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Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes

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ABSTRACT

Causes of mortality were described for 245 radio-marked Eurasian lynx (*Lynx lynx*) in five different Scandinavian study areas. Furthermore, the survival rates and the population growth rates were estimated for three of the study areas where 202 lynx were followed for a total of 314 radio-years. The main causes of mortality in adult Eurasian lynx in all our study areas were overwhelmingly anthropogenic, with starvation, vehicle collisions, intra- and interspecific killing and disease only having a minor role. The mean mortality rates for adults increased from 2% to 17% when hunting and poaching were included, i.e., an increase by a factor of eight. This in turn had a large impact on population growth rates, which changed from more than a 20% annual increase to only a 2–4% when hunting and poaching were included. Poaching accounted for 46% of the mortality in adult lynx. Poaching and legal harvest appear to be primarily motivated by conflicts; lynx depredation on semi-domestic reindeer in northern Scandinavia, competition with hunters for roe deer in southern Scandinavia, and depredation on free-ranging domestic sheep in all Norway. The lowest poaching rate was found in the Hedmark study area in Norway, which also had a high legal harvest. The poaching rate was higher in one of the Swedish study areas (Sarek) where legal hunting was lower than in other areas. On the other hand, both the poaching rate and the legal harvest were high in the Akershus/Østfold study area in Norway. Thus, there does not seem to be a simple relationship between an increased legal harvest and decreased poaching as is commonly expected. The most important conservation actions are to combat poaching through both law enforcement and measures designed to increase tolerance.

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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 Scandinvia, all of the four large carnivores (Eurasian lynx *Lynx lynx*, brown bear *Ursus arctos*, wolverine *Gulo gulo* and wolf *Canis lupus*) occur mainly outside protected areas in the surrounding matrix of multi-use landscapes (Swenson et al., 1994; Landa et al., 2000; Linnell et al., 2001; Wabakken et al., 2001) where the potential for diverse conflicts is high. Furthermore, most protected areas in Sweden and Norway are smaller than the home ranges of individual large carnivores (Linnell et al., 2001).

Lynx are found from south-central Sweden and northwards (Östergren et al., 1998; Liberg and Glöersen, 2000) and in most of Norway except in the south-western parts (Brøseth et al., 2003). 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). In areas outside the reindeer husbandry area roe deer (*Capreolus capreolus*) are the main prey (Haglund, 1966; Aanes et al., 1998), but sheep (*Ovis aries*) are also preyed upon in these areas (Odden et al., 2002). Because of the conflicts between lynx and reindeer husbandry, sheep farming, and hunters, many interest groups demand that lynx populations be actively managed, such that distribution and density of lynx populations is limited (Andersen et al., 2004; Herfindal et al., 2005). However, active management of any wildlife species requires a base of good scientific data, especially for low density species like large carnivores.

The rate of increase of large carnivore populations is most sensitive to changes in adult mortality (Hovey and McLellan, 1996; Sæther et al., 1996; Gaona et al., 1998; Sæther et al., 1998). Hunting mortality on large carnivores is often additive to other mortality (Brand and Keith, 1979; Bailey et al., 1986; Swenson et al., 1997; Krebs et al., 2004). 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, and can potentially prevent the recovery of species with low or moderate rates of increase, especially if they naturally live at low densities (Kenney et al., 1995; Nowell and Jackson, 1996; Servheen et al., 1999). Therefore, the aim of this paper is to describe causes of mortality in the Eurasian lynx populations in Scandinavia. We also raise the question whether increased hunting quotas can increase stakeholder acceptance (Ericsson et al., 2004) and thereby lower the poaching levels. This question is of major concerns for successful conservation and management of many species, not only large carnivores.

2. Study area

This study is based on telemetry data from five different study areas in Sweden and Norway; Sarek and Bergslagen in Sweden, Nord-Trøndelag, Hedmark and Akershus/Østfold in Norway (Fig. 1).

The northernmost study area (Sarek; 8000 km^2) is located in the county of Norrbotten around Kvikkjokk (67°00′N, 17°40′E) in northern Sweden. Part of the area is within Sarek National Park (2600 km^2). 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. Data on lynx survival for this study has been collected from 1994 to 2002.

The north-central study area is located within Nord-Trøndelag county in Norway (64°35′N, 12°20′E). The study area is about 6000 km^2 and includes agricultural land (<5% of the study area) in valley bottoms, boreal forest, and alpine tundra above the tree line. The forest is intensively managed for pulp and timber. The boreal forests are dominated by Norway spruce and Scots pine and large bogs. The area is located within the Sami reindeer husbandry area. Data on lynx survival for this study has been collected from 1994 to 1996.

The central area is situated in the county of Hedmark in south-eastern Norway (61°15′N, 11°30′E). The area is about 8600 km^2. The topography consists of several parallel river valleys running from north to south at about 200–500 m a.s.l., with hills ranging from 600 to 900 m a.s.l. The region is dominated by coniferous forest, covering about 72% of the

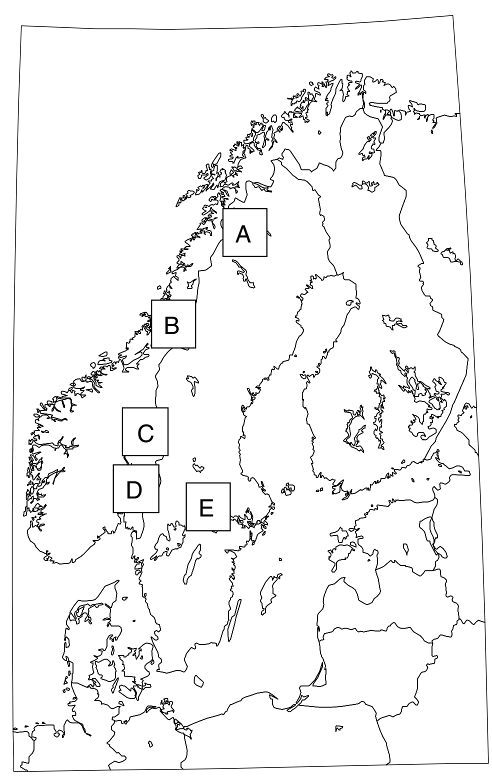

Fig. 1 – Map of Scandinavia showing the five study areas where data were collected. A – Sarek (in Norrbotten county), B – Nord-Trøndelag, C – Hedmark, D – Akershus/Østfold, E – Bergslagen (in Örebro county).

area. Scots pine and Norway spruce are the dominant tree species, but birch may also be well represented, especially in the forest-alpine interface and along rivers. Most of the forest is intensively managed, resulting in a mosaic of even aged forest stands. Data on lynx survival for this study has been collected from 1995 to 2002.

