sweden and Norway. - In People and wildlife: conflict or co-existence? eds. R. Woodroffe, S. Thirgood, and A. Rabinowitz, pp 323-339. Cambridge University Press.

Swenson, J.E., Sandegren, F., Söderberg, A., Bjärvall, A. and Franzén, R. 1997. Infanticide caused by hunting of male bears. - Nature 386: 450 – 451.

Swedish University of Agricultural Sciences

Mortality and poaching of wolverines in Sweden

Dödlighet och illegal jakt på järv i Sverige

Jens Persson, Geir Rune Rauset, Peter Segerström and Henrik Andrén

Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences (SLU), SE-730 91 Riddarhyttan, Sweden.

Corresponding author:
Jens Persson
Tel: + 581-69 73 05
E-mail: jens.persson@slu.se

A report to World Wide Fund for Nature, (Sweden).

Mortality and poaching of wolverines in Sweden

Jens Persson, Geir Rune Rauset, Peter Segerström and Henrik Andrén

Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences (SLU), SE-730 91 Riddarhyttan, Sweden.

The views in this report are the authors, and may not necessarily be the ones of WWF.

---

1. ABSTRACT

In this report, we assess causes of mortality and estimate annual survival for 234 wolverines (*Gulo gulo*) monitored for a total of 613 wolverine years in northern Sweden. The study area was located in a mountainous area in Norrbotten County in and around the Laponia World Heritage site. We found that poaching (including assumed poaching) was the main cause of mortality in adult wolverines (60 %). For adult wolverines the annual survival was 0.91 (0.88-0.95; 95% CI) when poaching was excluded, and 0.81 (0.76-0.86) when both confirmed and assumed poaching were included. The annual poaching rate in adult wolverines was 0.10 (0.06-0.14). Notably, the annual poaching rate was higher in adult males 0.21 (0.06-0.35) than females 0.08 (0.04-0.11; P = 0.031). We hypothesize that this difference is due to sex-specific movement patterns and indirect protection of denning females as a result for the current compensation program. Almost all poaching of adult wolverines (97 %) occurred during the snow-season (December-May), with a peak in March-May. In addition, three subadult wolverines were poached in March-May. Most juvenile mortality was caused by intraspecific predation and other natural factors (78 %). Both our assessment of subadult mortality causes and estimate of juvenile/subadult survival are presumably biased low because a high proportion of subadults disperse. Neither the annual survival, including all sex and age classes and all mortality causes nor the annual poaching rate differed between 1993-1999 and 2000-2011. Although poaching forms a significant part of wolverine population dynamics in Sweden, estimates of an increasing population suggest that the level of poaching is not high enough to halt population growth.

Dödlighet och illegal jakt på järv i Sverige

Jens Persson, Geir Rune Rauset, Peter Segerström och Henrik Andrén

Grimsö Forskninigsstation, Instituationen för Ekologi, Sveriges Lantbruksuniversitet (SLU), 730 91 Riddarhyttan.

---

1. SVENSK SAMMANFATTNING

I denna rapport rapporterar vi åldersspecifika dödsorsaker, med fokus på illegal jakt, och årlig överlevnad hos 234 järvar (*Gulo gulo*)som följts under totalt 613 radio-år i norra Sverige. Studieområdet var ett område med fjäll och fjällnära skogar i Jokkmokks and Arjeplogs kommun i Norrbottens län. Vi fann att illegal jakt (inklusive sannolik illegal jakt) var den viktigaste dödsorsaken bland vuxna järvar (60 %). Hos vuxna järvar var den årliga överlevnaden 91 % (88-95 %; 95 % CI) när illegal jakt var exkluderat från analysen. När illegal jakt inkluderades var den årliga vuxenöverlevnaden 81 % (76-86 %). Illegal jakt svarade för en årlig dödlighet på 10 % (6-14 %) vuxna järvar. Noterbart är att dödligheten orsakad av illegal jakt var högre hos hanar (21 % (6-35 %)) än hos honor (8 % (4-11 %; P = 0.031). Vi antar att denna skillnad kan bero på könsspecifika skillnader i rörelsemönster och att reproducerande honor får ett indirekt skydd som resultat av nuvarande ersättningssystem. Nästan all illegal jakt på vuxna järvar (97 %) skedde under snösäsongen (december-maj), med en tydlig topp i mars-maj. De tre subadulta (1-2 år gamla) järvar som dödades illegalt dödades även de i mars-maj. Den viktigaste dödsorsaken bland järvungar (0-1 år gamla) var inomartspredation. Både våra beräkningar av dödsorsaker och årlig överlevnad bland subadulta järvar är troligen underskattningar eftersom en stor andel av djuren i denna åldersklass utvandrade och förlorades från studien innan vi kunde avgöra vad som hänt med dessa djur. Varken årlig överlevnad inkluderande alla åldersklasser och dödsorsaker eller nivån på illegal jakt tycks ha förändrats från perioden 1993-1999 till 2000-2011. Våra analyser visar att illegal jakt är en viktig del i järvars populationsdynamik i Sverige. Emellertid tyder inventeringsresultaten på att populationen i landet ökar och att illegala jakten inte är tillräckligt omfattande för att stoppa populationen från att växa som helhet.

2. INTRODUCTION

The wolverine is relatively scarce across its circumpolar range, with regional conservation status ranging from secure to endangered and, in some locales, possibly extirpated. Globally, the wolverine is classified as Least Concerned (Abramov et al. 2009). There is also a diversity of conservation and management concerns in many areas where the wolverine occurs. These concerns include primarily habitat fragmentation, overexploitation, and depredation conflicts with sheep and reindeer husbandry (Landa et al. 2000, Slough 2007, Zhang et al. 2007). Recently, concern has also been raised about the potential negative impact of global warming on wolverine populations (Copeland et al. 2010). Some concerns about wolverine management/conservation are common to many areas of wolverine distribution, while some are more specific to particular regions.

The Scandinavian wolverine population size and distribution declined markedly during the 1900s (Flagstad et al. 2004). During the last 10 years the wolverine population has increased in both Sweden and Norway, and the total Scandinavian population size is estimated to be 880-1190 individuals, with 550-790 in Sweden (Persson et al. 2011). The distribution of wolverines in Sweden largely overlaps with that of semi-domestic reindeer (*Rangifer tarandus*), which is the predominant prey of wolverines (Persson, 2005; Mattisson 2011). The recovery of the wolverine population has been accompanied by increasing depredation on free-ranging sheep grazing unattended on summer pastures in Norway and semi-domestic reindeer in Sweden and Norway, leading to conflicts and high compensation costs (Swenson and Andrén, 2005). Currently, the wolverine population is listed as vulnerable in Sweden (Gärdenfors, 2010) and endangered in Norway (The Norwegian Biodiversity Centre). Current attempts to manage conflicts in Sweden are mainly based on a system of compensation for damage caused by wolverines, but also lethal harvest of wolverines and law enforcement against poaching (Persson et al. 2009). Compensation is based on the number of wolverines and other large carnivores within the reindeer grazing community. Lethal control of wolverines is only allowed in special cases as a final conflict-mitigating measure and is presumably of limited importance at population level. In Norway, conflicts are managed with compensation for livestock that is documented or assumed to be killed by wolverines, as well as an extensive annual harvest of wolverines. As a result of the conflict with animal husbandry, poaching and legal harvest forms a substantial part of wolverine population dynamics in northern Scandinavia (Persson et al. 2009). As wolverines typically occur at low densities and have a low reproductive potential (Persson, 2005; Persson et al. 2006), wolverine populations are expected to be sensitive to changes in survival rates (Weaver et al. 1996).

We have previously assessed age-specific mortality causes and estimated annual survival of wolverines (Persson et al. 2009). Therefore, the aim with this report is to update the knowledge about poaching of wolverines in Sweden.

3. STUDY AREA

The study area (8000 km^2) is located in the county of Norrbotten around Kvikkjokk (67°00' N, 17°40' E). Part of the area is within the Laponia World Heritage Site, including Sarek National Park. The study area ranges from coniferous forest (Norway spruce, *Picea abies* and Scots pine, *Pinus sylvestis*) in the eastern parts (about 300 m a.s.l.), through mountain birch forest (*Betula* sp.) and mountain meadows to high alpine areas with peaks around 2000 m a.s.l. The tree line is at about 800 m a.s.l. The area is located within the Sami reindeer husbandry area and includes mainly the reindeer management units: Tuorpon, Jåhkågasska, Sirges, Luokta-Mávas, and Sörkaitum. The study area has reproducing populations of lynx (*Lynx lynx*) and brown bear (*Ursus arctos*) that are also studied. Reindeer (*Rangifer tarandus*) is the main prey for wolverines in the area. Data on wolverine survival for this study was collected 1993-2011.

4. METHODS

4.1. Capturing and monitoring

During the study period we captured 256 wolverines, and 234 of these were used in analyses. Of these, 163 were monitored as juveniles, 107 as subadult (1–2 years), and 104 as adults (>2 years) for a total of 613 wolverine years (Table 1). Some animals are included in analyses of mortality causes, but not included in the survival analyses, e.g. because the monitoring frequency were too low to be included in the latter. We captured and equipped most juveniles with implanted VHF-transmitters at rendezvous sites in early May to early June (2–3 months old). Adults were captured on ground or were darted from helicopters (Arnemo and Fahlman, 2011) and equipped with implanted VHF-transmitters and in some cases GPS-collars. The study was approved by the Animal Ethics Committee for northern Sweden, Umeå. For details on capture and immobilization see Arnemo et al. (2011).

We detected death of radio-marked wolverines during biweekly radio-tracking from fixed-wing aircraft with supplemental ground tracking. When we detected a mortality signal the site was investigated to determine the cause of death. We estimated the time elapsed from the date last heard alive until death by the condition of the carcass and indications at the carcass site. When the state of a carcass indicated that the animal had died recently, we designated the date of death at 80% of the time between the date last heard alive and the date when mortality was detected. When there were no indications of how long the animal had been dead, we fixed the date of death at 40% (cf. Johnson, 1979) of the time between the last time the animal was known to be alive and the date when mortality was detected. We classified animals that we lost contact with into two different categories; assumed poaching and lost (i.e., unknown disappearance) using additional information. Assumed poaching was when the lost animal was a resident adult equipped with a transmitter with at least half of the expected battery life remaining, the transmitter showed no signs of technical problems (e.g., strange signals), and the study area was searched extensively for the animal on ground and from the air (cf. Andrén et al., 2006; Persson et al. 2009). Furthermore, in several cases we documented that a new individual had taken over the territory the winter following the disappearance of a resident individual, suggesting that the latter had been killed. Date of assumed mortality and censoring of lost animals were assigned the same way, i.e. one week after the last date the animal was heard alive (i.e., approximately intermediate between the last time heard and the next radio-tracking event).

4.3 Methods for estimating survival

Survival rates of radio-marked wolverines were calculated using the staggered entry design, which is a modified Kaplan-Meier estimate (Pollock et al. 1989, R-development core team 2010, R library *survival*). We estimated survival for two age classes; a) juveniles and subadults pooled, and b) adults. The juvenile/subadult age class included wolverines from approximately 3 months of age to the age of 2 years, and adults are wolverines older than 2 years. We also estimated survival separately for adult males and females. We estimated two survival rates. The first one includes all mortality and the second one excludes poaching and assumed poaching. The magnitude of poaching was estimated using cumulative incidence functions (Gray 1988, R library *cmprsk*). Competing risk regression (Fine and Gray 1999, R library *cmprsk*) was used to test for differences in poaching between age and sex classes and between time periods. If nothing else is mentioned, poaching includes both confirmed and assumed poaching in the text below.

5. RESULTS

5.1. Cause of mortality in radio-marked individuals.

In our study area in northern Sweden, we monitored 234 individual wolverines. We documented 68 mortalities, distributed on 33 adult, 5 subadult and 32 juvenile mortalities. In addition, we documented 22 cases of assumed poaching of adult wolverines. We lost contact with 120 individuals for which the fate could not be determined.

Confirmed adult mortality was dominated by hunting (i.e. lethal control) and poaching (Table 1). A third (33 %) of confirmed adult mortality was caused by poaching. If we include assumed poaching, poaching caused 60 % of adult mortality (Fig. 1). Poaching caused 94 % of adult male mortality and 46 % of adult female mortality (Fig. 2). Natural adult mortality was caused by disease, intraspecific strife, starvation, avalanche and unknown natural causes.

We documented mortality of 5 subadult individuals during the study (Table 1). Poaching was confirmed as the cause of death of three individuals. One subadult male was presumably killed by another wolverine. The cause of death for one female was unknown.

