Human caused mortality in the endangered Scandinavian wolverine population

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ABSTRACT

The wolverine is a relatively long lived mustelid species with low average annual reproduction which in theory makes them sensitive to changes in survival rates. In a multi-year study we monitored 211 radio-marked wolverines to estimate age-specific survival rates and mortality causes in an endangered population. Our data suggests that poaching forms a substantial part of wolverine population dynamics in northern Scandinavia causing up to 60% of adult mortality. Average annual adult survival rate was 0.91. Male and female survival rates did not differ. Twenty-five adult wolverines were confirmed to have died during the study. Fifty-two percent of confirmed adult mortality was human caused. The most important cause of adult mortality was poaching (9). Annual adult survival was lower (0.86) when 15 adult resident wolverines that were assumed to have died due to poaching were included in the analyses. Natural mortality among subadults and adults was less frequent in our study population compared to North American wolverine populations. Adult survival was significantly lower during the snow season (December–May) than during the snow-free season (June–November), while natural mortality was more evenly distributed between seasons. We explain this by the frequency of poaching which is higher during snow season. Our results underline the need to frame the underlying human dimension factors behind poaching to facilitate conservation and management of endangered populations.

1. Introduction

Conservation biology has been increasingly concerned with the dynamics of small populations. This is particularly true for small populations of carnivores, whose conservation is made difficult because of a wide array of conflicts with human interests, such as depredation on domestic animals and competition for game species. In the western world, many large carnivore populations persist in multi use landscapes at high human population densities and often outside protected areas (Linnell et al., 2001). For example, in Scandinavia, all four large carnivores (wolverine *Gulo gulo*, Eurasian lynx *Lynx lynx*, brown bear *Ursus arctos*, and wolf *Canis lupus*) occur mainly outside protected areas where the potential for conflicts is high (Andrén et al., 2006). Hence, effective management and conservation plans with a strong scientific basis are essential, and it is important to reveal factors, including human activities, that influence persistence of carnivore populations.

The wolverine is relatively scarce across its circumpolar range where it occupies tundra, taiga, and forest zones in North America and Eurasia (Banci, 1994). Globally it is classified as vulnerable since 1988 (Mustelid Specialist Group, 1996). Management concerns include primarily habitat fragmenta-

tion, overexploitation, and depredation conflicts with sheep and reindeer husbandry (Landa et al., 2000; Slough, 2007; Zhang et al., 2007). The Scandinavian wolverine population's distribution and size declined markedly during the 1900s (Flagstad et al., 2004). Currently, more than half of the Scandinavian wolverine population, estimated at about 780 individuals in total, resides in Sweden (Persson, 2007) where it is classified as endangered (Gärdenfors, 2000). 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). Locally, reindeer husbandry suffers from heavy predation by wolverines and other predators (Swenson and Andrén, 2005). 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, 2007). 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 on a population-level. During 1999–2005, 10 wolverines were legally harvested in Sweden (Persson, 2007).

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). It is therefore important to estimate survival rates and causes of mortality to understand variation in population growth. Only three previous studies provide estimates of wolverine survival rates, and information on causes of mortality is scant. Among juvenile wolverines in Scandinavia, intraspecific killing was the most important cause of mortality (Persson et al., 2003) while harvest, starvation, and predation were the most important causes of adult wolverine mortality in North America (Krebs et al., 2004; Squires et al., 2007).

Sound conservation of wolverines necessitates a solid knowledge about factors affecting demographic parameters. Data on demographic parameters are needed to model effects of management strategies (e.g. harvest rates) on viability of wolverine populations (e.g. Sæther et al., 2005; Lofroth and Ott, 2007). Therefore, in this study, we assess age-specific causes of mortality and estimate age-specific survival, as well as seasonal adult survival, to assess factors that could influence the conservation of an endangered wolverine population.

2. Study area

We carried out the study in and around the Laponia World Heritage Site in northern Sweden above the Arctic Circle (Kvikkjokk: 67°00′N, 17°40′E). The climate is continental and the ground is usually snow-covered from November to late May. The area is characterized by deep valleys, glaciers, and high alpine plateaus with peaks up to 1700–2000 m a.s.l. The valleys are dominated by mountain birch (*Betula pubescens*), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*), while mountain birch forms the tree line at 600–700 m a.s.l. (Grundsten, 1997). Semi-domestic reindeer is managed exclusively and extensively by the indigenous Sámi people in the study area. About 24% of documented wolverine reproductions in Sweden were documented in the Laponia area 1996–2002 (Sæther et al., 2005). The approximate density of wolverines were 1.4/100 km^2 in the study area (Persson et al., 2006).

