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Juvenile and subadult survival *in Scandinavian wolverines (Gulo gulo*) in relation to sex and small rodent abundance

Overlevelse av valper og ungdyr i den skandinaviske jervbestanden (Gulo gulo) med henhold til kjønn og smågnagerår

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Acknowledgements

This thesis has been a process of learning combined with my great interest of nature and wild life. It has given me an experience of scientific work, as analysing data and writing a longer thesis.

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Abstract

Although the wolverine (*Gulo* gulo) is regarded as more sensitive to habitat changes and human disturbance than the other large northern carnivores, it is the least investigated one. In Central Norway, fifteen adult female wolverines were monitored at their dens during 2002-2007, and their cubs, in total 37 individuals, were identified and monitored over several years by scat sampling. The juvenile survival was 0.49 for all cubs, 0.68 and 0.28 for males and females, respectively- with significant higher survival for males than females (P = 0.047). The survival of juveniles born prior to or in a rodent peak year (2004 and 2007 in this study) had a significantly higher survival rate than juveniles born in years with low numbers of rodents (S = 0.57 vs. 0.31; P = 0.030). This demonstrates that rodents are an important food source for wolverines in their first year of age, and that the rodent cycles have a substantial impact on wolverine juvenile survival. Because of conflicts between the wolverines and livelihoods such as sheep farming and reindeer herding, the wolverine population is managed to maintain a low, but sustainable population level. However, like other long-lived carnivores with low average annual productions, the wolverine is sensitive to changes in survival rates. The importance of rodent peak years for annual survival should therefore be considered in the management of this species.

Sammendrag

Selv om jerven (*Gulo gulo*) er ansett å være den mest sensitive arten i forhold til habitatforandringer og menneskelig forstyrrelse av de store rovdyrene i Norden, er jerven den som er minst utforsket. I Sør-Norge ble femten tisper overvåket ved hiet fra 2002 til 2007, hvor valpene, til sammen 37 individer, ble identifisert og overvåket over flere år ved hjelp av avføringsprøver. Overlevelsen til valpene var 0,49 for alle individer og henholdsvis 0,68 og 0,28 for hanner og hunner, med signifikant høyere overlevelse for hannene (P = 0,047). Overlevelsen av valper som er født i forkant eller i et smågnagerår (2004 og 2007 i dette studiet) hadde en signifikant høyere overlevelse rate enn valper som er født i år med lavt nummer av smågnagere (S = 0,57 vs. 0,31; P = 0,030). Dette viser at smågnagere er en viktig kilde til mat for jerven i dens første leveår, og at smågnagerår har en betydelig påvirkning på overlevelsen. På grunn av konflikter mellom jerven og næringer som sauehold og reindrift, blir jervpopulasjonen forvaltet for å opprettholde et lavt, men bærekraftig populasjonsnivå. Men som andre langlevede rovdyr med lav, årlig reproduksjonsrate, er jerven sensitiv til forandringer i reproduksjonsraten. Viktigheten av smågnagerår for den årlige reproduksjonen burde derfor bli vurdert når det gjelder forvaltning av denne arten.

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1. Introduction

Female survival is one of the most important parameters for population growth of long-lived mammals such as large carnivores (Persson et al. 2003; Wielgus et al. 2013). The survival of juveniles is however more variable and can have a stronger effect on the population dynamics (Persson et al. 2003). It is therefore important to estimate rates and causes of juvenile mortality to understand variations in population growth (Persson et al. 2003). Some studies assume that the most important naturally mortality causes for juveniles are intraspecific, such as infanticide or competition for territories (Swenson et al. 2001; Persson et al. 2003; Persson 2009). Other assumes that interspecific factors are more important, such as competition for food and other resources (Marucco et al. 2012).