We monitored 163 juvenile wolverines and documented 32 mortalities (Fig. 1). The predominant cause of death was intraspecific predation (44 %; n = 14). Other causes of juvenile mortality were lethal control, poaching, drowning, starvation or unknown. Human caused mortality represented 15 % of juvenile mortality, while 78 % of mortality was caused by natural factors.

5.3. Seasonal distribution of mortality
In adults, 97 % of confirmed and assumed poaching occurred during December-May, and 73 % occurred during March-May (Fig. 3). In contrast, 40 % of natural and unknown adult mortality occurred during December-May. All three cases of poached subadults occurred in March-May. In juveniles 94 % of the mortality occurred in May-September, but juveniles were not monitored in March-April.

5.2 Annual survival for radio-marked individuals
Annual survival for all sex and age classes pooled (Fig. 5) was significantly higher ($P<0.05$) when poaching was excluded 0.87 (0.84-0.91), compared to when poaching was included (0.78; 0.74-0.83).

For adult wolverines the annual survival was 0.91 (0.88-0.95) when poaching was excluded. If we included poaching the annual adult survival was 0.81 (0.76-0.86). When we analyzed adult survival separated on males and females, we found that female and male annual survival was 0.82 (0.77-0.88) and 0.77 (0.66-0.90), respectively, when all mortality causes were included.

Pooled annual survival for juveniles and subadults was 0.81 (0.75-0.87) excluding poaching, and 0.75 (0.68-0.83) when poaching was included.

If we look at the level of poaching separately, the overall level of poaching is 0.08 (0.05-0.11) when all age and sex classes are pooled. The annual rate of poaching was 0.03 (0.01-0.06) for juveniles and subadults combined, whereas the annual poaching rate was 0.10 (0.06-0.14) for adult wolverines. The annual poaching rate was higher in adult males 0.21 (0.06-0.35) than females 0.08 (0.04-0.11) (Competing Risk Regression; $P = 0.031$).

Overall annual survival, including all sex and age classes and all mortality causes, did not differ between the two periods 1993-1999 and 2000-2011 ($\chi^2 = 0$, $df = 1$, $P = 0.93$; Fig. 6). Similarly, the annual poaching rate did not differ between 1993-1999 and 2000-2011 (0.07 and 0.08, respectively; Competing Risk Regression, $P = 0.54$).

6. DISCUSSION

We focus the discussion on adult survival because; a) adult survival is the demographic parameter that has most influence on population growth, b) adults is the age class that is most influenced by human caused mortality, c) we have the most robust data on adults and juveniles.

Adult survival and mortality causes
Poaching, including assumed poaching, was the most important cause of adult wolverine mortality in northern Sweden (60 %; Fig. 1.). If we include lethal control, human caused mortality represents 71 % of adult mortality. Annual survival both when all age classes were pooled and for adult wolverines were significantly lower when confirmed and assumed poaching was included compared to survival without poaching. This suggest that poaching is the most important limiting factor for the Swedish wolverine population, considering that adult survival is the most important parameter influencing population growth rate in long-lived mammals (e.g. Stearns 1992). For example, the influence of adult survival on wolverine population growth is estimated to be 4.5 times larger

than that of reproduction (Persson 2007). Importantly however, the level of poaching is not large enough to hinder the population from growing, as suggested by an increasing size of the population the last 10 years (Persson et al. 2011).

Notably, mortality caused by poaching was significantly lower in adult female wolverines than for adult males. We hypothesize that this difference is due to, 1) sex-specific differences in movement patterns, and 2) indirect protection of females as a result of the current compensation system. First, male home ranges in our study area are typically about four times larger than those of females (Persson et al. 2010). Wolverine males also appear to increase their movements before and during the mating season (April–August) (Hornocker and Hash, 1981; Magoun, 1985), which partly overlaps with the period when most poaching occurred. Hence, more extensive movements presumably make males more exposed to (incidental) poaching than females. Second, as a result of the current compensation system denning females have an economical value (200 000 SEK), which could contribute to indirect protection. In addition, monitoring of wolverine reproductions is an integral part of the compensation system that leads to increased activity of County administration personnel around denning areas, which may further contribute to indirect protection by deterring poachers. We hypothesize that the current system for compensation reindeer losses to carnivores can have a positive influence on wolverine female survival and thus wolverine conservation. Adult females and their survival is the most important segment of the population. Thus, our results suggest that the observed level of poaching on females is a better reflection of the influence of poaching on the wolverine population than the pooled survival of females and males.

Seasonal differences in adult mortality

The number of poached wolverines was highest during the snow season, with a peak in March-April. This is the factor explaining why adult survival is lower during the snow season than during the snow-free season (Persson et al. 2009). Poaching is presumably facilitated by snow cover that enables tracking and hunting by snow-machines in remote areas with low risk of detection. This is especially true for the later part of the snow season (March–May) when snow conditions are ideal and daylight is longer, increasing the chances of spotting wolverines and their tracks. A similar temporal pattern is documented for poaching of lynx in our study area (Andrén et al. 2006).

Juvenile and subadult survival and mortality causes

Although we monitored 107 individuals as subadults, we could only confirm 5 mortalities in this age class (Table 1). A high proportion of subadults disperse from the study area and it is therefore logistically hard and expensive to monitor these individuals and their destiny (establishment and/or death). Furthermore, dispersing carnivores are young, inexperienced animals that make extensive movements in new areas and are often subject to higher mortality than residents (Waser, 1996; Fuller et al., 2003; Blankenship et al., 2006). Therefore, it is likely that our results underestimate subadult mortality and particularly mortality caused by poaching.

Juvenile mortality (n = 32) was dominated by natural causes (78 %). Of these, 14 were confirmed and one was presumably killed by conspecifics. A thorough discussion about intraspecific predation on juvenile wolverines is provided in Persson et al. (2003). Poaching caused only 6 % of juvenile mortality. The low level of poaching in juveniles is expected as they are monitored in most cases from early June to 1 March (when they become subadults). Thus, juveniles were mainly monitored outside the period when poaching is most frequent.

Pooled annual survival for juveniles and subadults was lower than that of adult wolverines when poaching was not included. This difference is primarily explained by the higher natural mortality in juvenile wolverines. When including poaching, juvenile/subadult survival was still lower than that of adults, but the difference was smaller because the level of poaching was low in juveniles and the fate of many subadults could not be determined.

Lost animals and reliability of our estimates

In total, we lost contact with 120 wolverines for which we could not determine their fate. These animals were censored from all survival analyses. The explanation for these disappearances could be dispersal, failure of radio-transmitters or poaching (with subsequent destruction of transmitters). It was primarily subadults that were lost from the study; 48 % (n = 57) of all lost animals were subadults and 54 % of subadults were lost from the study. The reason for this is that most wolverines that disperse do so when they are subadults (Vangen et al. 2001). A high proportion of dispersing animals are lost because of the difficulties to monitor dispersal. In addition, for animals that have not been determined as being established, it is hard to separate dispersal, poaching and transmitter failure. As mentioned above, young dispersers is the category that is expected to be most exposed to poaching and other mortality factors, suggesting that we underestimate subadult mortality in general and poaching in particular. This is supported by two subadults that were classified as lost subsequently were incidentally found poached, suggesting that our estimates of poaching could be biased low (i.e., animals classified as lost were in fact killed).

Representativeness for wolverines outside the study area

Our study area represents a small proportion of the distribution of the Swedish wolverine population. Over time, our study area is likely to have been influenced by survival of marked animals, i.e. a selection process where we monitor more individuals in areas where survival is relatively high, and it is not unlikely that our research activity could inflate survival of marked animals. This suggests that our estimates of poaching could be biased low. Furthermore, our study area is not representative regarding the level of lethal control. Since the start of the study our radio-marked wolverines constitute 32 % of all lethal control conducted in Sweden. Thus, the level of lethal control is lower on a national level than indicated by our estimates in this report.

6.5. Conclusions

Poaching is the main cause of mortality in adult wolverines. Almost all poaching occur during the snow-season with a peak in March-May. Most juvenile mortality is caused by intraspecific predation and other natural factors. Our estimate of subadult survival and mortality causes is presumably biased low because a high proportion of subadults disperse beyond the study area and it is therefore hard to determine the fate of most subadults. Although poaching forms a significant part of wolverine population dynamics, estimates of an increasing population suggest that the level of poaching is not high enough to halt population growth. Finally, we hypothesize that the current compensation system for losses of reindeer to carnivores provides indirect protection of denning wolverine females and thereby to the conservation of the Swedish wolverine population.

6. ACKNOWLEDGEMENTS

WWF (Sweden) has funded this report. The research project was funded by The Swedish Environmental Protection Agency; The Norwegian Directorate for Nature Management; the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Formas); WWF (Sweden); European Association for Zoo and Aquaria; Marie-Claire Cronstedt Foundation.

7. REFERENCES

Abramov, A., Belant, J. & Wozencraft, C. 2009. *Gulo gulo*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. <www.iucnredlist.org>. Downloaded on 20 April 2011.

Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., Franzén, R., Segerström, P., 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation 131, 23–32.

Arnemo, J.M, Evans, A. and Fahlman, Å. (editors). 2011. Biomedical Protocols for Free-ranging Brown Bears, Wolves, Wolverines and Lynx. - NINA, Norway, 14 pages (available at http://www.rovviltportalen.no/content.ap?thisId=500039688.

Blankenship, T.L., Haines, A.M., Tewes, M.E., Silvy, N.J., 2006. Comparing survival and cause-specific mortality between resident and transient bobcats *Lynx rufus*. Wildlife Biology 12, 297–303.

Fine, J.P. and Gray, R.J., 1999. A proportional hazards model for the subdistribution of a competing risk. Journal of the American Statistical Association 94: 496-509

Flagstad, Ö., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., Segerström, P. & Ellegren, H. 2004. Colonization history and non-invasive monitoring of a re-established wolverine (*Gulo gulo*) population. Conservation Biology 18(3): 1-13.

Fuller, T.K., Mech, L.D., Cochrane, J.F., 2003. Wolf population dynamics. In: Mech, L.D., Boitani, L. (Eds.), Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, pp. 161–191.

Gärdenfors, U. 2010. The 2010 Red list of Swedish species. Swedish Species Information Centre, Swedish University of Agricultural Sciences.

Gray, R.J., 1988. A Class of K-sample tests for comparing the cumulative incidence of a competing risk. The Annals of Statistics 16(3): 1141-1154

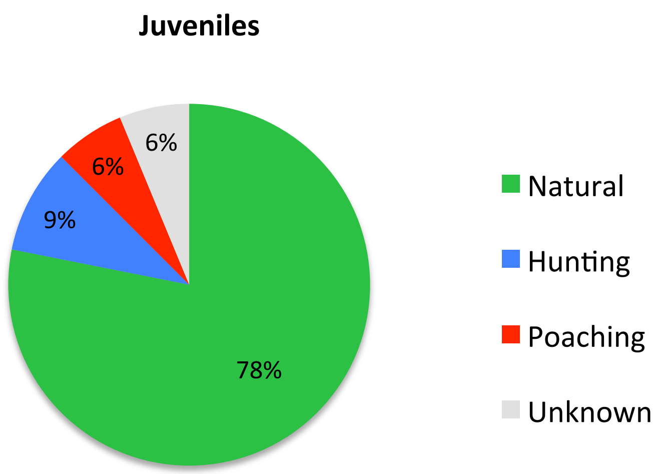
Hornocker, M.G., Hash, H.S., 1981. Ecology of the wolverine in northwestern Montana. Canadian Journal of Zoology 59, 1286– 1301.