3. Methods

3.1. Capture and radio-marking

We captured 224 wolverines. Of these, six juveniles were too small to be equipped with transmitters and seven animals lost their transmitters or died too soon after capture to be included in the analyses. Hence, 211 different individuals entered the analyses. We monitored 144 juvenile, 77 subadult (1–2 years), and 94 adult (>2 years) wolverines during a total of 377 wolverine years (Table 1). Individuals were monitored for an average of 614 radio-days (SE 50.8). Eighty of the monitored juvenile wolverines were used for analyses of survival and mortality causes presented in Persson et al. (2003). We captured and equipped most juveniles with transmitters at rendezvous sites in early May to early June (2–3 months old). All animals categorized as subadults were captured as juveniles and were hence of known age when they entered

Table 1 – Mortality causes of the 144 juvenile, 77 subadult and 94 adult wolverines studied in the Laponia area during 1993–2008.

Age	Capture		Radio-years	Cause of death					
	Sex	N		Poaching	Lethal control	Natural	Unknown	Assumed mortality	Lost
0–1 Years	M	65	40	2	2	3	1	0	15
	F	79	44	0	1	13	3	0	13
	Total	144	84	2	3	16	4	0	28
1–2 Years	M	32	14	2	0	1	0	1	20
	F	45	27	1	0	0	1	0	21
	Total	77	41	3	0	1	1	1	41
>2 Years	M	37	68	4	0	1	0	7	17
	F	57	184	5	4	9	2	8	10
	Total	94	252	9	4	10	2	15	27

the subadult class on March 1 the year following birth. Adults were captured on ground or were darted from helicopters (Arnemo and Fahlman, 2007). The study was approved by the Animal Ethics Committee for northern Sweden, Umeå.

3.2. Survival and mortality causes

We detected death of radio-marked wolverines during bi-weekly 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 mortality and lost (i.e., unknown disappearance) using additional information. Assumed mortality was when the lost animal was a resident adult equipped with a transmitter with at least half of the expected battery life remaining, and when the transmitter showed no signs of technical problems (e.g., strange signals), and the study area was searched carefully for the animal on ground and from the air (cf. Andrén et al., 2006). Furthermore, in four of these 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. One reproductive female was lost during the denning season and no tracks were found in the area. One subadult was classified as assumed mortality when additional local information supported the assumption that the animal was killed. In the survival analyses, assumed mortalities were treated as deaths in scenario a and were censored in scenarios b–d. Lost animals for which we had no indications of the fate of the animal were censored in all analyses (i.e., they were categorized as lost). Date of assumed mortality and censoring were assigned the same date, 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).

3.3. Data analysis

We pooled data from all years to obtain a sufficient sample size for Kaplan–Meier estimates modified for a staggered-entry design to estimate survival rates (Pollock et al., 1989). Approximate confidence intervals (95%) for the survival rates were derived according to Pollock et al., 1989. We grouped data by sex and age class and by season (December–May and June–November) for adult survival. Juvenile survival was measured from June 1st to March 1st the following year. We started the analysis from June 1st to obtain an unbiased Kaplan–Meier estimate (Murray, 2006) correlated with the estimates of wolverine female birth rate (Persson et al., 2006).

We calculated survival on a monthly basis to correspond to the frequency of relocation (Winterstein et al., 2001). Juvenile survival in May was calculated using the Mayfield Method (Winterstein et al., 2001). We calculated four different adult survival scenarios corresponding to the categorization of mortality causes. Unless mentioned otherwise, survival estimates include all mortality causes except assumed mortality. We used the robust, conservative Fisher's exact test (Siegel and Castellan, 1988) to analyze differences among mortality causes. We used Z-tests to test for differences in point estimates of annual survival between groups and seasons (Pollock et al., 1989). By treating different mortality causes as censored in the different Kaplan–Meier analyses we analyzed cause-specific mortality (Winterstein et al., 2001). We performed our statistical analyses in SAS (SAS institute, 1989).

4. Results

4.1. Mortality causes

Of the 94 adult wolverines, 25 were confirmed to have died during the study (Table 1). About half (52%; $n = 13$) of all confirmed adult mortality was human caused. The most important cause of death was poaching (36%; 5 females and 4 males). Four females were legally removed in conjunction with depredation control. One male and nine females died from natural causes. The male died from infection. The females died from inflammation secondary to injury (autopsy suggested injury from bites) ($n = 2$), intraspecific strife ($n = 1$), starvation ($n = 1$), starvation secondary to injury ($n = 1$), avalanche ($n = 1$), and unknown natural causes ($n = 3$). Two females died from trauma caused by unknown natural or anthropogenic causes. In addition, three wolverines were found dead incidentally after they were lost and censored in the survival analyses. Two were lost as subadults and found poached the following year. One adult male was found killed by trauma, possibly inflicted by another wolverine.