The wolverine (*Gulo gulo*) is the largest terrestrial mustelid, and one of the four large carnivores found in Scandinavia besides the brown bear (*Ursus arctos*), grey wolf (*Canis lupus*) and lynx (*Lynx lynx*) (Landa et al. 1997). Compared to the other northern large carnivores, the wolverine is thought to be the most sensitive species with regard to habitat changes and human disturbance (May et al. 2006). Wolverines are found in remote areas with arctic and alpine tundra, as well as in boreal forests in the Northern hemisphere (May et al. 2006; Hedmark et al. 2007; Persson 2009; Rauset et al. 2013). The wolverine is a facultative scavenger with competition for scarce and defendable food resources (Landa et al. 1997; van Dijk et al. 2008; Broseth et al. 2010), but it is also an active hunter (Landa et al. 1999; van Dijk et al. 2008). Wolverines show strong intrasexual territoriality with agonistic interactions among territory holders (Broseth et al. 2010). Females occupy territories that overlap to a small extent, whereas males can have larger territories that can encompass the home ranges of several females (Hedmark et al. 2007; Broseth et al. 2010).

The natural survival of adult wolverines is high (Broseth et al. 2010), and the mortality is often related to human activity (Vangen et al. 2001; Krebs et al. 2004; Persson et al. 2006; Squires et al. 2007; Broseth et al. 2010). In the 1900s, the wolverines were hunted down for its fur and for being regarded as a pest species (Landa & Skogland 1995; Hedmark et al. 2007), and it was about to be extinct when it was protected in Scandinavia from the late 1960's; 1967 in Sweden, 1973 in the Southern Norway and 1982 in Northern Norway (Landa & Skogland 1995; Hedmark et al. 2007). The government in Sweden and Norway has a goal of 90 and 39 annual reproductions respectively, to maintain a viable population, as they are obligated to by the Bern convention (Nilsson 2013). The Norwegian government, however, takes out the excess by hunting, usually in late winter/early summer (Swenson & Andren

2005). Eight regional predator boards are responsible for the management of the populations of large carnivores, and are in charge when it comes to hunting and issuing of hunting permissions within their own region, in accordance with the agendas of population goals, and for taking out wolverines that make large damage on farmer's livestock (Vangen et al. 2001).

As for most other mammals with low adult mortality, the wolverine has a low reproductive rate with long inter-birth intervals (Persson et al. 2006; Broseth et al. 2010). The females have litters of 2-3 and more rarely 4 cubs, with an increasing litter size with age (Banci 1994; Landa et al. 1997). Also time intervals between successful breeding attempts increase with age (Banci 1994; Landa et al. 1997). Adult female wolverines give birth from January to April, with most of them at the end of February and at the beginning of March (Persson et al. 2006) . The age of the cubs when they disperse is on average 11 months (Rauset 2013). The juveniles have a late maturity at 2 years of age (Banci 1994).

Juvenile wolverines are likely to have higher mortality rates when they leave their mothers' territory, because they do not longer benefit from hunting in familiar home ranges, and because of increased risk of being killed by other territorial wolverines (Banci 1994; Krebs et al. 2004). Juvenile survival may thus be strongly affected by annual fluctuations in food supply. Small rodents are keystone species in the arctic ecosystems, with large interannual fluctuations in population size. Rodents normally have population cycles of 3-4 years, but the cycles have been less pronounced some places in Europe since 1980, likely as a result of global climatic changes (Cornulier et al. 2013). This could affect many species that are dependent on small rodents (Cornulier et al. 2013). It is well known that several birds of prey, such as buzzards (Buteo spp) and owls, as well as smaller carnivores, such as the arctic fox (*Alopex lagopus*), the least weasel (*Mustela nivalis*) and the stoat (*Mustela Erminea*), depend on rodents to survive and breed, and thus increase in number in or after rodent peak years. Persson et al (2009), however, suggested that also the performances of larger carnivores, such as the wolverine, are affected by rodent abundance.

Rather few studies suggest that the rodent peak years may have an influence on wolverine production or juvenile mortality. Broseth et al. (2010) suggest that juvenile survival is correlated with reproduction parameters in ungulates. Wolverines have been regarded mainly as scavengers on large ungulates, and their survival may thus be affected by the presence of other large predators, such as the lynx (Mattisson et al. 2011) and the wolf (van Dijk et al. 2008), which will increase the scavenging opportunities. Landa et al. (1997) suggested that the lack of other large carnivores make the wolverines reproduction more dependent on small rodents. Banci (1994), on the other hand, considered wolverines to be too large to survive on small prey, and Lofroth et al. (2007) found that small mammals were relatively unimportant in the wolverines’ diet.

In this study, I examine the dispersal and survival of juvenile wolverines and if there are any differences between the sexes. Secondly, I investigate if there are any connection with juvenile survival and rodent peak years as an alternative food source.