Landa, A., Linell, J.D.C., Linde´n, M., Swenson, J.E., Røskaft, E., Moksnes, A., 2000. Conservation of Scandinavian wolverines in ecological and political landscapes. In: Griffiths, H.I. (Ed.), Mustelids in a modern world, Management and Conservation Aspects of Small Carnivore: Human Interactions. Backhuys Publishers, Leiden, pp. 1–20.
Magoun, A.J., 1985. Population characteristics, ecology and management of wolverines in Northwestern Alaska. Ph.D. Thesis, University of Alaska, Fairbanks.
Mattisson, J.M., 2011. Interactions between Eurasian lynx and wolverines in the reindeer husbandry area. . - Doctoral thesis No. 2011:10, Faculty of Natural Resources and Agricultural Sciences, Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden
Persson, J., 2005. Wolverine female reproduction: reproductive costs and winter food availability. Canadian Journal of Zoology 83, 1453–1459.
Persson, J., Willebrand, T., Landa, A., Andersen, R., Segerstro¨m, P., 2003. The role of intraspecific predation in the survival of juvenile wolverines *Gulo gulo*. Wildlife Biology 9, 21–28.
Persson, J., Landa, A., Andersen, R. & Segerström, P. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. Journal of Mammalogy 87(1):75-79.
Persson, J. 2007. Järvens status och ekologi i Sverige. Rapport Till berörda parter Rovdjursutredningen.
Persson, J., Ericsson, G. & Segerström, P. 2009. Human caused mortality in an endangered wolverine population. Biological Conservation 142: 325-331.
Persson, J., Wedholm, P. & Segerström, P. 2010. Space use and territoriality of wolverines (Gulo gulo) in northern Scandinavia. European Journal of Wildlife Research 56(19): 49-57.
Persson, J., Brøseth, H. och Svensson, L. 2011. Den skandinaviska järvpopulationen – status och utbredning. – Gemensam rapport från Järvprojektet, Viltskadecenter och Rovdata 2011-1, Grimsö forskningsstation, SLU. 23 sidor. ISBN: 978-91-8633129-0
Waser, P.M., 1996. Patterns and consequences of dispersal in gregarious carnivores. In: Gittleman, J.L. (Ed.), . In: Carnivore Behaviour, Ecology, and Evolution, Vol. 2. Cornell University Press, Ithaca, pp. 267–295.
Saether, B.-E., Engen, S., Persson, J., Brøseth, H., Landa, A. and Willebrand, T. 2005. Management strategies for the Scandinavian wolverine: practical application of stochastic models in Population Viability Analysis. Journal of Wildlife Management 69: 1001-1014.
Slough, B., 2007. Status of the wolverine *Gulo gulo* in Canada. Wildlife Biology 13 (Suppl. 2), 76–82.
Vangen, K.M., Persson, J. Landa, A. Andersen, R. & Segerström, P. 2001. Characteristics of dispersal in wolverines. Canadian Journal of Zoology 79: 1641-1649.
Zhang, M., Liu, Q., Piao, R., Jiang, G., 2007. The wolverine Gulo gulo population in the Great Kinghan Mountains, northeastern China. Wildlife Biology 13 (Suppl. 2), 83–88.

Table 1. Causes of mortality of radio-marked wolverines in northern Sweden, 1993-2011.

Age (years)	N monitored	Natural	Hunting	Poaching	Assumed poaching	Unknown cause	Unknown fate*
<1	163	25	3	2	0	2	26
1-2	106	1	0	3	0	1	57
> 2	104	13	6	11	22	3	37
Total		39	9	16	22	6	120

* Four wolverines classified as unknown fate and censored from the study were subsequently confirmed to have died. One adult male was killed in intraspecific strife or injury from falling down a cliff after his radio transmitter failed. One adult female was killed illegally. One male and one female were lost as subadults and were subsequently found poached and dropped in a hydropower dam.



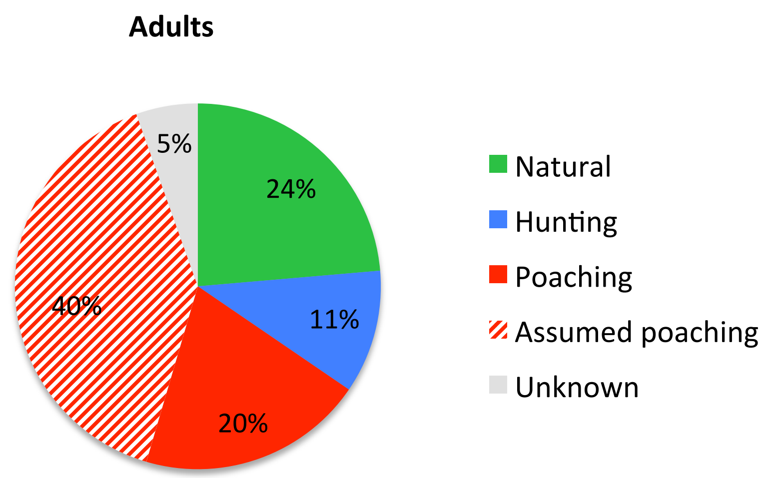


Figure 1. Causes of mortality in juvenile (upper chart) and adult (lower chart) wolverines in northern Sweden, 1993-2011.

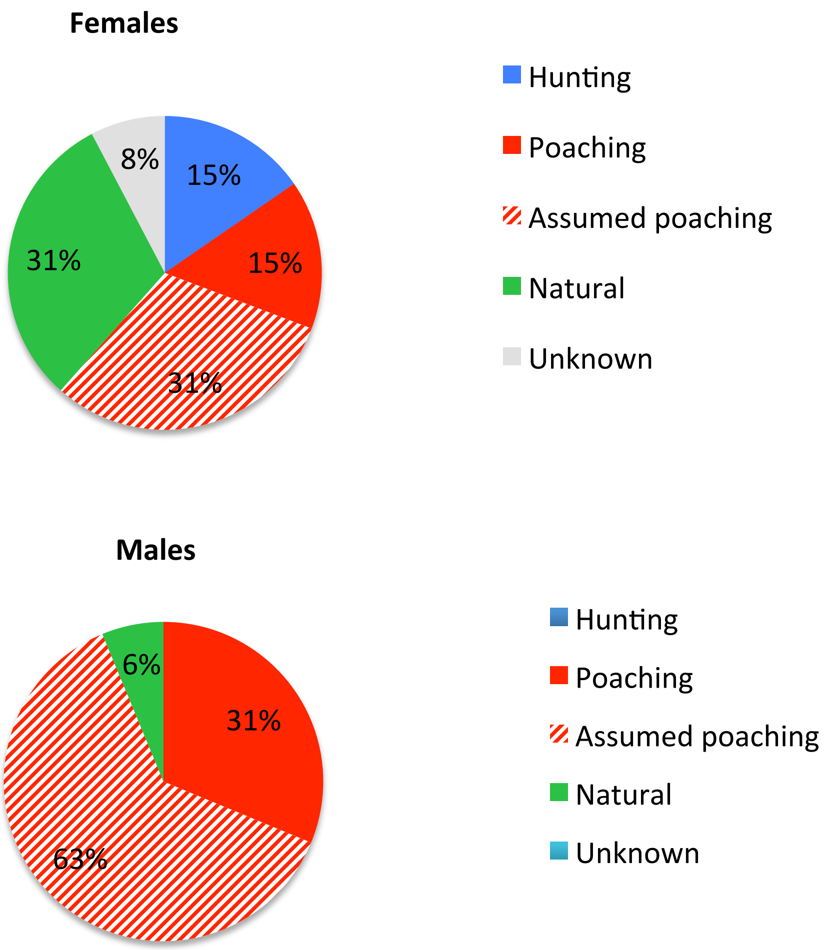


Figure 2. Causes of mortality in adult female (upper chart) and male (lower chart) wolverines in northern Sweden, 1993-2011.

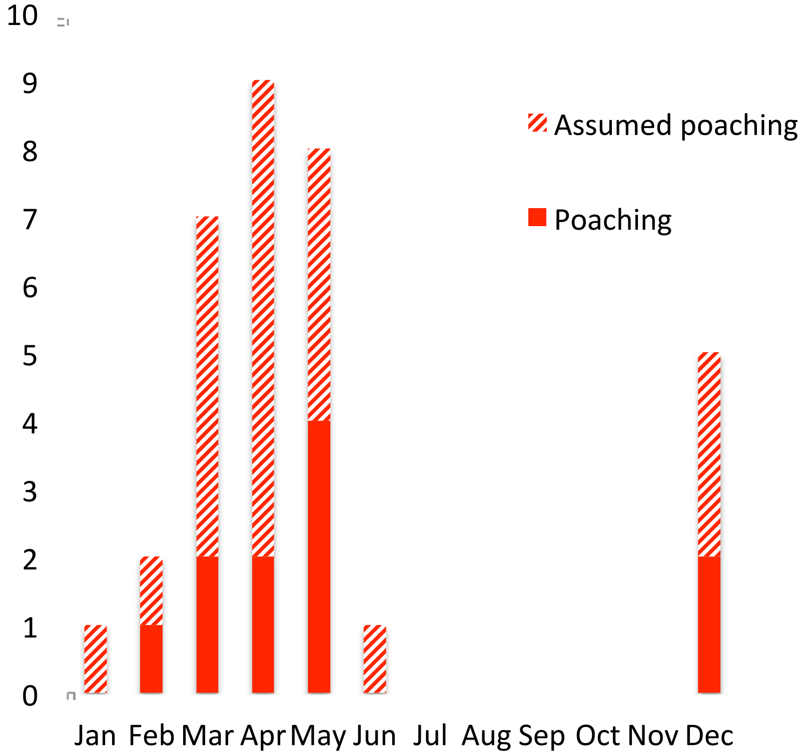


Figure 3. Number of radio-marked adult wolverines that died from confirmed poaching (red; n = 11) and assumed poaching (red-striped; n = 22) in relation to month of the year 1993–2011.

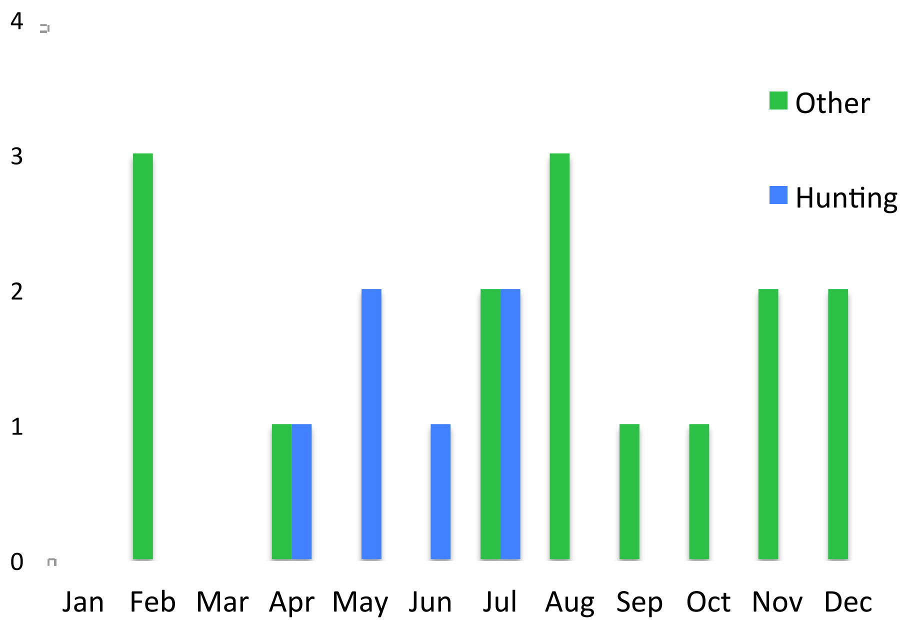


Figure 4. Number of radio-marked adult wolverines that died from natural and unknown causes (green bars; n = 15) and lethal control (blue bars; n = 6) in relation to month of the year 1993-2011.

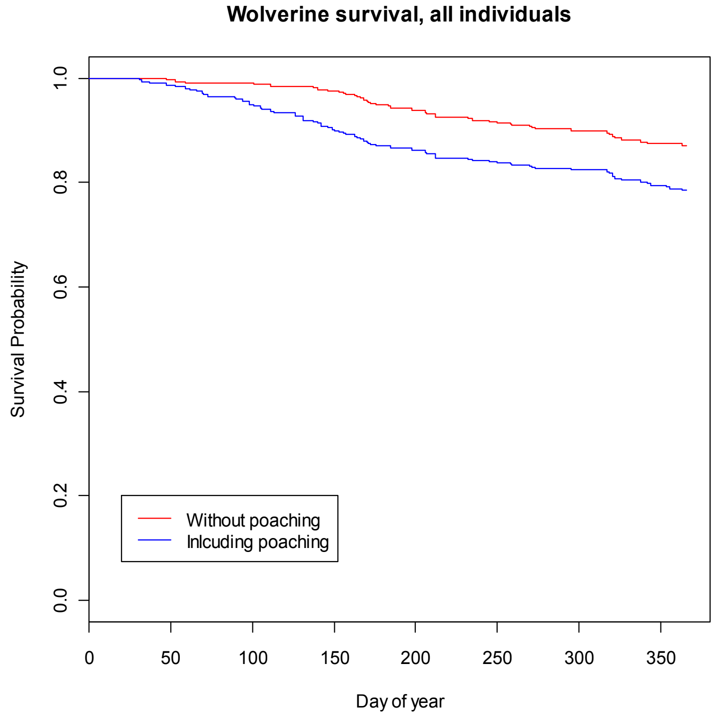


Figure 5. Survival curve illustrating survival probability for all sex and age classes pooled, with and without poaching included in the analysis. Survival is significantly lower when poaching (including assumed poaching) is included ($P < 0.05$).