Moreover, 15 adult resident wolverines were assumed to have died, according to our criteria (Table 1). Assuming that all assumed mortality was caused by poaching, 70% of adult mortality ($n = 40$) was human caused. Ninety-seven percent of documented poaching and assumed mortality of subadults and adults ($n = 31$) occurred during December–May (Fig. 1), while 43% of natural and unknown mortality occurred during the same period.
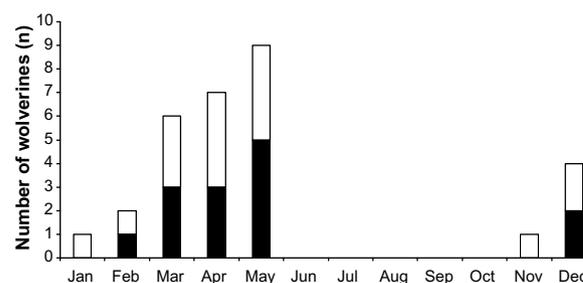

Fig. 1 – Number of radio-marked subadult and adult wolverines that died from poaching (black bars; $n = 14$) and assumed mortality (white bar; $n = 16$) in relation to the month of the year in the Laponia area during 1993–2008.

The proportion of adult wolverines that were killed by humans was 11% for males and 16% for females (Fisher's exact test, $P = 0.56$). Including assumed mortality the proportion of both males and females killed by humans were 30%. The proportion of adult males that were poached was 11% (including assumed mortality, 30%) and females 9% (including assumed mortality, 16%) (Fisher's exact test; $P = 0.73$ and $P = 0.13$, respectively). In contrast, the proportion of individuals that died from natural and unknown causes was higher in females (19%) than in males (3%) (Fisher's exact test; $P = 0.03$). The proportion of adult males (46%) that were lost was higher than that of females (17%) (Fisher's exact test, $P < 0.01$).

Of the 77 subadult wolverines, mortality of five individuals was confirmed during the study (Table 1). Poaching was confirmed as the cause of death of three individuals. One male died in June from a skull fracture caused by a bite, probably inflicted by another wolverine. Cause of death for one female was unknown. In addition, one lost subadult was assumed to have died. Fifty-three percent of the 77 subadults were lost (20 males; 21 females).

Of the 144 monitored juvenile wolverines, 25 died during the study (Table 1). The predominant cause of juvenile death was intraspecific predation (48%; $n = 12$). Other confirmed mortality causes were legal harvest ($n = 3$), starvation ($n = 3$), poaching ($n = 2$), and unknown predator ($n = 1$). Of the three juveniles that died from starvation, two presumably died as a consequence of losing their mother and one died from starvation secondary to fractures on both front legs. Four juveniles died from unknown causes. Of all juvenile mortality, 96% occurred before October (Fig. 2).

4.2. Survival rate

Average annual adult survival rate was 0.91 (Table 2). Annual male and female survival rates did not differ (0.93 and 0.90, respectively, $Z = 0.63$, $P = 0.53$). However, average survival rate for both sexes was lower (0.86) when assumed mortality was included in the analysis ($Z = 1.97$, $P = 0.05$). Annual male and female survival rate when assumed mortality was included was 0.84 and 0.87, respectively, ($Z = 0.61$, $P = 0.54$). Adult survival rate when human caused mortality was excluded was 0.96, which is higher than the survival rate when poaching and assumed mortality was included ($Z = 4.16$, $P < 0.01$).
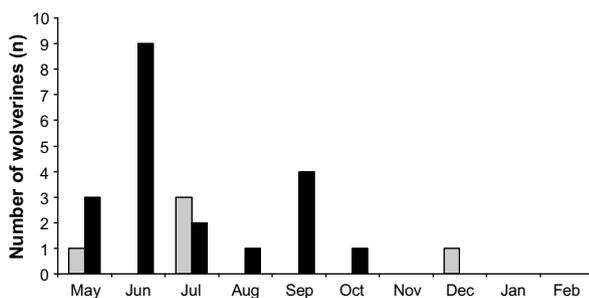

Fig. 2 – Number of radio-marked juvenile wolverines that died from human caused (grey bars; $n = 5$) and natural causes (black bars; $n = 20$) in relation to month (May–February) of the year in the Laponia area during 1993–2008.