The Akershus/Østfold study area (59°45′N, 11°15′W) is situated around the Norwegian capitol Oslo, and is broadly similar to the Hedmark area. However, the proportion of farmland and the human density is far higher. Data on lynx survival for this study has been collected from 2000 to 2003.

The southernmost 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 of south-central Sweden, mainly in Örebro county. 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). Data on lynx survival for this study has been collected from 1996 to 2002.

Roe deer are the main prey in the Hedmark, Akershus/Østfold and Bergslagen study areas (Haglund, 1966; Aanes et al., 1998; Liberg and Glöersen, 2000), while semi-domestic reindeer is the main prey in the Sarek area (Haglund, 1966; Pedersen et al., 1999). In the Nord-Trøndelag study area both roe deer and semi-domestic reindeer are equally important prey for lynx (Sunde et al., 2000).

3. Methods

This study is based on radio-collared lynx. 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 were treed with the use of dogs. The lynx were immobilised with a mixture of ketamine (5 mg/kg) and medetomidine (0.2 mg/kg; Kreeger et al., 1999) and equipped with either a radio-collar (Telonics Mod 335 or Mod 400 or Televilt TXH-3) or an implanted transmitter (Telonics Imp 400L). We also radio-marked neonatal kittens at the age of 5–6 weeks with implanted radio-transmitter (Telonics Imp 150L; Arnemo et al., 1999) in the Hedmark and Bergslagen areas. The handling protocol for lynx has been examined by both the Swedish Animal Welfare Agency and the Norwegian Experimental Animal Ethics Committee and fulfils their ethical requirements for research on wild animals.

The lynx were 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. In Sweden the lynx carcasses were send to the Swedish National Veterinary Institute for examination of the cause of mortality. In Norway lynx carcasses were sent to the Norwegian Institute for Nature Research and examined in co-operation with the Norwegian Veterinary Institute to identify the cause of mortality.

Cause of mortality was classification into natural (i.e., starvation, sarcoptic mange, 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), probable poaching (see below), or unknown cause of mortality (i.e., lynx certainly dead but the cause could not be determined, in most cases unmarked kittens that were lost during the period from the natal lairs in June to radio-marking in February).

Poaching is very difficult to quantify. Sometimes it was 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 in strange places, e.g., the bottom of a lake and the collar had been cut off the lynx, or else a collar was found smashed. We also conclude 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 suddenly disappeared and we had been radio-tracking the area very carefully after the disappearance.

However, to separate between probable poaching and unknown disappearance (such as rapid long distance dispersal or transmitter failure) we used several criteria. Poaching was probable if a resident adult lynx suddenly disappeared and we had been radio-tracking the area very carefully from the air immediately after the disappearance. Furthermore, there were no signs of technical problems with the radio-transmitter (e.g., strange or weak signals), at least half of the expected lifetime of the radio-transmitter was still available and we had searched the area carefully for signals (usually from the air). Young lynx that had not established their own home range and were in the phase of dispersal were classified as probable 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 very carefully from the air immediately after the disappearance. Otherwise, the lynx was classified as unknown fate.

Survival rates of radio-marked lynx were calculated using the staggered entry design, which is a modified Kaplan–Meier estimate (Pollock et al., 1989). As lynx are long-lived animals, several individuals were used for more than one year to estimate the number of individuals at risk. However, in order to avoid pseudo-replication we only used the number of unique individuals to estimate the standard error. For kittens that were only counted or tattooed in natal dens, rather than being radio-marked with implanted transmitters, we estimated the survival rate from birth to radio-marking in February using the Mayfield estimate (Krebs, 1999). Age specific mortality estimates were divided into males and females, three age classes (kittens <12 months old, yearlings 12–24 months old and adults >24 months old). Enough data was available to calculate these estimates for three study areas (Sarek, Hedmark and Bergslagen).

We estimated three survival rates. The first one includes natural and unknown causes of death. The second one also includes traffic, poaching and probable poaching, i.e., uncontrolled human caused mortality. Finally, the third one also includes hunting, i.e., mortality which is controlled by the management agencies. In the Hedmark study areas hunters were encouraged to not kill radio-marked lynx during the hunting season, which will lead to a downward bias in estimated harvest rate, whereas in the other areas no restrictions were made to protect the lynx from being shot. The data from

Nord-Trøndelag and Akershus/Østfold were only used to describe the causes of mortality in lynx, as the relatively small sample sizes (14 and 29 lynx, respectively) were too small to estimate reliable survival rates. Differences in mortality rates were tested according to Pollock et al. (1989).

The effect of hunting and poaching on the rate of increase was described by calculating the rate of increase (λ) using the different survival estimates (Table 2). When the survival was 1.00 for a category the highest survival value from the same category but from another study area was used. Data on reproduction was taken from Andrén et al. (2002). The mean number of kittens per litter was 0.625 (±0.420 SE) and 1.603 (±0.158 SE) for 2 year old females and $\geqslant$3 year old females in Sarek, respectively. Corresponding numbers for Hedmark were 0.375 (±0.376 SE) and 1.364 (±0.251 SE) for 2 year old females and $\geqslant$3 year old females, respectively. In Bergslagen the reproductive rate was 2.048 (±0.288 SE) kittens per litter for females $\geqslant$2 years old.