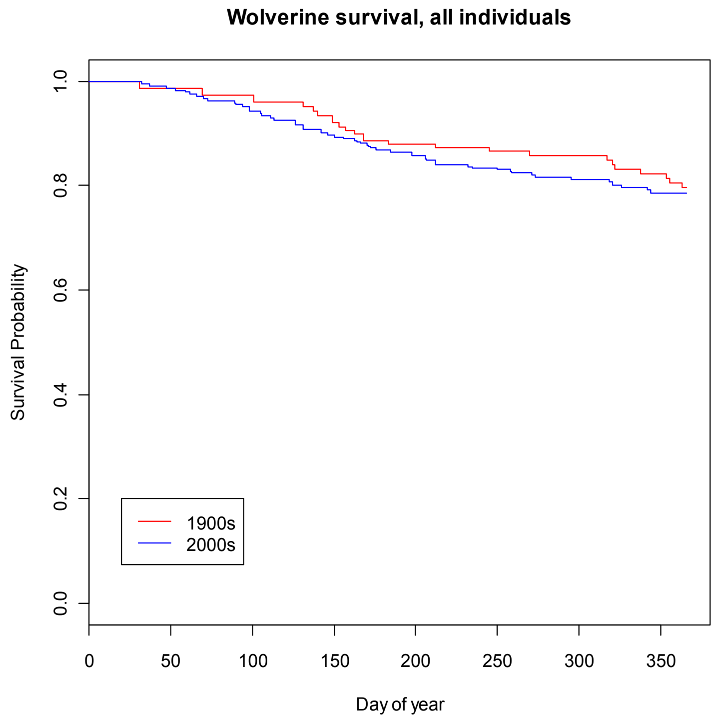


Figure 6. Survival curve illustrating survival probability for all sex and age classes pooled, 1993-1999 (1900s) and 2000-2011 (2000s) respectively, with poaching (including assumed poaching) included. The survival probability did not differ between the two periods.

Illegal killing of wolves in Scandinavia 1998 – 2011: variation in space and time.

Olof Liberg, Håkan Sand, Petter Wabakken, Guillaume Chapron

A report to World Wide Fund for Nature, WWF, (Sweden).

Authors:

Olof Liberg[1], Håkan Sand[1], Petter Wabakken[2], Guillaume Chapron[1]

Affiliation:

[1] Grimsö Research Station, Dept of Ecology, Swedish University of Agricultural Sciences, SE 730 91 Riddarhyttan, Sweden

[2] Hedmark University College, Faculty of Forestry and Wildlife Management, Evenstad N 2480 Koppang, Norway

Corresponding author: Olof Liberg, olof.liberg@slu.se

Photo front page: Åke Granqvist

ABSTRACT

Mortality and illegal killing was investigated in the Scandinavian wolf population for the period December 1998-February 2011. We quantified the illegal killing of wolves in order to test for differences between Sweden and Norway and to test whether the gradual changes in Swedish wolf policy from 2004 and onwards have had any effect on the extent of illegal killing. The main method was analysis of cause specific mortality in radio-collared wolves. Retrieved dead wolves were examined post mortem for cause of death. All cases of lost radio contact were checked against a number of standardized criteria for classification of the disappearance to illegal killing or any other cause. A total of 123 wolves were radio collared, producing data from a total of 160.9 “radio-years”. At the end of the study we still had contact with eight of the 123 wolves. Six wolves died in connection with capture and handling and were excluded from analysis. 29 wolves were confirmed dead with radio collars still functioning of which 9 were due to natural causes, 5 were killed by road and railway traffic, 10 were legally shot, and 5 cases were verified illegal killing. We lost radio contact with 80 wolves of which 19 were classified as probably illegally killed.

Total annual wolf mortality rate for Scandinavia for the total study period was 0.26. Mortality from illegal killing was 0.13 and from other causes 0.13. Both total mortality (Norway 0.36; Sweden 0.22) and illegal killing (Norway 0.18; Sweden 0.11) was higher in Norway than in Sweden. There was a large inter-annual variation in the rate of illegal killing, but in Sweden there was a decreasing trend with time. Analysis of a possible well defined break point in this trend gave significance for 31st Dec in 2003, 2004 and 2005, with the highest probability for 2005, which we then used to split the material into two periods, 1998-2005 and 2006-2011. Both total mortality (0.31 vs 0.17) and illegal killing (0.16 vs 0.08) decreased from 1998-2005 to 2006-2011 in Scandinavia. However, the extent of illegal killing in Norway and Sweden showed opposite trends over the two time periods. Whereas Norway had a non-significant increase in this type of mortality after 2005, Sweden had a significant almost seven-fold decrease, from 0.169 to 0.025, which corresponds to a reduction with almost two thirds of the total number of wolves illegally killed per year. The decrease in illegal killing of wolves in Sweden after 2005 was supported by a larger dataset based on verified cases of illegal killing including both collared and un-collared wolves, but only weakly so by data on old shot wounds found during post mortem autopsy of dead wolves.

An alternative method for determining mortality for the whole Scandinavian population, based on annual censuses of the population combined with data on reproduction, gave support for a reduction of total mortality (corresponding figures given for the dataset based on radio collared wolves within brackets); 0.26 (0.31) in 1998-2005 and 0.20 (0.17) in 2006-2011. The decrease in total mortality rate of wolves in Sweden between the two time periods probably was the most important reason for an increase in the average annual growth rate of the Swedish wolf population from 14 % in the period 1998-2005 to 19 % in the period 2006-2010.

SAMMANFATTNING PÅ SVENSKA

Dödlighet och illegalt dödande av varg undersöktes i Skandinavien under perioden december 1998-februari 2011. Studiens syfte var att kvantifiera omfattningen av illegalt dödande av varg och eventuella skillnader mellan Sverige och Norge samt huruvida den gradvisa förändringen av vargpolitiken i Sverige från och med 2004 har haft någon effekt på nivån av illegalt dödande i Sverige. Huvudmetoden var analys av orsaksspecifik mortalitet hos radio-märkta vargar. Alla döda vargar som återfanns blev obducerade för fastställande av dödsorsak. Alla fall av förlorad radio kontakt kontrollerades mot ett antal standardiserade kriterier för klassificering av försvunna individer som antingen *sannolikt* illegalt dödande eller försvunna av annan orsak. Totalt omfattade vårt dataset 123 radio-märkta vargar vilket resulterade i totalt 160,9 s.k. "radio-år". När studien avslutades hade vi fortfarande kontakt med åtta vargar. Sex vargar dog i samband med fångst/märkning och exkluderades från vidare analys. 29 vargar registrerades döda medan deras radiosändare fortfarande fungerade. Nio av dessa dog av naturliga orsaker, 5 dödades av tåg eller bil, 10 sköts lagligen och 5 blev illegalt dödade. Vi förlorade radiokontakten med 80 vargar. Nitton av dessa klassificerades som *sannolikt* illegalt dödade.

Total årlig dödlighet i Skandinavien för hela studieperioden var 25,9 %. Illegalt dödande utgjorde 12,8 % och andra orsaker 13,1 % av den totala dödligheten. Norge hade högre nivåer än Sverige, både för total dödlighet (Norge 35,6 %; Sverige 22,4 %) och för illegalt dödande (Norge 17,9 %; Sverige 11,1 %). Mellanårsvariationen var stor både för total dödlighet och för illegalt dödande, men i Sverige visade den senare en klart avtagande tendens med tiden. Vi analyserade om det statistiskt gick att visa någon bestämd brytpunkt över tiden för denna dödlighet. Vi fann en säkerställd sådan för 31 december åren 2003, 2004 och 2005, med störst sannolikhet för 2005. På basis av denna analys delade vi därefter in materialet i två tidsperioder, 1998-2005 resp. 2006-2011.

Både total dödlighet (30,5 % vs 16,8 %) och illegalt dödande (15,7 vs 7,7 %) minskade från perioden 1998-2005 till 2006-2011 i Skandinavien. Den illegala dödligheten uppvisade dock motsatta tidstrender i Norge och Sverige. Norge hade en icke-säkerställd ökning av denna typ av mortalitet efter 2005, medan Sverige hade en statistiskt säkerställd, nästan sjufaldig, minskning från 16,9 % till 2,5 %, vilket motsvarar en minskning av antalet illegalt dödade vargar per år med två tredjedelar. Den s.k. censusmetoden för bestämning av total dödlighet (baserad på de årliga inventeringarna av hela populationen samt reproduktionsdata) gav samma trend för total dödlighet i Skandinavien som materialet från radio-märkta vargar, med 26 % för perioden 1998-2005 och 20 % för perioden 2006-2011.

Nedgången av illegalt dödande av varg i Sverige efter 2005 stöds även av data på verifierade fall av illegalt dödande i ett större datamaterial omfattande både radio-märkta och omärkta vargar men endast svagt stöd från data på gamla skottskador som upptäcktes vid obduktioner av vargar som dött av andra orsaker. Ett ytterligare stöd för en nedgång av illegalt dödande av varg i Sverige är en demonstrerad ökning av den genomsnittliga årliga populationstillväxten av den svenska vargstammen, från 14 % under perioden 1998-2005 till 19 % under perioden 2006-2010.

Background

Large carnivores (LC) are controversial animals in most places where they occur (Treves and Karanth 2003). A consequence of this controversy is that human caused killing and specifically intentional illegal killing (poaching) often is a large problem for small threatened LC populations (Woodroffe and Ginsberg 1998, Creel & Creel 1998, Damania et al. 2003, Altrichter et al. 2006). There has been identified several different cause factors behind illegal killing of LC, but in affluent countries with low commercial incentives to poach, its existence might be an expression of disapproval of the prevailing conservation policy (Eliasson 2004). One major question of interest for the conservation of LC is whether a relaxed legal protection would lead to a decrease in illegal killing. A few studies have reported results that support a negative correlation between the extent of legal hunting of LC and illegal killing (Wielgus et al. 1994, Huber 2002, Andrén et al 2006), but the existence of such a trade-off also has been rejected (Treves 2009). Good data on this question are still lacking, although much needed considering its high relevance for the management of LC. In this report we use data from a long-term research project on wolf ecology to explore this subject, using differences in wolf policy between two countries sharing the same wolf population, but with a radical shift of wolf policy in one of the countries during the study period.

Sweden together with Norway constitutes the 837,000-km^2 Scandinavian peninsula, here referred to as Scandinavia (55°-72° N, 5°-31°; Fig. 1). The present wolf range covers 100 000 km^2 in the south-central part of the peninsula, but with the main part (c. 80%) in Sweden (Fig. 1). The two countries have rather different political and economic situations which also have formed their management policies for LC (Swenson and Andrén 2005). Sweden is highly industrialized and farming is strongly rationalized in large units with rural society proportionately small, and thus of less political influence. Norway, on the other hand, has pursued a policy of preserving and promoting rural communities and culture by subsidies for small-scale agriculture. As a result, a greater proportion of the Norwegian human population inhabits rural areas, and consequently is more politically empowered relative to its Swedish counterpart. In addition, Sweden is a member of the European Union and is bound to the strong protective legislation for large carnivores whereas Norway is not. Consequently, Norwegian wolf policy is more influenced by rural interests and less by those of nature protectionists as compared to Sweden.

These different situations in the two countries have led to different policies regarding the management of LC. The Swedish wolf management policy is regulated by the Predator Act “En sammanhållen rovdjurspolitik” passed by the Parliament in 2001 (Swedish Ministry of Environment 2000; MJU9, rskr 2000/01:174). The Act states that a preliminary national goal for wolves is to reach a minimum of 20 breeding packs. Before this goal is reached control of wolves (e.g. to reduce depredation or mitigate conflicts in other ways) should be kept to a minimum. Wolves shall be allowed to occur all over the country wherever there is suitable habitat, but with the restriction that breeding packs should not be allowed within the reindeer summer grazing range (mainly the alpine areas).

Before 2004 even the right to defend domestic animals from large carnivore attacks was very restricted, but from this year and onwards a number of steps were taken to liberalize this strict legislation. Earlier the care-taker was not allowed to kill the attacking carnivore before any of his livestock was wounded or dead but in 2004 this requirement was relaxed if the attack occurred inside a fenced area. After the election in 2006 a new Swedish government continued the movement towards a more liberal predator policy, starting with further relaxing conditions for control harvest of depredating carnivores, and for self-defense of domestic animals. Now it became allowed to kill an attacking carnivore before any damage had occurred, even outside fenced areas, also including defense of hunting dogs. This change in legislation resulted in an increase in the annual number of legally killed wolves from 1.3 annually during 1999-2006 to 4.0 during 2007-2010. In 2009 the national goal of 20 annual wolf reproductions was attained. In this year the Parliament passed an addendum to the Predator Act, introducing a temporary upper limit of the wolf population of 210 animals (but with the aim at still keeping a minimum of 20 annual reproductions, corresponding to approximately 200 individuals), and opened for a quota-based harvest to actively regulate the population to this upper limit. The first quota hunt occurred in January 2010 when 28 wolves were shot and in January 2011 another 19 wolves were harvested. The new wolf policy also included a decentralization of large carnivore management decisions and invitation to representatives for local stake holding interests to participate in these decisions.