Survival of adult wolverines was lower during December–May (0.93 [95% CI: 0.90–0.96]) compared to June–November (0.98 [95% CI: 0.96–0.99]; $Z = 2.42$, $P = 0.01$). The difference in survival between the seasons was larger when assumed mortality was included (0.88 [95% CI: 0.85–0.92] and 0.97 [95% CI: 0.95–0.99], respectively, $Z = 4.20$, $P < 0.01$).

Average annual survival rate for subadult wolverines was 0.90 (95% CI: 0.80–1.00; $n = 77$). Male and female subadult survival was 0.85 (0.62–1.00; $n = 32$) and 0.94 (0.84–1.00; $n = 45$), respectively, ($Z = 0.67$; $P = 0.50$). Annual survival was 0.89 (0.78–0.99) with one case of assumed mortality included. Subadult survival rate when poached animals were treated as censored observations was 0.95 (0.87–1.00). The estimates of subadult survival are presumably biased high because of the high number of censored animals.

Average survival rate for juveniles from 1 June–28 February was 0.83 (95% CI: 0.76–0.90; $n = 139$). Female and male juvenile survival were 0.79 (0.69–0.90; $n = 75$) and 0.88 (0.79–0.97; $n = 64$), respectively, ($Z = 1.26$, $P = 0.21$). Juvenile survival in May was 0.87. Corresponding (monthly) juvenile survival from June–February was 0.98 (Mayfield Method).

5. Discussion

5.1. Human caused mortality

Poaching was the single most important cause of mortality for adult wolverines, while natural mortality was most important for juveniles. Similar pattern has been described for populations of other large carnivores (e.g., Stahl and Vandel, 1999; Andrén et al., 2006). Thirty-six percent of confirmed adult wolverine mortality was caused by poaching. In addition, 15 adult wolverines were assumed to have died. Our criteria-based assumption that mortality caused by poaching caused their disappearance was supported by the fact that they were lost during the period when all confirmed poaching of subadults and adults occurred (December–May). Assuming that these animals were poached, 60% of adult mortality was caused by poaching. Including four adult females that were lethally controlled to mitigate depredation conflicts, 70% of adult mortality was human caused.

In essence, adult survival was strongly influenced by human caused mortality and the proportion of mortality that was caused by humans was higher in our study (70%) than in trapped populations in North America (47%) (Krebs et al., 2004). Still, adult survival when confirmed and assumed poaching was included (0.86) is higher than that of trapped populations (0.73 and 0.74 for females and males, respectively) in North America. This is presumably explained by a higher natural and unknown mortality in trapped wolverine populations in North America (0.21 mortalities per radio year; recalculated from Krebs et al., 2004) than in our study area (0.05). Similarly, annual survival rate in our study area when human caused mortality was excluded (0.96) was higher than in untrapped North American populations (0.88; Krebs et al., 2004).

Three subadult wolverines were confirmed poached. The high proportion of censored subadults (53%) is presumably due to a high frequency of dispersal at this age (Vangen et al., 2001). Dispersal is often initiated during the period

Table 2 – Annual adult survival rates (females and males pooled and separated) for four sets of scenarios based on mortality causes included in the analysis: (a) includes all mortality causes, (b) includes all mortality causes except assumed mortality, (c) include natural and unknown mortality as well as lethal control and finally (d) includes only natural and unknown mortality causes.

Group	Scenario	Wolverines (n)	Radio-years	Mortalities	Annual survival rate (95% CI)
Pooled	(a)	94	252	40	0.86 (0.82–0.89)
Females	(a)	57	184	28	0.87 (0.82–0.91)
Males	(a)	37	68	12	0.84 (0.75–0.92)
Pooled	(b)	94	252	25	0.91 (0.88–0.94)
Females	(b)	57	184	20	0.90 (0.86–0.94)
Males	(b)	37	68	5	0.93 (0.87–0.99)
Pooled	(c)	94	252	16	0.94 (0.91–0.97)
Females	(c)	57	184	15	0.93 (0.89–0.96)
Males	(c)	37	68	1	0.99 (0.96–1.00)
Pooled	(d)	94	252	12	0.96 (0.93–0.98)
Females	(d)	57	184	11	0.95 (0.92–0.98)
Males	(d)	37	68	1	0.99 (0.96–1.00)

when most poaching occurs (Vangen et al., 2001). Dispersers are young, inexperienced animals making 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. Our assumption is supported by that two subadults classified as lost were subsequently incidentally found poached. It suggests that our estimates of adult survival could be biased high as well (i.e., animals classified as lost were in fact killed).