Data on the number of lynx in the counties where the study areas are located were obtained from the regular lynx surveys conducted by the respective wildlife management authorities (Liberg and Glöersen, 2000; Odden et al., 2000; Liberg and Andrén, 2005; Linnell et al., in press). The lynx quotas and number of shot lynx were obtained from the Swedish Environmental Protection Agency and the Norwegian Directorate for Nature Management.

4. Results

In the Nord-Trøndelag study area 14 lynx were radio-marked between January 1994 and June 1996 and tracked for 9 radio-years. The cause of mortality could be documented in three cases, 5 radio-transmitters stopped sending signals and 6 radio-collars were still working when the study ended in December 1996. The data from Sarek, Hedmark, Akershus/Østfold and Bergslagen was based on 84, 55, 29 and 63 radio-marked lynx that have been followed for a total of 136, 86, 34 and 92 radio-years, respectively.

For all study areas pooled, the causes of mortality differed among age classes (data pooled into three groups; 1 – natural and unknown; 2 – traffic, poaching and probable poaching; 3 – hunting; $G = 87.1$, $df = 4$, $p < 0.0001$, Table 1). Adult lynx died more often because they were shot, legally or illegally (Fig. 2). This was also true for the yearlings, however, natural causes and traffic were also important mortality causes. Most lynx kittens died of unknown causes. Most of these were marked or counted as neonates in June, whereas at first snow (December to January) the kittens were no longer with their mothers (no radio instrumented kittens dispersed at this young age). The natural causes of death identified include six cases of starvation, two cases of sarcoptic mange and two kittens (siblings) found dead with high levels of internal parasites, presumed to be the ultimate cause of death through starvation. Another five lynx died from interactions with other carnivores, one adult male was killed by another male during the mating season, a young female was probably killed by another lynx, and one young male was probably killed by a wolverine.

The time of the year (data pooled into two groups; 1 – January to June and 2 – July to December) at which lynx were illegally killed differed significantly between the northernmost study area (Sarek) compared to the other four study areas (Nord-Tröndelag, Hedmark, Akershus/Østfold and Bergslagen; Fig. 3; $G = 3.96$, $df = 1$, $p = 0.047$). In the northernmost study area (Sarek) most lynx were illegally shot during the first half of the year (January–June), whereas in the three other study areas most lynx were illegally shot during the second half of the year (July–December).

Legal hunting and poaching, including probable poaching, were the only causes of mortality for yearling females in Sarek, for yearling males and adult males and females in Hedmark and Akershus/Østfold, as well as for yearling males in Bergslagen (Table 1). The survival rates for the different age classes were clearly affected by hunting and poaching, especially for the older (>1 year old) lynx. The mean survival rates (adult males and females and all three study areas pooled together) decreased by 15% units, from 98% survival to 83% survival (Table 2). Or, expressed the other way around, the mean mortality rate for adult lynx increased from 2% to 17%, i.e., an increase by a factor of eight (Table 2).

The mean annual rates of increase (λ) were significantly above 1 for all three study area when only natural and unknown causes of mortality were included in the survival estimates (Sarek, $Z = 3.44$, $p < 0.001$, Hedmark, $Z = 2.30$, $p = 0.02$ and Bergslagen, $Z = 3.74$, $p < 0.001$; Table 2). The mean annual rates of increase (λ) decreased by about 10% units as traffic and poaching were included in the survival estimates. Hunting further decreased the mean annual rates of increase (λ) with another few percent units. The final mean annual rates of increase (λ) including all causes of mortality were not significantly different from 1 for Sarek and Hedmark (Sarek, $Z = 0.96$, $p = 0.34$, Hedmark, $Z = 0.15$, $p = 0.88$), whereas it was significantly higher than 1 for Bergslagen ($Z = 1.96$, $p = 0.05$; Table 2).

The poaching rate on the radio-marked lynx in a given year within the Sarek study area was not significantly related to the quota rate that year in Norrbotten county (Spearman rank, $R_s = 0.11$, $p = 0.79$, $n = 7$). Also in the Bergslagen study area there was no significant relationship between the poaching rate in a given year on the radio-marked lynx and the quota rate that year in Örebro county (Spearman rank, $R_s = -0.05$, $p = 0.91$, $n = 6$).

The mean hunting rates on the radio-marked lynx in the Sarek study area and in the Bergslagen study area were not significantly different from the mean hunting rate (i.e., the number of shot lynx in relation the estimated population size) in Norrbotten county and Örebro county ($Z = 0.34$, $p = 0.73$ and $Z = 0.13$, $p = 0.90$, respectively; Table 3). The quota rates (i.e., the number of lynx given in a quota in relation to the estimated population size) were highest in the counties of Akershus and Østfold (56%; Table 3), followed by Hedmark (28%), and the counties of Norrbotten and Örebro (6.7% and 8.8%, respectively). The poaching rate on the radio-marked lynx was almost significantly lower in the Hedmark study area than in Sarek ($Z = 1.76$, $p = 0.08$; Table 3). There were no significant differences in poaching rate between Hedmark and Akershus/Østfold ($Z = 0.52$, $p = 0.61$), Hedmark and Bergslagen ($Z = 0.17$, $p = 0.86$), Akershus/Østfold and Sarek ($Z = 0.84$, $p = 0.41$) and Akershus/Østfold and Bergslagen ($Z = 0.39$, $p = 0.70$).