Norwegian predator policy is regulated by the Predator Act “Rovvilt i Norsk Natur” (Norwegian Ministry of the Environment 2003), passed by the parliament in 2004. In this act the Norwegian Parliament established a specified “wolf zone” in south-eastern Norway, along the Swedish border, where wolves should be tolerated. Within this zone the sub-population goal was three Norwegian breeding packs, not including packs holding territories across the border to Sweden. When this goal is reached, control of additional wolves in the zone might be allowed if local authorities find it necessary to mitigate conflicts. Outside the zone, local governments may allow removal of wolves after they have received complaints, irrespective of whether the goal within the wolf zone is reached or not. Since 2004 there have been only minor changes of the Norwegian wolf policy.

Our objective in this study was to quantify the extent of illegal killing of wolves in Scandinavia during the period December 1998 - February 2011. Specifically, we investigated if there has been a change over time and we examined our data to find possible break points in our time series. Further, we used different datasets to test whether any changes in the rate of illegal killing may be due to a selective tendency among poachers for or against killing specifically radio-collared wolves. Finally, we discuss if the change found in the rate of illegal killing over time may have a causal relation to the shift in the Swedish wolf policy starting with 2004.

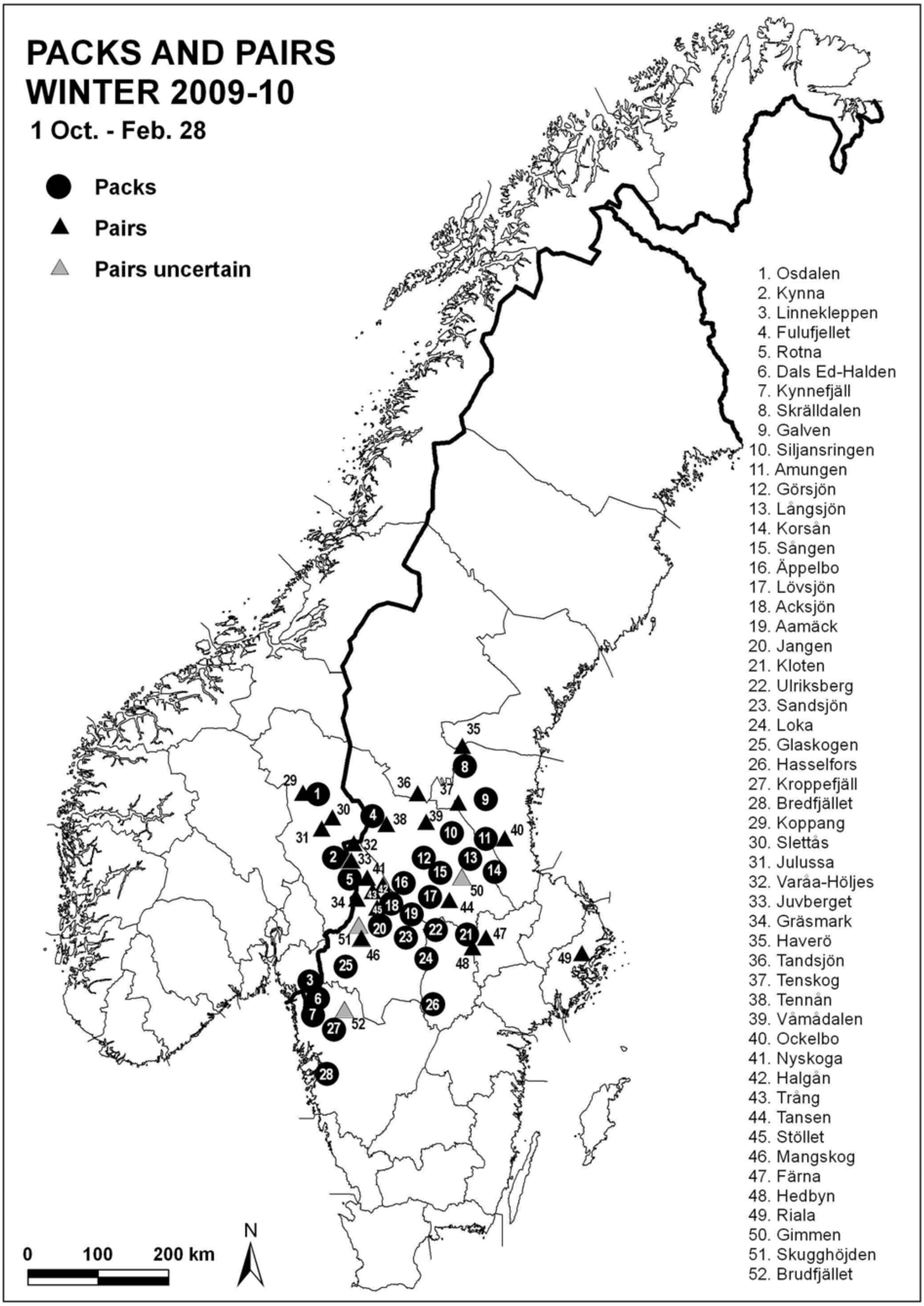


Figure 1. The distribution of wolf territories in Scandinavia the winter 2009-2010.

STUDY AREA

The present wolf range in central Scandianvia covers approximately 100 000 km^2 (Fig. 1). Altitude varies between 100 and 1000 m a.s.l. Average temperature in February is -3 to -9 C, and in July 13 to 16 C. Annual precipitation is 700-900 mm. Snow cover lasts 2-5 months with maximum depths 50-100 cm (SNA 1991). Boreal forest dominates the landscape, and most of it is intensively managed with a dense network of forest gravel roads. In the north-west the wolf range includes some alpine tundra. The human population is sparse, from <1 human/km^2 in the northwest to 10 in the southeast where agriculture might make up as much as 40 % of the area (Swedish National Atlas 1991).

Coexisting large mammalian predators include brown bear (*Ursus arctos*) and European lynx (*Lynx lynx*). Wolverine (*Gulo gulo*) occurs sparsely in the northern part of the wolf range. The most important wild prey species is moose (*Alces alces*)) and roe deer (*Capreolus capreolus*). Wolves also prey on domestic animals, primarily sheep. Approximately 1200 sheep per year are economically compensated as killed by wolves in Norway, and 100-200 in Sweden. Also 30-50 dogs, mainly hunting dogs, have been killed or wounded by wolves annually the last five years in Sweden and Norway. Another source of conflict is competition with human hunters over game, especially moose. More than 150 000 moose are harvested annually in Scandinavia.

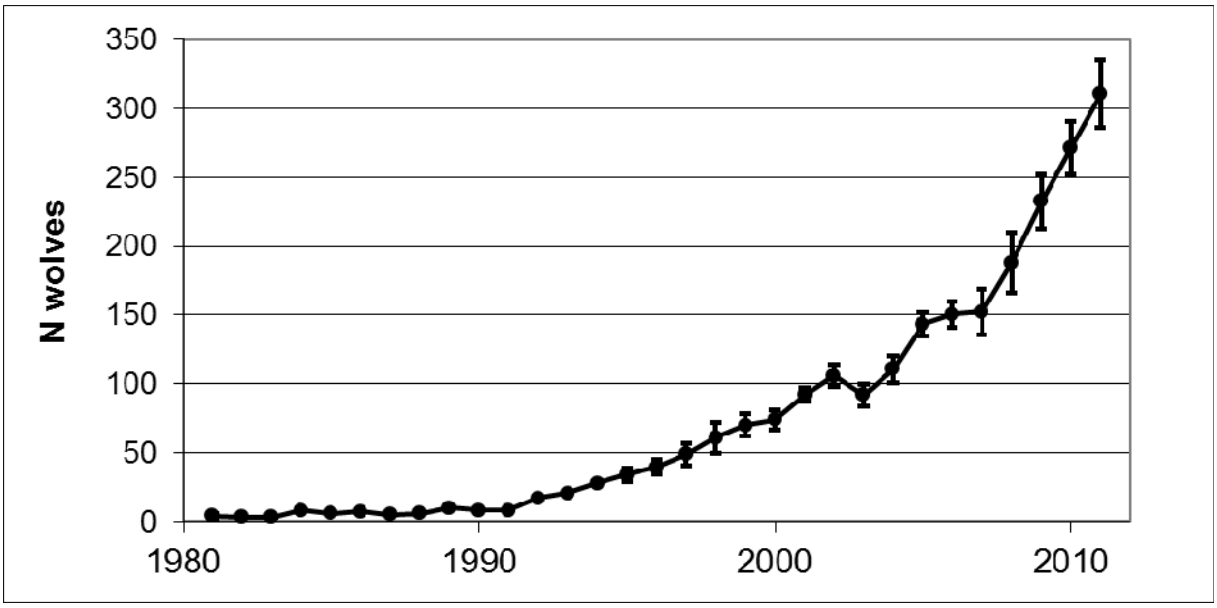


Figure 2. Development of the Scandinavian wolf population size 1981-2011. Data points give number of wolves in early winter for each year whereas bars give minimum and maximum estimates from census data, respectively.

Wolf population development

The Scandinavian wolf population started declining during the 19th century, and when finally protected, 1966 in Sweden and 1972 in Norway, the wolf was functionally extinct in Scandinavia (Wabakken et al. 2001). The nearest source population occurred in Russian Karelia along the eastern border of Finland. During the 1970's wolves expanded into eastern Finland, and by 1977 several wolves were recorded in northern Sweden. In 1982 a pair was formed in south-central Scandinavia and successful breeding was recorded in 1983 (Wabakken et al. 2001). This breeding pair and a third male immigrant arriving in 1990, also with origin in Finland/Russia, were the sole founders of the recent Scandinavian wolf population until 2008 (Liberg et al. 2005). In 2008 another two immigrants from the Finnish/Russian population entered the breeding Scandinavian population, making total number of founders by March 2011 to five. In spite of an increasing degree of inbreeding with negative effects on reproduction (Liberg et al. 2005), the wolf population has expanded (Fig. 2) and in early winter 2010/11 the total population size in Scandinavia was preliminary estimated to 286-335 wolves, of which 89 % occurred in Sweden or in border territories (Wabakken et al. 2011). Preliminary figures for reproductions in 2010 are 25 in Sweden, three in trans-border territories, and three in Norway.

METHODS

Estimation of population size and reproduction

Annual monitoring of wolf numbers and distribution was performed by volunteers and research project personnel until 2002, when the responsibility for performing annual census estimates was taken over by the regional county boards in Sweden. In Norway, Hedmark University College and the Norwegian Nature Inspectorate have been responsible for similar monitoring during the complete period of this study. Since 1998, Swedish and Norwegian wolf monitoring have been coordinated, evaluated and results concluded for each country and total Scandinavia in a joint published, annual Swedish-Norwegian status report (e.g. Wabakken et al. 2010). Field personnel search actively for wolf tracks on snow during the census period (1 October - 28 February), and follow several thousand kilometres of wolf tracks each season. Tracking data are registered including location and length (km) of tracking route, and details of the tracked wolves including number and social status. The search for tracks is aided by reports from hunters and the general public. As a complement to tracking data telemetry data from radio-collared wolves is used and provided by the research project within SKANDULV, and since 2002/03 DNA-analyses of mainly scats also constitutes an important source of information (Liberg et al. 2005, Wabakken et al. 2010).

In each territory the number of wolves was recorded during winter by repeated tracking efforts. We employed DNA and telemetry techniques to help distinguishing between wolves in adjacent territories. In cases where there was uncertainty of exact number in a group, a maximum and a minimum figure was given. All recorded wolves were summed up for a total population estimate, where mean, maximum and minimum figures were given (figure 1, Wabakken et al. 2010). Annual reports on the size of the Scandinavian wolf population have been produced since 1999 (Wabakken et al. 2010).

Recruitment of pups was determined if at least one of the following criteria was satisfied: 1) ocular observations of pups during summer (before October 1); 2) an active den with faeces from pups was found; 3) reproduction confirmed by DNA-analyses; 4) more wolves in the pack on snow than during the previous winter; 5) at least five wolves in the pack confirmed during the annual monitoring, October, 1th - February, 28th.