Annual mortality caused by poaching was about two times higher for adult males (0.06–0.15) than females (0.03–0.07) (Table 3). This difference could be explained by two factors. Male home ranges in our study area were typically about four times larger than those of females (Hedmark et al., 2007). In addition, wolverine males 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, we suggest that more extensive movements make males indirectly more exposed to poaching. Furthermore, denning females may receive indirect protection from poaching by the monitoring of wolverine reproductions by the County Administration and our research activity centred on female denning areas, i.e., increased activity of people around denning areas might deter poachers and inflate adult female survival rates.

Table 3 – Cause-specific mortality for adult wolverines studied in the Laponia area 1993–2008.

Cause	Pooled	Females	Males
Assumed mortality	0.05	0.04	0.09
Poaching	0.04	0.03	0.06
Lethal control	0.01	0.02	0.00
Natural and unknown	0.04	0.05	0.01
Total	0.14	0.13	0.16

Adult survival was lower during the snow season (December–May) than during the snow-free season (June–November). This pattern is explained by the frequency of poaching (Fig. 2). Poaching is presumably facilitated by snow cover that facilitates tracking and hunting by snow-machines in remote areas with low risk of detection. Most poaching occurred during the later part of the snow season (March–May) when snow conditions were ideal and daylight was longer, increasing the chances of spotting wolverines and their tracks. Furthermore, this period coincides with increased reindeer–herding activity around calving grounds in alpine areas where most wolverines are resident. A similar temporal pattern is documented for poaching of lynx in our study area (Andrén et al., 2006).

5.2. Natural mortality

Intraspecific killing was the most important cause of juvenile mortality but seems to occur in all age classes. One adult female was found killed by another wolverine close to the border of her territory. In addition, autopsy suggested trauma that could have been inflicted by other wolverines as the cause of death of three adult females that were classified as unknown mortality. In addition, four juvenile females were killed by conspecifics in August and September outside their mother's home range. In none of these cases the perpetrator could be identified. However, female wolverines are territorial (Banci, 1994; Wedholm, 2006), suggesting that both adult and juvenile females were killed by resident females in defence of territories (Persson et al., 2003).

One subadult male was found killed by injuries presumably inflicted by a wolverine. In addition, autopsy indicated that an adult male (≥8 years) found incidentally after we lost contact with him was also killed by another wolverine. Both were found in June, during the peak of the mating season (Mead et al., 1991). Similarly, Lofroth (2001) found one subadult and two adult males killed by conspecifics in BC, Canada, during the mating season. Male wolverines are as well territorial (Banci, 1994; Wedholm, 2006), suggesting that intraspecific strife occurs as a result of territoriality also in males.

The timing of the deaths and observations of males regularly exhibiting fresh wounds before and during the mating season (Magoun, 1985; unpublished data) suggest an increase in aggression during this period. Intraspecific strife has been documented in several other territorial carnivores, such as wolf (Mech, 1994), Florida panther (*Puma concolor;* Taylor et al., 2002) and Eurasian lynx (Andrén et al., 2006).

5.3. Conclusions

Our results confirm that the wolverine with a low average annual reproduction may be susceptible to variation in adult survival caused by human induced mortality, with poaching as a significant part. This verifies that conservation of wolverines needs to acknowledge strategies to limit poaching in their plans, even in protected populations. Large demographic stochasticity is an important characteristic of wolverine population dynamics, influencing population viability (Sæther et al., 2005). Also, population viability is generally strongly influenced by changes in population growth rate (e.g., Lande et al., 2003). Thus our results emphasize the conclusion of Sæther et al. (2005) that limiting poaching will increase population specific population growth rate and reduce stochastic influences on population viability. Furthermore, our study suggests that the mortality patterns for each sex may be linked to their life history strategies as well as indirect protection of females by monitoring and research activities.

The conservation of wolverines in Scandinavia represents a unique conservation challenge with an endangered species living in conflict with an indigenous reindeer–herding culture. In essence, the cultural norms within the indigenous reindeer–herding culture are in conflict with the cultural norm within the dominating society not allowing wolverines to be killed as a proactive depredation action. Instead, the dominating society favouring conservation actions and only allows reactive depredation in a handful cases; only 10 wolverines were legally harvested in Sweden during 1999–2005 (Persson, 2007). We conclude that the human dimension challenge for the conservation of the endangered wolverine population is to reveal the underlying social, psychological, and economic factors behind poaching among different groups (*sensu* Ericsson et al., 2007).

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