Table 1 – Causes of death in radio-marked lynx in five different study areas in Scandinavia

Study area sex and age class	Natural	Unknown cause of death	Traffic	Poaching	Probable poaching	Hunting	Unknown fate
Sarek							
Males (0–1 year)	–	19	–	–	1	–	2
Males (1–2 years)	3	–	–	–	–	1	8
Males (>2 years)	2	–	1	1	6	1	3
Females (0–1 year)	4	16	–	–	2	–	–
Females (1–2 years)	–	–	–	–	1	–	6
Females (>2 years)	2	–	–	2	6	–	4
Nord-Trøndelag							
Males (0–1 year)	–	–	–	–	–	1	–
Males (1–2 years)	–	–	–	–	–	–	–
Males (>2 years)	–	–	–	1	–	–	–
Females (0–1 year)	–	–	–	–	–	–	–
Females (1–2 years)	–	–	–	–	–	–	–
Females (>2 years)	–	–	–	–	–	1	–
Hedmark							
Males (0–1 year)	1	3	–	–	–	–	–
Males (1–2 years)	–	–	–	1	1	1	3
Males (>2 years)	–	–	–	–	–	3	–
Females (0–1 year)	1	3	–	–	–	–	1
Females (1–2 years)	1	–	1	–	1	–	2
Females (>2 years)	–	–	–	–	2	4	1
Akershus/Østfold							
Males (0–1 year)	–	–	1	–	–	1	4
Males (1–2 years)	–	–	–	–	–	1	2
Males (>2 years)	–	–	–	1	–	3	–
Females (0–1 year)	–	1	–	–	–	–	2
Females (1–2 years)	–	–	–	–	1	–	–
Females (>2 years)	–	–	–	–	1	4	–
Bergslagen							
Males (0–1 year)	1	11	2	1	–	2	4
Males (1–2 years)	1	–	1	–	–	–	–
Males (>2 years)	–	–	–	1	1	5	2
Females (0–1 year)	–	10	1	–	–	–	1
Females (1–2 years)	–	1	–	–	1	–	2
Females (>2 years)	–	1	–	2	–	1	–
Total							
Males (0–1 year)	2 (4.5%)	33 (75.0%)	3 (6.8%)	1 (2.3%)	1 (2.3%)	4 (9.1%)	10
Males (1–2 years)	4 (40.0%)	–(0%)	1 (10.0%)	1 (10.0%)	1 (10.0%)	3 (30.0%)	13
Males (>2 years)	2 (7.7%)	–(0%)	1 (3–8%)	4 (15.4%)	7 (26.7%)	12 (46.2%)	5
Females (0–1 year)	5 (13.2%)	30 (78.9%)	1 (2.6%)	–(0%)	2 (5.3%)	– (0.0%)	4
Females (1–2 years)	1 (14.3%)	1 (14.3%)	1 (14.3%)	–(0%)	4 (57.1%)	– (0.0%)	10
Females (>2 years)	2 (7.7%)	1 (3.8%)	–(0%)	4 (15.4%)	9 (34.6%)	10 (38.5%)	5

5. Discussion

This study reveals that anthropogenic cause of mortality were very important for adult lynx in all five study areas, whereas natural causes were most important for kittens (Table 1, Fig. 1). Few other large carnivore studies have comparative data on juvenile survival, however, this pattern of human caused mortality being dominant for adults is similar to that of other large carnivores living in multi-use landscapes, and even in protected areas (Woodroffe and Ginsberg, 2000). Although European data is sparse traffic and poaching were the most common causes of mortality in Eurasian lynx in Switzerland (Schmidt-Posthaus et al., 2002) and Poland (Jedrzejewski et al., 1996), Iberian lynx *Lynx pardinus* in Spain (Ferreras et al., 1992) and wolves in Croatia (Huber et al., 2002). Similarly in North America, traffic and legal and illegal killing were identified as important causes of mortality in the Florida panther (*Puma concolor coryi*; Taylor et al., 2002), wolves (Fuller, 1989; Forbes and Theberge, 1995) and grizzly bears (Knight et al., 1988).

The average mortality rates for adult lynx in our studies increased 5–10 times when hunting and poaching were included. This in turn had an impact on the rate of increase. The rate of increase changed from more than 20% increase per year to 2–4% increase per year, when hunting and poaching were included in the survival estimates. Similarly, the total mortality for wolverines in North-America differ largely between trapped and un-trapped populations (Krebs et al., 2004), which resulted in declining wolverine populations in trapped areas ($\lambda = 0.88$), but in increasing wolverine

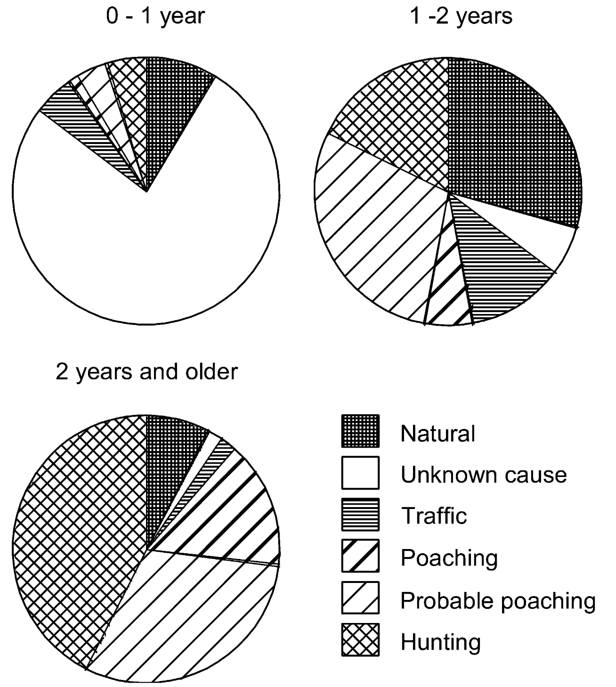

Fig. 2 – Causes of mortality in 0–1 year old (n = 82), 1–2 year old (n = 17) and ⩾2 year old (n = 52) lynx in Scandinavia.