In primi-parous packs, the total number of wolves minus the breeding pair was registered as the number of pups recruited into the winter. In packs that had reproduced before (itero-parous), the number of pups were calculated the same way, but reduced by 15 % to account for remaining older offspring.

Capture of study animals

Wolves were captured on snow during the winter season. They were first located on ground by searching for tracks in known wolf territories, and then immobilized from helicopter using a CO_2-powered dart gun and a standard dose of drugs, either 500 mg of tiletamine-zolazepam (Zoletil®, Virbac) per animal or a combination of 5 mg of medetomidine (Zalopine®, Orion Pharma Animal Health) and 250 mg of ketamine (Narketan®, Chassot) per animal. All wolves captured were measured, sexed, aged, weighed, and ear tagged. Blood and hair samples were collected. Before 2003, wolves were equipped with conventional VHF radio collar (Telonics, Mod. 500, Mesa, Arizona). However, after we got indications that wolves were radio tracked by unauthorized persons, and suspecting that this practice could be used to facilitate illegal killing, in 2003 we replaced all old transmitters with GPS-collars that can not be abused. The GPS collars were manufactured by either TVP International, Sweden (GPS-Simplex) or by Vectronic Aerospace, Germany (GPS-plus). The handling protocol for wolves has been approved by both the Swedish Animal Welfare Agency and the Norwegian Experimental Animal Ethics Committee and fulfils their ethical requirements for research on wild animals.

Radio tracking and recording of mortality

Wolves with VHF-collars were positioned minimum once a week from ground or air, and during intensive predation study periods 1-5 times per day from the ground. GPS-collars were programmed for positioning 2-6 positions per day, and during intensive study periods at hourly or half-hourly intervals.

Most of the transmitters had a mortality function that enabled us to retrieve dead wolves soon after death which enhanced our chances of determining the cause of mortality. Wolves found dead in Sweden were sent to the Swedish National Veterinary Institute for examination of the cause of mortality, and in Norway carcasses were sent to the Norwegian Institute for Nature Research and examined in co-operation with the Norwegian Veterinary Institute. Mortality causes were classified as: *natural causes* (drowning and other non-human caused accidents, intra-specific strife, disease and malformations), *traffic* (both road and railway), *legal killing* of wolves, in most cases in form of predator control, *verified illegal killing* and *probable illegal killing*. For definition of the last two, see below.

Bodies also were examined for other signs of disease or malformations. At the Swedish National Veterinary Institute all wolf bodies were x-rayed to search for shots, bullets or other traces of metal (Mörner et al. 2005). In Norway this praxis has not been consequent all through the study period.

Criteria for classifying wolves as poached

Criteria for *verified illegal killing* (enough if one criterion is satisfied):

1. The body is recovered and the post mortem show that is was deliberately killed by a human, and that this did not happen during a legal hunt.

2. The transmitter collar was found cut over where the only possible explanation was that this was done by a human being without reporting it to the authorities.

3. Wolf tissue (skin, muscle, bone etc.) determined by DNA-analysis to originate from the recent Scandinavian wolf population, was found in possession of a person that could not explain how he had acquired it

4. Snow tracking of a wolf chased by humans, where it with certainty could be concluded that the wolf was killed, even if the body was not found, e.g. by presence of a typical strong arterial bleeding in the snow (so called “pipe bleeding”).

These criteria were used both for wolves with radio-collars, and for non-instrumented wolves.

Criteria for *probable illegal killing* (either all of criteria 1-3 are satisfied, or criterion 4 is satisfied):

1. Sudden loss of radio contact where there is no reason to suspect transmitter failure (well working transmitter with more than half battery life left). For GPS-collars status of the battery voltage were checked just before contact was lost. A sudden reduction in voltage was used a strong indication that the loss of contact was due to malfunction of the collar.

2. The radio contact could not be re-established in spite of at least two aerial searches over a much larger area than the wolf’s territory (for GPS/GSM-collars this was not necessary).

3. The wolf was stationary and it could with certainty be determined missing in its territory after repeated snow tracking, and/or after DNA-analyses of faeces found in the territory.

4. Radio contact was suddenly lost and special circumstances indicated with a high degree of probability that the most plausible explanation was illegal killing (used only in two cases).

These criteria were used only for radio-collared wolves, and criterion 2 and 3 only for radio-collared territorial wolves.

All other cases of lost radio contact were classified either as *failure of radio collar*, if we had strong indications of that (expected life-time for battery expired, irregular or abnormal VHF-signals just before contact were lost, type of radio-collar known to be un-reliable, the wolf was observed alive with its radio collar after the signal was lost, or found dead and the time of death was determined to have occurred after the signal was lost), or otherwise as *unknown fate*.

Calculation of mortality rates

We used two methods to determine mortality rates, *the radio method* and *the census method.* With the *radio method* we used survival data from our radio-collared wolves and have estimated cause specific mortality rates and tested for difference among groups. We used the competing risk approach proposed by Heisey and Patterson (2006) and ran computations in R. The two competing risks analysed (i.e. cause-specific mortality rates) were illegal killing versus non-illegal killing ("other mortality") for periods 1998-2005 and 2006-2011 and for Sweden and Norway. A competing risk approach is required, as traditional survival analysis methods (e.g Kaplan Meier) introduce a bias when several different mortality causes operate simultaneously. In addition, statistical procedures used in biomedicine cannot be applied in this case because they often do not allow for staggered entry of individuals in the dataset (left censorship).

With the *census method* we could only calculate total mortality. It is based on the difference between consecutive annual censuses of the population and an expected population size based on data on recruitment rate. The mathematical formula we used for the calculation was

$$D = ((P\ t_1 + R_2) - P\ t_2) / P\ t_1$$

where:

D = total annual mortality in the population between year 1 and 2

$P\ t_1$ = population size year 1

$P\ t_2$ = population size year 2

R_2 = number of pups recruited to year 2

With this method no confidence limits could be calculated, nor cause specific mortality rates.

Analysis of possible break points in the material

We used the same competing risk analysis as above but broke the dataset into two sub-datasets with year break point changing from 2001 to 2009. For each sub-dataset, we computed cause-specific mortality rates and tested for statistical differences between the two periods.

RESULTS

Cause specific mortality in radio-collared wolves and lost radio contacts

During the study period we radio-collared a total of 123 wolves in both Norway and Sweden representing 160.9 “radio years” (Table 1). The number of “radio years” was three times as many in Sweden compared to Norway, but the number of recorded mortalities was less than double. At the end of the study 29th February 2011 we still had contact with eight of the radio collared wolves. Six wolves died during, or in connection with, handling of immobilized wolves and were not included in the analysis. Of the remaining 109 wolves, 29 were confirmed dead while their collars still were working, 9 died of natural causes (drowning or other accidents, disease and age), 5 were killed by road and railway traffic, 10 were shot legally, and 5 died in *verified* cases of illegal killing. We lost radio contact with 80 wolves. Nineteen of these were classified as *probably* illegally killed.

Table 1. Number of radio collared wolves (N ind), number of “radio years”, total number of deaths among radio collared wolves, and cause specific deaths. Radio years, and deaths, excluding project related deaths, are also specified on countries and time periods. Number of radio collared individuals could not be specified in this way because the same animal might appear in both countries and/or time periods.

	N ind	N radio-years	N dead tot (excl. project related)	Natural causes	Traffic	Legal hunting	Illegal killing	Prob-able illegal	Project related
Sweden 1998 – 2005		71.0	25	6	3	2	3	11	
Sweden 2006 – 2011		51.1	6	2	1	2	0	1	
Norway 1998 – 2005		29.8	11	1	1	4	2	3	
Norway 2006 – 2011		9.0	6	0	0	2	0	4	
Scandinavia 1998 -2005		100.8	36	7	4	6	5	14	
Scandinav ia 2006-2011		60.1	12	2	1	4	0	5	
Sweden total		122.1	31	8	4	4	3	12	
Norway total		38.8	17	1	1	6	2	7	
Scandinavia total	123	160.9	48	9	5	10	5	19	6

Variation in time and space of annual rates of total mortality and illegal killing in radio collared wolves

Total annual mortality rate in the Scandinavian wolf population (Sweden and Norway together) for the whole study period 1998-2011 was 0.259 (25.9 %) (Table 2). Mortality from illegal killing was 0.128 (12.8 %) and from other causes 0.131 (13.1 %). Norway had a higher mortality rate than Sweden, mainly because of a higher rate of illegal killing.

Table 2. Mean annual rates of illegal killing (verified and probable illegal killing pooled), and other mortality (legal control, traffic, natural) in Scandinavian wolves, in two countries during two time periods (1998-2005 and 2006-2011). Log-rank tests of differences in illegal killing between groups are presented at the bottom of the table.

Data	Illegal killing	±SD	Other mortality	±SD
All	0.128	0.026	0.131	0.025
Sweden	0.111	0.028	0.113	0.026
Norway	0.179	0.054	0.177	0.053
All 1998-2005	0.157	0.033	0.148	0.033
All 2006-2011	0.077	0.034	0.091	0.029
Sweden 1998-2005	0.169	0.042	0.133	0.036
Sweden 2006-2011	0.025	0.025	0.075	0.028
Norway 1998-2005	0.134	0.056	0.181	0.061
Norway 2006-2011	0.323	0.114	0.116	0.078

Tests of differences in illegal killing:
Sweden vs Norway $p = 0.11$
All 1998-2005 vs All 2006-2011 $p = 0.10$
Sweden: 1998-2005 vs 2006-2011 $p = 0.0066$ (**)
Norway: 1998-2005 vs 2006-2011 $p = 0.13$

Annual illegal killing rates in Sweden varied heavily between single years due to small sample sizes, but with a clear decreasing trend in the latter part of the study period with a start of the decline in 2004 (Table 3). In the period 2006-2011 there was only one case of illegal killing among our radio-collared wolves in Sweden. Statistical tests for a change (break point) in this time series gave support for a significant change either after 2003, after 2004 or after 2005 (Fig. 3).

Table 3. Annual mortality rates from illegal killing and other mortality causes in Swedish wolves for the period 1999-2010.

Year	Illegal killing	Variance	Other mort	Variance	N dead	N poached	N radio years
1999	0.314	0.161	0.171	0.156	3	2	5.0
2000	0.318	0.116	0.068	0.068	3	2	9.7
2001	0.000	0.000	0.221	0.098	3	0	12.8
2002	0.234	0.093	0.134	0.044	7	5	16.9
2003	0.214	0.095	0.071	NA	4	3	10.8
2004	0.129	0.120	0.100	NA	2	1	7.4
2005	0.139	0.129	0.266	0.115	3	1	8.2
2006	0.000	0.000	0.071	NA	1	0	12.6
2007	0.000	0.000	0.000	NA	0	0	10.5
2008	0.000	0.000	0.234	0.107	2	0	5.7
2009	0.118	0.110	0.059	NA	2	1	11.5
2010	0.000	0.000	0.067	NA	1	0	9.5

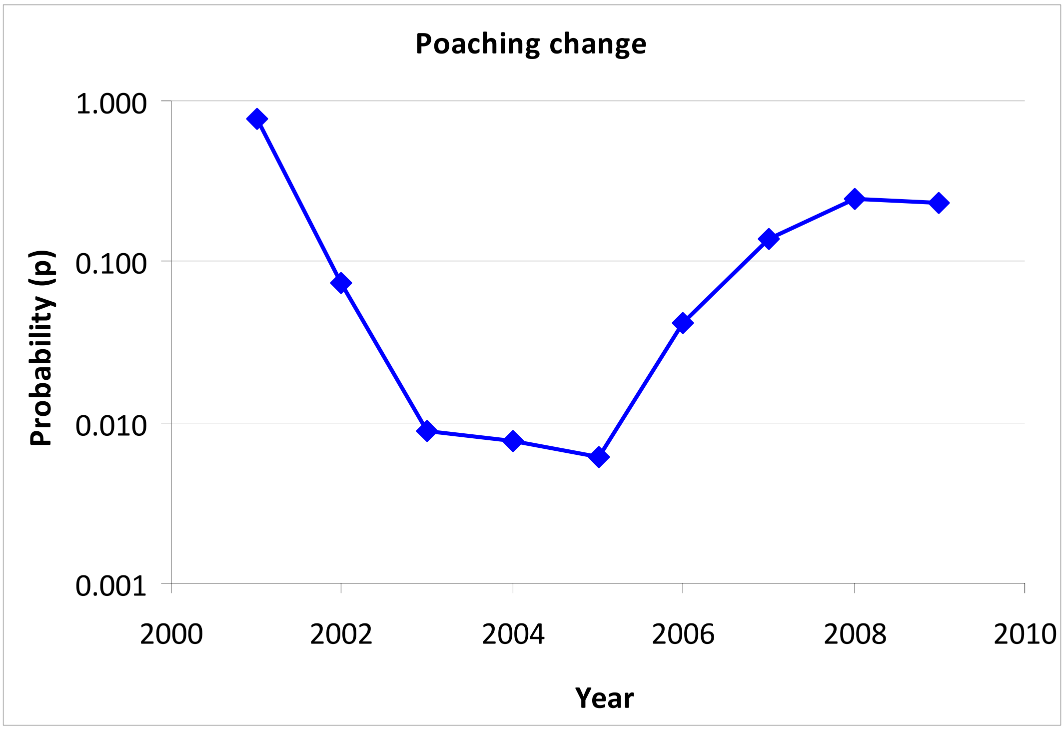


Figure 3. P-values for log-rank test of a break point in time trend of the rate of illegal killing (verified and probable illegal killing pooled) in Sweden. The time points indicate Dec 31st of the respective year.