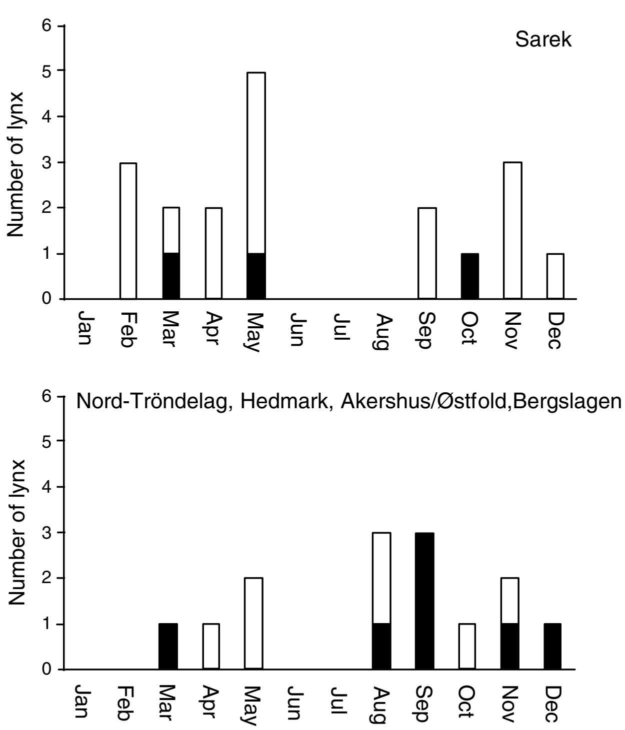

Fig. 3 – Number of poached lynx (black parts of the bars) and probably poached lynx (open parts of the bars) in relation to the month of year in the Sarek study area (upper graph, n = 19) and in the four other study areas combined (lower graph, n = 14).

populations in un-trapped areas ($\lambda = 1.06$). Krebs et al. (2004) also concluded that human-caused mortality was mostly additive to natural mortality.

The population growth rates calculated from the radio-marked lynx and including poaching seems to be the best description of the changes in the lynx population in Scandinavia. Survey data from Sweden (Liberg and Andrén, 2005) shows an almost stable population in the northernmost county, which includes our northern study area (Sarek; estimated $\lambda = 1.07 \pm 0.071$ SE) and an increasing population in south-central Sweden, which includes our southern study area (Bergslagen; estimated $\lambda = 1.19 \pm 0.097$ SE). However, our estimate of the rate of increase in the Hedmark study area is probably an overestimation (estimated $\lambda = 1.01 \pm 0.086$ SE), as radio-marked lynx in that study area were actively protected during the hunting season. Data from lynx surveys in Hedmark indicate a decreasing lynx population (Brøseth et al., 2003). Obtaining unbiased estimates of poaching rates is very difficult, even with the use of radio-telemetry. Interestingly, our estimated rates of increases are actually slightly higher than the observed ones. Thus, the mortality rates were probably not overestimated, which may also suggest that the poaching rates were not overestimated.

Poaching (including probable poaching) accounted for 46% of the mortality in adult lynx. There are several potential reasons for humans to want to decrease a local lynx population. Within the reindeer husbandry area lynx are responsible for heavy depredation on reindeer. The estimated losses to predation are about the same as the number of slaughtered reindeer (Swenson and Andrén, 2005). Although the reindeer owners are compensated for the loss of reindeer to predators, there still might be an economical benefit for illegally killing a lynx, because it might lower the losses. The estimated loss per lynx was about 40 reindeer per lynx and year (Swenson and Andrén, 2005). The kill rate for a lynx family group in winter was about 6 reindeer per month (Pedersen et al., 1999), corresponding to a yearly kill rate of about 36 reindeer per lynx. Thus, the estimated losses are not unrealistic. The Swedish reindeer owners' organisation claims that the compensation paid for predator-killed reindeer is too low. For Sweden, they have estimated that large carnivores cause a direct production loss of 7.3 million USD, i.e., fewer reindeer slaughtered. This is almost 30% more than the compensation paid in 2000 (4.9 million USD). However, the true costs of having large carnivores, according to the Swedish reindeer owners' organisation, also considering future production loss due to female reindeer being killed and an increased cost of herding the reindeer due to carnivore disturbance, is 4–5 times larger (18.2 million USD) than the compensation paid today. Based on this logic, some reindeer herders believe that it is better to reduce the lynx population rather than get the compensation – an evaluation that assumes the chances of being caught and fined for poaching are minimal. Furthermore, it is unclear to what extent economic remuneration can compensate for predation when meat production lies at the heart of Sami culture (Nilsson-Dahlström 2003).

The depredation of sheep by lynx in Norway is extensive. The Norwegian authorities compensated for the loss of about 8500 sheep killed by lynx in 2000 to a cost of 2.6 million USD. The estimated number of sheep killed per lynx was 15.2, which correspond to data obtained from quantifying the kill rates of radio-tracked lynx (Odden et al., 2002). Studies in Norway have shown that legal hunting of lynx has real effects on

Table 2 – Mean yearly survival estimates and their standard errors (Pollock et al., 1989) for lynx males and females in three age classes (0–1, 1–2, >2 years old) for the Sarek, Hedmark and Bergslagen study areas

Sex	Age-class (years)	Natural, and unknown	+ Traffic, poaching and probable poaching	+ Hunting
Sarek				
M	0–1	0.490 ± 0.078	0.463 ± 0.076	=
M	1–2	0.817 ± 0.143	=	0.735 ± 0.154
M	>2	0.950 ± 0.053	0.791 ± 0.090	0.771 ± 0.092
F	0–1	0.446 ± 0.071	0.407 ± 0.067	=
F	1–2	1 ± 0	0.900 ± 0.090	=
F	>2	0.965 ± 0.039	0.830 ± 0.073	=
Growth rate (λ)		1.21 ± 0.062	1.07 ± 0.070	1.07 ± 0.071
Hedmark				
M	0–1	0.365 ± 0.097	=	=
M	1–2	1 ± 0	0.729 ± 0.170	0.583 ± 0168
M	>2	1 ± 0	=	0.883 ± 0.103
F	0–1	0.593 ± 0.126	=	=
F	1–2	0.750 ± 0.217	0.429 ± 0.187	=
F	>2	1 ± 0	0.944 ± 0.065	0.861 ± 0.078
Growth rate (λ)		1.19 ± 0.081	1.09 ± 0.078	1.01 ± 0.086
Bergslagen				
M	0–1	0.405 ± 0.118	0.282 ± 0.090	0.215 ± 0.072
M	1–2	0.667 ± 0.222	0.571 ± 0.216	=
M	>2	1 ± 0	0.940 ± 0.064	0.787 ± 0.101
F	0–1	0.544 ± 0.102	0.511 ± 0.099	=
F	1–2	0.875 ± 0.109	0.766 ± 0.131	=
F	>2	0.962 ± 0.050	0.890 ± 0.079	0.855 ± 0.087
Growth rate (λ)		1.33 ± 0.088	1.22 ± 0.095	1.19 ± 0.097

Three different mean yearly survival estimates are given.The first estimate includes natural and unknown mortality, the second one also includes poaching and probable poaching, and the third also includes hunting (Table 1). The growth rate is estimated using data on reproduction from Andrén et al. (2002).
=, means the same survival rate as in the column to the left.

Table 3 – Mean hunting and poaching rates on radio-marked lynx in four Scandinavian study areas

Radio-marked lynx			Lynx in the county					
Number of individuals (radio-years)	Poaching rate (%)	Hunting rate (%)	Quota	Hunting	Family groups	Population size	Quota rate (%)	Hunting rate (%)
Sarek			Norrbotten					
84 (136 years)	14.0	1.5	14.7	2.3	36	219[a]	6.7	1.0
Bergslagen			Örebro					
63 (92 years)	6.5	8.7	5.1	5	–	60.3	8.8	8.3
Hedmark			Hedmark					
55 (86 years)	5.8	9.3[b]	14.9	12.3	9	55.3[c]	28.0	23.1
Akershus/Østfold			Akershus/Østfold					
29 (34 years)	8.9	26.7	13.5	8.5	4.4	24.0[d]	56.2	35.4

The data on quotas and hunting are yearly means from the period 1996–2002 for Norrbotten county, 1996–2002 for Örebro county, for 1996–2002 for Hedmark county and for 2000–2003 for Akershus and Østfold counties combined.
a The population size for the county of Norrbotten was estimated by multiplying the number of family groups by 6.14 following Andrén et al. (2002).
b Hunting rate for Hedmark is underestimated for radio-marked lynx, because hunters were requested to avoid killing radio-marked lynx during the hunting season in this study area.
c Population size for the county of Hedmark was estimated by multiplying the number of family groups by 6.24 following Andrén et al. (2002).
d Population size for the county of Akershus/Østfold was estimated by multiplying the number of family groups by 5.48 following Andrén et al. (2002).

depredation, but only when the population size is reduced (Herfindal et al., 2005).

Finally, as lynx prey upon roe deer there is also a conflict with hunters. The roe deer hunting bag records have experienced greater declines in areas with lynx as compared to areas without lynx. The number of shot roe deer in Sweden has declined by 90% in counties with lynx and by 50% in counties without lynx (Andrén et al., 1999). Data on lynx predation on roe deer has shown that even at low roe deer densities lynx are able to maintain relatively high kill rates resulting in potentially heavy predation impacts on low density roe deer populations (Andersen, Odden and Linnell unpublished data). However, lynx have not caused the decline in the roe deer population alone. Red fox (*Vulpes vulpes*) populations in Scandinavia that were hit by sarcoptic mange during the 1980s have begun to recover, leading to increased predation on roe deer fawns (Lindström et al., 1994; Kjellander and Nordström, 2003; Jarnemo and Liberg, 2005).

These causes of intolerance might explain the differences in the time of the year that poaching occurs. In the northernmost study area (Sarek) lynx were mainly poached from February to May. At this time of the year there is snow in northern Sweden and it is relatively easy to access remote areas with snowmobiles, which allows poachers to locate and kill lynx with a low risk of detection. In the three other study areas poaching occurred mainly in the autumn. This is during the roe deer and moose (*Alces alces*) hunting seasons. Some hunters may take the opportunity to illegally shoot a lynx that appears in front of them. This would mean that lynx poaching is conducted in an opportunistic, rather than a planned manner.

Within regions we could not find any significant relationship between the given hunting quota rate in a given year and the poaching rate on radio-marked lynx that same year. However, the year-by-year comparison is based on mortality estimates calculated from only 25–30 radio-marked lynx per year such that one more or less poached radio-marked lynx will have an enormous effect on the estimated poaching rate. Therefore, the sample size might be too small for within region comparisons. However, when comparing between regions and study areas, the lowest poaching rate was found in the Hedmark study area in Norway where the hunting quota rate was higher than in Sweden. On the other hand poaching levels were not lower in Akershus/Østfold with the highest hunting quota. Furthermore, the lynx hunting quota in both Hedmark and Akershus/Østfold was not sustainable and causes a decline in the lynx population (Brøseth et al., 2003). Thus, it is very unclear whether an increased lynx hunting quota will result in a lower poaching.

Poaching has received most international attention in connection with tigers (*Panthera tigris*) and bears (*Ursus* sp.) where the main motivation is to harvest high value tiger bone and bear gall for the Asian market in traditional medicines (Kenney et al., 1995; Servheen et al., 1999; Nowell, 2000; Shepherd and Magnus, 2004). In these cases very poor and uneducated people, are tempted to break the law to access a high value product in an environment where law enforcement is often either minimal or corrupt, or both. The case of lynx poaching in Scandinavia is interesting in that it occurs in a rich country with high standards of living, high levels of education, with relatively honest and effective law enforcement, and is motivated only slightly by economic gain. While a desire to minimise economic loss or perceived economic loss may act as a proximate reason, it is apparent that the underlying ultimate motivation is a lack of acceptance of the presence of lynx as a predator in the modern landscape. Working on these underlying value based attitudes will take concentrated effort and much time (Breitenmoser, 1998), and illustrates that attention should be paid to social aspects of carnivore-human conflicts as well as to the material aspects (Andersen et al., 2004; Kleiven et al., 2004; Nilsson-Dahlström, 2003).