Because the statistical test gave strongest support for a change after 2005, we have used Dec 31st 2005 as a break point and compared mortality rates of the two time periods 1998-2005 and 2006-2011 in our further analyses. Both illegal killing and other mortality showed a tendency to be lower during 2006-2011 compared to 1998-2005 also for the total dataset from Scandinavia (Table 2). However, the time trends were opposite in Norway and Sweden. Norway had an increase in illegal killing in the latter period, while Sweden had an almost seven-fold decrease, from 0.169 (16.9 %) to 0.025 (2.5 %). This corresponds to 9-20 animals illegally killed per year during 1998 to 2005 and 3-7 animals illegally per year during 2006 to 2010, which is a 65% reduction of the number of poached wolves per year. This change of illegal killing mortality in Sweden was the only difference that was statistically significant (p=0.007). In the period 1998-2005 there were 14 cases of illegal or probably illegal killing recorded in radio-collared wolves in Sweden, whereas there was only one case in the 2006-2011 period. Corresponding figures for Norway were 4 and 5.

Non radio-tracking data on mortality and illegal killing, and population growth over time in Sweden

There was a statistically significant reduction in total number (both radio-collared and non-collared wolves) of detected verified cases of illegal killing of wolves or obvious attempts (one case) of illegal killing in relation to exposure in the form of “wolf years” (see text Table 4) in Sweden from 1998-2005 to 2006-2010 (Table 4). We did not include 2011 as we needed complete years for this analysis. Poisoning attempts were not included.

Table 4. Number of cases of detected verified illegal killing plus attempts of illegal killing detected in both radio-collared and un-collared wolves in Sweden in two time periods. ”Wolf years” are defined as the sum of annually censused wolves in Sweden for all the years in respective period (X^2 = 6.48, p=0.011, Pearson´s two-sided chi-square test).

Period	N cases	N "wolf years"	N cases/1000 "wolf years"
1999 -2005	10	545	18.3
2006 -2010	4	883	4.5

Frequency of wolves with old shot wounds (number of cases in relation to exposure time, see table text for explanation), i.e. wolves that had survived a shooting attempt and in which traces of bullets or shots were found during a post mortem after the death of the wolf, also was slightly lower in the second period compared to the first period for wolves examined post mortem in Sweden, but the difference was not significant (Table 5). If an examined wolf had an old shot wound that it could have contracted in either of the two periods, the case was weighted according to the proportion of the total exposure time in each of the two periods respectively.

Table 5. Cases of old shot wounds found at post mortem examinations of dead wolves from other causes, in two time periods in Sweden. Exposure time was measured as the sum of the portions of longevity in the two periods respective, for all wolves examined post mortem. Shot wounds that could have been afflicted a wolf in either of the two periods were weighted according to exposure time of the concerned wolf in the two periods respectively ($X^2 = 0.168$, $p=0.682$, Pearson´s two-sided chi-square test).

Period	N observed cases of old shot wounds	Exposure time (years)	N cases per 100 years exposure
1999-2006	7.9	143	5.5
2007-2011	9.1	202	4.5

The "census method" for determining wolf mortality in Scandinavia, based on census and reproduction data, produced a total mortality for the whole study period of 0.23, which is close to the rate for the radio-collared wolves (0.26). The census method also indicated a reduction of mortality with time, giving a total mortality of 0.26 in 1998-2005, as compared to 0.20 in 2006-2011. The census method does not allow for calculation of cause specific mortality rates, nor for splitting of the data on Sweden and Norway.

The average annual growth rate of the Swedish part of the Scandinavian wolf population was 16 % for the whole study period. The average for the period 1998-2005 was 14 %, and for the period 2006-2010 it was 19 % (excluding the effect of the license hunts 2010 and 2011) (Figure 4).

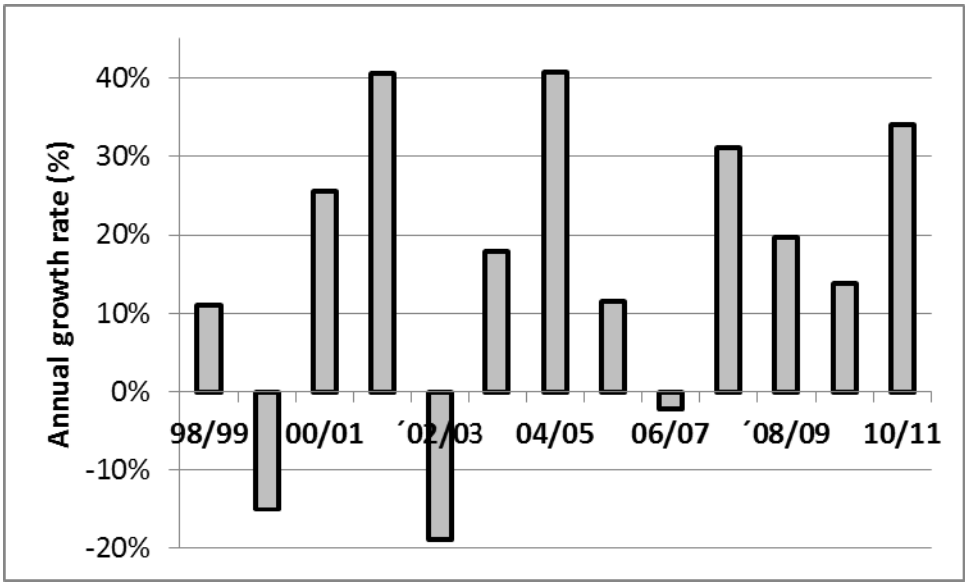


Figure 4. Annual growth rates in the Swedish part of the Scandianvian wolf population 1998-2010. The growth rates concern growth from early winter one year to early winter next year. The years on the x-axis indicate growth from year t-1 to year t (i.e. the growth of 08/09 in the figure refers to the growth from winter 07/08 to winter 08/09). The effects of the quota hunts are excluded from the growth rates of 09/10 and 10/11.

DISCUSSION

Are data on illegal killing and its demonstrated time trend in Sweden, reliable?

Illegal killing was the dominant mortality cause in Scandinavian wolves. Almost half of all dead wolves died from this type of mortality. One problem is that most of the illegal killings among radio-collared wolves could not be verified by the retrieval of a dead body, but were instead based on circumstantial evidence. However, several independent datasets support the high incidence of illegal killing. The "census method" gave a total mortality rate that was close to the one calculated from radio-collared wolves. If our calculation of illegal killing from radio-collared wolves had been a strong overestimate, there must exist some other unknown cause of mortality of similar magnitude that was not registered in our sample of collared wolves, and that simultaneously also would cause radio failure. We have not been able to identify any such alternative mortality cause. In a recently published paper (Liberg et al. 2011) we have presented a more elaborate model based on census and reproduction data where we could also single out illegal killing rate. Total illegal killing rate for Scandinavia 1998-2009 according to this model (0.149) did not differ much from the rate calculated from radio-collared wolves (including VHF-transmitters, see below) for the same period (0.134). The reason that these rates are somewhat higher than in the present report (0.128) probably is that the latter include also data from 2010 and 2011 when we had no cases at all of illegal killing among our radio-collared wolves. We believe this is the strongest support for the validity of the estimate of illegal killing rate and evidence against any suggested bias to this, e.g. the possibility that transmitter type might have influenced our data on illegal killing rate (see below). Our estimated level of illegal killing and total mortality also fits well with the figures we have on population growth. Finally, the data on cases of verified illegal killing and on old shot wounds demonstrate that illegal killing and illegal killing attempts are indeed prevalent in high frequency in the Swedish wolf population.

The data also clearly indicate a reduction of illegal killing of wolves in Sweden starting in the period 2004-2006. The decrease of mortality from illegal killing in radio-collared wolves in Sweden was dramatic, from almost 17 % annually in 1998-2005 to 2.5 % in 2006-2011. This reduction was supported by several independent or partially-independent data sets. Number of verified cases of illegal killing or attempts of illegal killing in wolves is for obvious reasons low, as we expect poachers to make efforts to conceal their activities. Still, in the first period there was more than one case detected each year. After 2005, the frequency of cases in relation to how many wolves that were exposed decreased with 80 %, a difference that was also statistically significant. Two of the cases that occurred in the first period concerned farmers that shot wolves moving close to their life stock, but although they believed they had a right to do this and reported to the police themselves, they were convicted in court according to the hunting laws at that time. These cases would have been legal after the liberalizations of the concerned laws in 2004 and 2006.

Also mortality estimates based on the census method, and data on annual population growth in Sweden gave support to a decrease of illegal killing in the latter part of the study period.

The only data set that did not give a clear indication of a declining illegal killing in Sweden was number of old shot wounds. It decreased after 2005, but the reduction was small, less than 20 %, and not statistically significant. We cannot explain why we do not see the same trend here as in the other data sets. Most of the old shot wounds were superficial, consisting of one or a few small shots from a shot gun, often found in the skin or other superficial tissues (in one case the only shot discovered was found in an ear), probably results of shooting at wolves with shot guns from too large distances to be mortal (mortal range for a shot gun is below 35 m). Perhaps this type of behaviour does not follow the same dynamics as illegal killing with decided mortal intent.

Interestingly, data did not show a corresponding decrease of illegal killing in Norway. However, because more than 80 % of the Scandinavian wolves live in Sweden, the reduction of illegal killing there had an overall effect on total mortality in Scandinavia, from 30 % in the first period to 17 % in the second. This decrease showed a relatively good fit with calculation of total mortality based on census data (from 26 to 20 %), which supports the notion that this reduction was in fact true and to a large extent caused by a reduction of illegal killing.

There was also a decrease in traffic mortality and natural deaths, both in Sweden and Norway between the two time periods, which indicates that there was little, if any, compensatory effects in illegal killing, meaning that most of it was additive to other mortality. This pattern was also supported by the increase in growth rate observed in the Swedish part of the wolf population after 2005.

Possible reasons for the decline of illegal killing in Sweden

The coincidence of the gradually changing wolf policy in Sweden and a reduction in illegal killing of wolves can support the hypothesis that there is a cause-effect, but is not conclusive evidence of this. There are a number of suggested alternative reasons for the decline in illegal killing, where some have support by data while others have not.

One possibility is that there all through our study period have been a relatively constant small number of people that have been prepared to commit themselves to this type of criminal activities. If this is the case, the relative impact of illegal killing would have been reduced as the wolf population grew and expanded its distribution, and a gradual decrease of illegal killing rate with the continuous increase of the wolf population would be expected all through the study period. Indeed, when plotting illegal killing rates in Sweden against population size, there was a significant decreasing trend ($R^2 = 0.37$, $p = 0.035$, linear regression), albeit with a large inter-annual variation (Fig. 5). We compared this trend with a simulated trend where we have assumed a constant number of wolves killed illegally each year and received a relatively good fit between the two trends (Fig. 5).

Alternatively there could also have been a change in behaviour within the group of offenders. It has been suggested that their motivation to continue killing wolves illegally might gradually have eroded when they have realized that they are fighting a hopeless fight, as the wolf population has continued to grow in spite of their efforts. Also a gradually increasing law enforcement activity against illegal killing of large carnivores during the last decade might have had effect.