To conclude, the main task for long-time survival of lynx in Scandinavia is to increase the tolerance towards the lynx and thereby reduce the poaching (Kleiven et al., 2004). Preliminary population viability analyses (Andrén and Liberg, 1999) indicate that the present Scandinavian lynx population of approximately 1600 individuals (1200–1400 in Sweden, Liberg and Andrén, 2005; and 300–350 in Norway, Brøseth et al., 2003) has a very low probability of extinction. However, an undetected increase in the poaching level can change this conclusion. This is not a problem specific to Scandinavia. A recent European-wide survey of lynx status identified poaching as the most important threat across all populations (von Arx et al., 2004).

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REFERENCES

Aanes, R., Linnell, J.D.C., Perzanowski, K., Karlsen, J., Odden, J., 1998. Roe deer as a prey. In: Andersen, R., Duncan, P., Linnell, J.D.C. (Eds.), The European Roe Deer: The Biology of Success. Scandinavian University Press, Oslo, Norway, pp. 139–159.

Andersen, R., Linnell, J.D.C., Hustad, H., Brainerd, S., 2004. Large Carnivores and Human Communities: A Guide to Coexistence in the 21st Century. Norwegian Institute for Nature Research 25, 1–48.

Andrén, H., Liberg, O., 1999. Demography and minimum viable population in Eurasian lynx. In: Ebenhard, T., Höggren, M. Viable Carnivore Populations. Swedish Biodiversity Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden, Publication 1. pp. 119–123 (in Swedish).

Andrén, H., Liberg, O., Sand, H., 1999. The impact of large carnivores on their wild prey. In: Appendix to A Coherent Predator Policy. The Swedish Parliament SOU 1999,146, Stockholm, Sweden, pp. 119–183 (in Swedish).

Andrén, H., Linnell, J.D.C., Liberg, O., Ahlqvist, P., Andersen, R., Danell, A., Franzén, R., Kvam, T., Odden, J., Segerström, P., 2002. Estimating total lynx (*Lynx lynx*) population size from censuses of family groups. Wildlife Biology 8, 299–306.

Arnemo, J.M., Linnell, J.D.C., Wedul, S.J., Ranheim, B., Odden, J., Andersen, R., 1999. Use of intraperitoneal radio-transmitters

in Lynx (*Lynx lynx*) kittens: anaesthesia, surgery and behaviour. Wildlife Biology 5, 245–250.
Bailey, T.N., Bangs, E.E., Portner, M.F., Malloy, J.C., McAvinchey, R.M., 1986. An apparent overexploited lynx population on the Kenai peninsula Alaska. Journal of Wildlife Management 50, 279–290.
Brand, C.J., Keith, L.B., 1979. Lynx demography during a snowshoe hare decline in Alberta. Journal of Wildlife Management 43, 827–849.
Breitenmoser, U., 1998. Large predators in the Alps: the fall and rise of man's competitor. Biological Conservation 83, 279–289.
Brøseth, H., Odden, J., Linnell, J.D.C., 2003. Minimum number of family groups, population size and population trend for lynx in Norway during 1996–2002, Norwegian Institute for Nature Research (in Norwegian).
Ericsson, G., Heberlein, T.B., Karlsson, J., Bjärvall, A., Lundvall, A., 2004. Support for hunting as a means of wolf *Canis lupus* population control in Sweden. Wildlife Biology 10, 269–276.
Ferreras, P., Aldama, J.J., Beltrán, J.F., Delibes, M., 1992. Rates and causes of mortality in a fragmented population of Iberian lynx *Felis pardina* Temminck, 1824. Biological Conservation 61, 197–202.
Forbes, G.J., Theberge, J.B., 1995. Influences of a migratory deer herd on wolf movements and mortality in and near Algonquin Park Ontario. In: Carbyn, L.N., Fritts, S.H., Seip, D.R. (Eds.), Ecology and Conservation of Wolves in a Changing World. Canadian Circumpolar Institute, Alta., Canada, pp. 303–314.
Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs 105, 1–41.
Gaona, P., Ferreras, P., Delibes, M., 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). Ecological Monograph 68, 349–370.
Haglund, B., 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. Swedish Wildlife Research 4, 81–310 (in Swedish with English summary).
Herfindal, I., Linnell, J.D.C., Moa, P.F., Odden, J., Austmo, L.B., Andersen, R., 2005. Does recreational hunting of lynx reduce depredation losses of domestic sheep. Journal of Wildlife Management 69, 1034–1042.
Hovey, F.W., McLellan, B.N., 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. Canadian Journal of Zoology 74, 1409–1416.
Huber, D., Kusak, J., Frkovic, A., Gužvica, G., Gomercic, T., 2002. Causes of wolf mortality in Croatia in the period 1986–2001. Veterinarski Arhiv 72, 131–139.
Jarnemo, A., Liberg, O., 2005. Red fox removal and roe deer fawn survival – a 14-year study. Journal of Wildlife Management 69, 1090–1098.
Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schmidt, K., Bunevich, A.N., Milkowski, L., 1996. Population dynamics (1869–1994), demography, and home range of lynx in Bialowieza Primeval Forest (Poland and Belarus). Ecography 19, 122–138.
Kenney, J.S., Smith, J.L.D., Starfield, A.M., McDougal, C.W., 1995. The long term effects of tiger poaching on population viability. Conservation Biology 9, 1127–1133.
Kjellander, P., Nordström, J., 2003. Cyclic voles, prey switching in red fox, and roe deer dynamics – a test of the alternative prey hypothesis. Oikos 101, 338–344.
Kleiven, J., Bjerke, T., Kaltenborn, B.P., 2004. Factors influencing the social acceptability of large carnivore behaviours. Biodiversity and Conservation 13, 1647–1658.
Knight, R.R., Blanchard, B.M., Eberhardt, L.L., 1988. Mortality patterns and population sinks for Yellowstone Grizzly bears, 1973–1985. Wildlife Society Bulletin 16, 121–125.
Krebs, C.J., 1999. Ecological Methodology, second ed. Benjamin/Cummings, Menlo Park, CA. 620 pages.
Krebs, J., Lofroth, E., Copeland, J., Banci, V., Golden, H., Magoun, A., Mulders, R., Shults, B., 2004. Synthesis of survival rates and causes of mortality in North American wolverine. Journal of Wildlife Management 68, 493–502.
Kreeger, T.J., Arnemo, J.M., Raath, J.P., 1999. Handbook of Wildlife Chemical Immobilization. Wildlife Pharmaceuticals, Incorporated, Fort Collins, CO, USA.
Landa, A., Linnell, J.D.C., Lindén, 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 Publisher, Leiden, pp. 1–20.
Liberg, O., Andrén, H., 2005. The lynx population in Sweden 1994–2004. An evaluation of the census data and methods. Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences Report.
Liberg, O., Glöersen, G., 2000. Lynx and wolf survey in Sweden in 2000. Swedish Association for Hunting and Wildlife Management. (in Swedish with English Summary) 18 pages.
Lindström, E., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K., Swenson, J., 1994. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. Ecology 75, 1042–1049.
Linnell, J.D.C., Andersen, R., Kvam, T., Andrén, H., Liberg, O., Odden, J., 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., Odden, J., Andrén, H., Liberg, O., Andersen, R., Moa, P., Kvam, T., Ahlqvist, P., Schmidt, K., Jedrejewski, W., Okarma, H., in press. Distance rules for minimum counts of Eurasian lynx *Lynx lynx* family groups under different ecological conditions. Wildlife Biology.
Nilsson-Dahlström, A., 2003. Negotiating wilderness in a cultural landscape: predators and Saami reindeer herding in the Laponian world heritage area. Uppsala Studies in Cultural Anthropology No. 32. Uppsala University Library, Uppsala, Sweden.
Nowell, K., 2000. Far From a Cure: The Tiger Trade Revisited. TRAFFIC International, Cambridge.
Nowell, K., Jackson, P., 1996. Wild Cats: Status Survey and Action Plan. IUCN, Gland, Switzerland.
Odden, J., Solvang, H., Maartman, E., Wabakken, P., Linnell, J., Andersen, R., Haagenrud, H., Lundqvist, O., Solberg, H.O., 2000. Survey of lynx and wolf in Hedmark county in 1999. Hedmark County Board, Report No. 1/2000, 36 pages (in Norwegian).
Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T., Andersen, R., 2002. Lynx depredation on domestic sheep in Norway. Journal of Wildlife Management 66, 98–105.
Östergren, A., Bergström, M.-R., Attergaard, H., From, J., Mellquist, H., 1998. Wolverine, lynx and wolf in the reindeer husbandry area of Sweden. Results from the 1998 inventory. Västerbotten County Board. Report No. 3, 34 pages (in Swedish with English summary).
Pedersen, V., Linnell, J.D.C., Andersen, R., Andrén, H., Segerström, P., Lindén, M., 1999. Winter lynx predation on semi-domestic reindeer in northern Sweden. Wildlife Biology 5, 203–212.
Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53, 7–15.
Sæther, B.-E., Ringsby, T.H., Røskaft, E., 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. Oikos 77, 217–226.
Sæther, B.-E., Engen, S., Swenson, J.E., Bakke, Ø., Sandegren, F., 1998. Assessing the viability of Scandinavian brown bear,

Ursus arctos populations: the effect of uncertain parameter estimates. Oikos 83, 403–416.
Servheen, C., Herrero, S., Peyton, B., 1999. Bears: Status Survey and Conservation Action Plan. IUCN Publications, Cambridge, United Kingdom. p. 309.
Schmidt-Posthaus, H., Breitenmoser-Würsten, C., Posthaus, H., Bacciarini, L., Breitenmoser, U., 2002. Causes of mortality in reintroduced Eurasian lynx in Switzerland. Journal of Wildlife Disease 38, 84–92.
Shepherd, C.R., Magnus, N., 2004. Nowhere to Hide: The Trade in Sumatran Tiger. TRAFFIC Southeast Asia. p. 108.
Sunde, P., Kvam, T., Bolstad, J.P., Bronndal, M., 2000. Foraging of lynxes in a human-exploited boreal alpine environment. Ecography 23, 291–298.
Swenson, J.E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P., Franzén, R., 1994. Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. Biological Conservation 70, 9–17.
Swenson, J.E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R., 1997. Infanticide caused by hunting of male bears. Nature 386, 450–451.
Swenson, J.E., Andrén, H., 2005. A tale of two countries: large carnivore depredations and compensation schemes in Sweden and Norway. In: Woodroffe, R., Thirgood, S., Rabinowitz, A. (Eds.), People and Wildlife: Conflict or Co-existence? Cambridge University Press, pp. 323–339.
Taylor, S.K., Buergelt, C.D., Roelke-Parker, M.E., Homer, B.L., Rotstein, D.S., 2002. Causes of mortality of free-ranging Florida panthers. Journal of Wildlife Diseases 38, 107–114.
von Arx, M., Breitenmoser-Würsten, C., Zimmermann, F., Breitenmoser, U., 2004. Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. KORA Bericht 19, 1–330.
Wabakken, P., Sand, H., Liberg, O., Bjärvall, A., 2001. The recovery, distribution abd population dynamics of wolves on the Scandinavian Peninsula. Canadian Journal of Zoology 79, 710–725.
Woodroffe, R., Ginsberg, J.R., 2000. Ranging behaviour and vulnerability to extinction in carnivores. In: Gosling, L.M., Sutherland, W.J. (Eds.), Behaviour and Conservation. Cambridge University Press, Cambridge, United Kingdom, pp. 125–140.