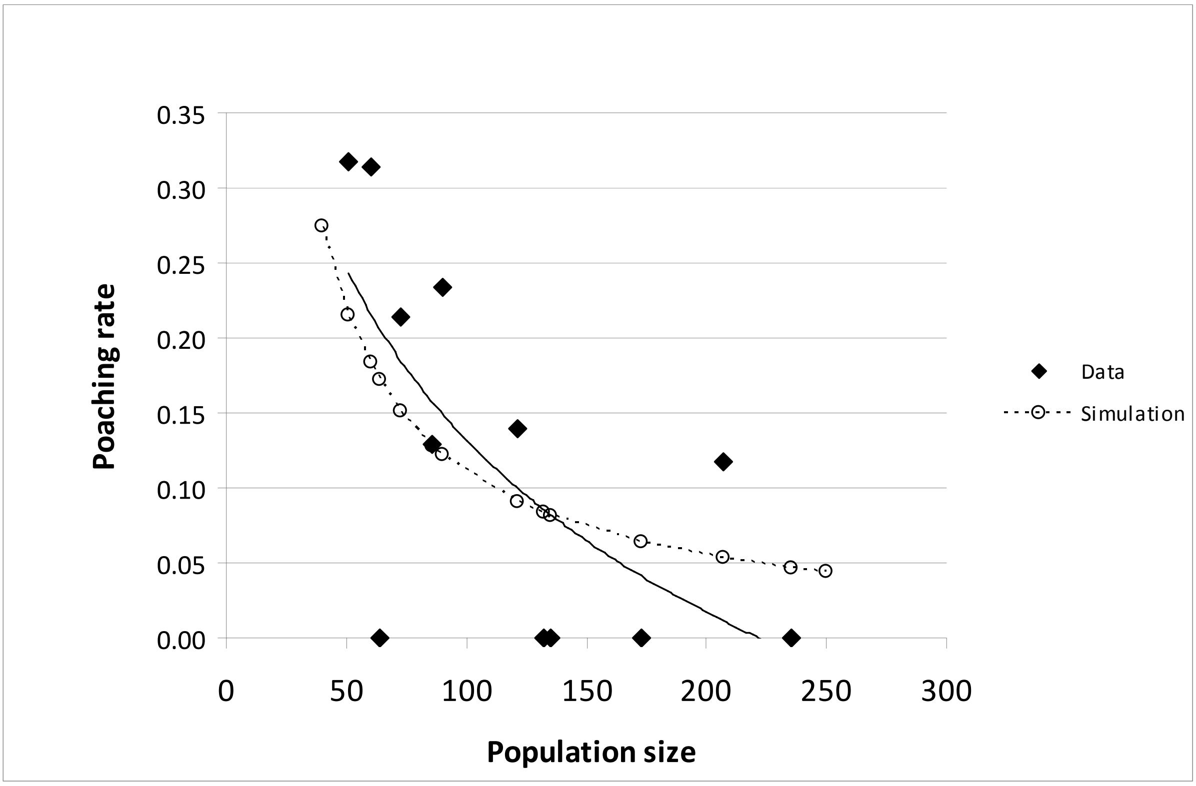


Figure 5. The rate of illegal killing in relation to population size of wolves in Sweden. Also included is a simulation of illegal killing rates when number of wolves killed per year is kept constant. The best fit with data occurred when this constant number was 11 wolves.

There is less support for the assumption that poachers gradually have learned to avoid radio-collared wolves and increasingly focused on non-instrumented animals in an effort to conceal their activity. If this had been the case, the decline of illegal killing would only have occurred in our radio-collared wolves, not in the whole population. The two independent data sets used in this study both infer a real decline of illegal killing in the whole population thus contradict the possibility of a selective killing of animals

Another suggested reason for a declining trend in illegal killing is our change of transmitter type during the study period. In the first years we used VHF-transmitters where poachers may have had the possibility to scan the collar frequency and exploited the transmitter to get in range of the carriers to kill them. However, in winter 2001/02 we started to exchange this type of transmitters to a more secure type of GPS-transmitters, which do not emit signals that can be misused, and by March 2003 all transmitters in operation were of the new type. If this had been an important source of error, our estimates of illegal killing up to 2003 would have been overestimates. However, our modelling based on independent data does not support this possibility (Liberg et al. 2011). Also, the lack of a decline in illegal killing in Norway, supports the conclusion that this possible bias, if real, had a small magnitude.

Although Norway all through the study period had a more liberal legal hunting policy of wolves than Sweden, it had a higher incidence of illegal killing. This could seem to contradict the idea that more legal hunting reduces illegal killing, but in fact it is rather the opposite. Most of the illegal killing of wolves in Norway occurred inside the Norwegian wolf zone in south-eastern Norway along the border to Sweden where wolves enjoy an even stronger degree of protection than in Sweden. After the Norwegian Parliament established the wolf zone in 2004, the Norwegian management authorities have not given any permission to wolf control within the zone. All legal hunting has taken place outside the zone, where there are very liberal regulations for control, and no permanent establishment of wolf territories are allowed. So, most illegal killing occurs inside the zone where there is no legal hunting, while there is almost no illegal killing outside where legal hunting is very liberally issued.

It is not possible to point out a single factor that explains the reduction of illegal killing in Sweden, but we think there is strong evidence that a reduction really has occurred, i.e. ruling out the possibility that it is just an artefact caused by our replacement of one transmitter type with another or a change in poacher focus towards non-instrumented wolves. The different alternative explanations suggested here for a declining trend in illegal killing are not mutually exclusive. In fact, they may all have contributed to this positive trend.

Unfortunately there is very little data on the association between legal and illegal killing of large carnivores in the literature. Treves (2009) found no evidence for such a trade-off, but he based his conclusion on only three publications. One of these (Andrén et al. 2006) actually was ambiguous on this point, and the other two (Adams et al. 2008, Person & Russell 2008) studied wolf populations in remote areas in North America with relatively little contact with people. There are a few papers that indicate a certain association between legal and illegal take off of large carnivores (Wielgus et al. 1996, Huber 2002), but firm conclusions may not be drawn. This issue if of such great importance for conservation policy makers and large carnivore managers worldwide, that there is a great need for more studies to focus on these aspects. Ideally ecological/demographic data should be complemented with studies of attitudes of local people concerned, especially studies of attitudes in the same group of people before and after certain management changes towards large carnivores has been implemented in their area.

CONCLUSIONS

Illegal killing was the dominant mortality cause for wolves in Scandinavia during 1998-2011 and accounted for half of total mortality. We found differences in the extent of illegal killing between Norway and Sweden and between the two time periods 1998-2005 and 2006-2011, but with opposite trends in the two countries. The only difference that was statistically significant was the reduction of illegal killing in Sweden after 2005 (from 16.9 % in 1998-2005 to 2.5 % in 2006-2011). Several different independent data sets show the same pattern and support that there has indeed occurred a reduction of illegal killing in Sweden, and we could rule out that it was an artifact caused by a change of radio transmitter technique or a selective behavior of poachers towards radio-collared wolves. We conclude that we cannot point out a single factor explaining this positive trend, but suggest that several factors might have contributed, including lack of numerical/functional poaching response to the increasing wolf population and a falling motivation in poachers as well as the various elements in a changed wolf policy after 2004, such as increased control of depredating wolves, a temporal freezing of the population with a regulating quota-based hunt, more local participation of management decisions and a strengthened law enforcement. In fact, there is a possibility that several, or all of these factors have contributed to the observed trend, and that they have influenced each other so that, for example number of poachers or intensity of poaching have failed to increase with the expanding wolf population due to one or several of the changes in wolf policy.

ACKNOWLEDGEMENTS

This report was prepared after request by the World Wide Fund for Nature (Sweden), which also provided a specific grant for its preparation. We are indebted to J. M. Arnemo, P. Ahlqvist and P. Segerström, who captured and handled the wolves. We also want to thank the large number of field workers in Norway and Sweden, and their leading officers at the local county offices ("länsstyrelser" and "fylkesmen") and at SNO, as well as other field workers and students connected to the wolf research for their enormous amount of work with tracking, sampling and reporting. We specifically want to mention T. Berglund, A. Blixgard, S.E. Bredvold, A. Bye, L.E. Carlsson, J Carlsson, M. Dötterer, J. Enerud, B. Fransson, F. Holen, G. Jansson, N. Johansson, P. Kirkeby, P. Larsson, W. Lundin, L-A. Magnusson, A. Nordin, S. Nordlund, E. Maartmann, C. Moberg, B. Olsson, M. Rapp, H. Rønning, R. Skyrud, T. H. Strømseth, O-K. Steinset and C. Wikenros. The DNA-work was performed by M. Åkesson and A. Danielsson at the DNA-laboratory at Grimsö. L. Svensson and Å. Aronson at the Swedish Wildlife Damage Center compiled census data. The Swedish National Veterinary Institute (SVA) and the Veterinary Laboratory at the Norwegian Institute for Nature Research performed the post mortem investigations of retrieved dead wolves. The study was supported by the Swedish Environmental Protection Agency, the Swedish Association for Hunting and Wildlife Management, World Wildlife Fund for Nature (Sweden), Swedish University of Agricultural Sciences, Norwegian Directorate for Nature, Management, Norwegian Research Council, Norwegian Institute for Nature Research, Hedmark University College, County Governors of Hedmark and Värmland, Borregaard Skoger, Glommen Skogeierforening, Norskog, Norges Skogeierforbund, Olle and Signhild Engkvists Stiftelser, Carl Tryggers Stiftelse, Marie Claire Cronstedts Stiftelse, Swedish Carnivore Association, and Stor-Elvdal, Åmot, Åsnes and Trysil municipalities. All research presented complies with the current laws of the country in which the experiments were performed.

References

Adams, L.G., Stephenson, R.O., Dale, B.W., Ahgook, R.T. and Demma, D.J. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska Wildlife Monographs, 170: 1–25.

Altrichter, M., Boaglio, G. and Perovic, P. 2006. The decline of jaguars Panthera onca in the Argentine Chaco. Oryx 40(3): 302-309.

Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, Y., Franzén, F. and Segerström, P. 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. – Biological Conservation 131: 23-32.

Creel, S. and Creel, N. 1998. Six ecological factors that may limit African wild dogs. Animal Conservation 1: 1-9.

Damania R., Stringer R., Karanth K.U. and Stith B. 2003. The economics of protecting tiger populations: linking household behavior to illegal killing and prey depletion. Land Economics 79: 198–215.

Eliason, S.L. 2004. Accounts of wildlife law violators: motivations and rationalizations. Human Dimensions of Wildlife 9: 119-131.

Heisey D.M. and Patterson B.R. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. Journal of Wildlife Management 70(6): 1544-55.

Huber, D., Kusak, J., Guzvica, G., Gomeric, T. and Frkovi, A. 2002. Causes of wolf mortality in Croatia in the period 1986-2001. Veterinarski Arhiv 72: 131-139

Liberg, O., Andrén, Pedersen, H-C., Sand, H., Sejberg, D., Wabakken, P., Åkesson, M. and Bensch, S. 2005. Severe inbreeding depression in a wild wolf (Canis lupus) population. Biol. Lett. 1: 17-20.

Liberg, O., Sand, H., Wabakken, P and Pedersen, H.C. 2008. Dödlighet och illegal jakt i den skandinaviska vargstammen. Rapport från Grimsö forskningsstation och Viltskadecenter. 42 sidor.

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. and Sand, H. 2011. Shoot, shovel and shut up: cryptic illegal killing slows restoration of a large carnivore in Europe. Proc. Roy. Soc. B. doi:10.1098/rspb.2011.1275

Person, D.K. and Russell, A.L. 2008. Correlates of mortality in an exploited wolf population. Journal of Wildlife Management, 72: 1540–1549.

Peters, R.P., and Mech, L.D. 1975. Scent marking in wolves: a field study. American Science 63: 628-637.

Swedish National Atlas (1991). Befolkningen (The population). Svensk National Atlas Förlag, Stockholm.

Swenson, J.E. and Andrén, H. 2005. A tale of two countries: large carnivore depredations and compensation schemes in Sweden and Norway. - Pp 323-339 in: Woodroffe, R., Thirgood, S. & Rabinowitz, A. (eds.). People and Wildlife: Conflict or Co-existence? Cambridge University Press.

Treves, A. 2009. Hunting for large carnivore conservation. Journal of Applied Ecology 46: 1350–1356.

Treves A, and Karanth, K.U. 2003. Human carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17: 1491–1499.

Wielgus, R.B., Bunnell, F.L., Wakkinen, W.L. and Zager, P.E. 1994. Population dynamics of Selkirk Mountain grizzly bears**.** Journal of Wildlife Management. 58: 266-272.

Wabakken, P., Aronson, Å., Sand, H., Steinset, O. K. and Kojola, I. 1999. Ulv i Skandinavia: Statusrapport for vinteren 1998-99. Høgskolen i Hedmark, rapp. 19/99. 46s.

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.

Wabakken, P., Aronson, Å., Strømseth, T.H., Sand, H. E. Maartmann, L. Svensson, Ø. Flagstad, E. Hedmark, O. Liberg and I. Kojola 2010. Ulv i Skandinavia: Statusrapport for vinteren 2005-2006. Oppdragsrapport nr. 4 - 2010. Høgskolen i Hedmark.

Woodroffe, R. and Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. Science 280: 2126-2128.