2. Methods

2.1. Study area

The present distribution of wolverines in Scandinavia encompasses two countries, Norway and Sweden. The area includes boreal forest with low mountain ranges, alpine- and subalpine areas (Landa et al. 1998; Broseth et al. 2010). The western and central parts are characterized by deep valleys, glaciers and higher mountain summits at around 2000 metres above the shore line (m.a.s.l), whereas the east has more accessible areas with forest. The tree line is situated at 800-1000 m.a.s.l. and decreases northwards. Snow covers the ground from October-November until May-June depending on elevation (Broseth et al. 2010). The area has cold winters with average daily temperatures of -10 to -13 °C in January and moderate summer temperatures with 13-14 °C in July.

The area includes the presently southernmost part of the wolverine distribution in Western Europe, and the only place where the species co-exists with wild reindeer (*Rangifer tarandus*) (van Dijk et al. 2008; Broseth et al. 2010). There is also farming in the area, as free-ranging sheep graze unattended during summer from June-September in Norway, and semi-domestic reindeer graze whole year around in the north-eastern part of the study area in both Norway and Sweden. Reindeer and moose (*Alces alces*) constitute the wolverine's most important food source during winter (Landa et al. 1997). Roe deer (*Capreolus capreolus*), hare (*Lepus timidus*), ptarmigan (*Lagopus muta*), lemming (*Lemmus lemmus*), various rodents (*Microtus* spp. and *Myodes* spp.) and insectivores (*Sorex* spp.) are other possible food sources either by hunting or scavenging (van Dijk et al. 2008). The domestic sheep is also an alternative food source during summer, when the sheep are grazing unattended. There are semi-domestic reindeer grazing unattended throughout the year, and they may be an important food source further North, but the wolverine is a less effective predator on wild reindeer (Swenson & Andren 2005). The wolverines coexist with other large carnivores, i.e. wolf, lynx and brown bear, mainly in the eastern part of Norway and in Sweden (May et al. 2010).

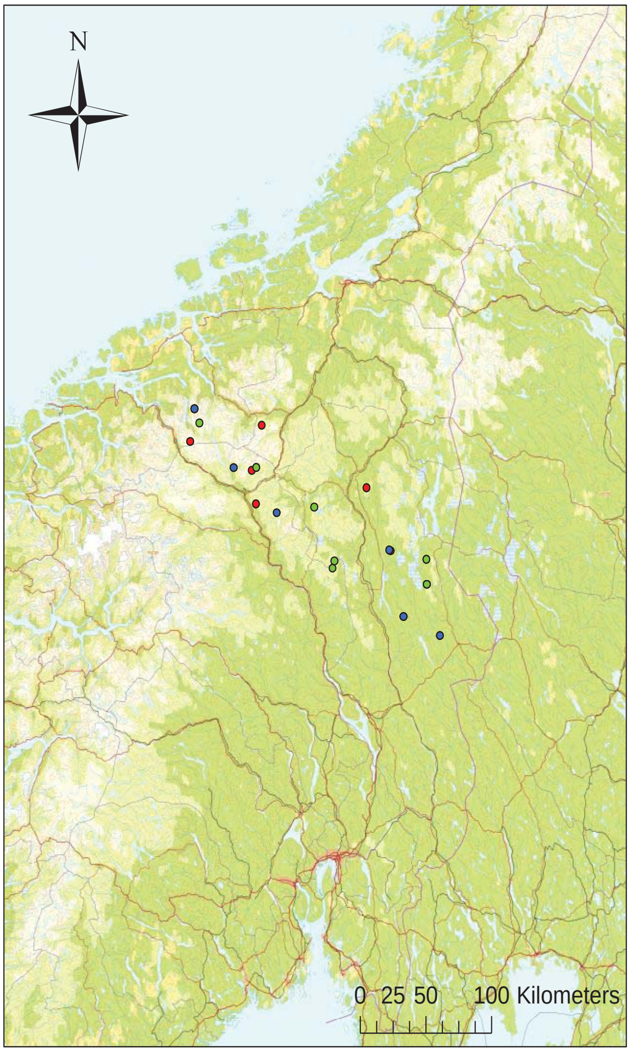

Figure 1. Overview of the locations of the wolverines' dens used for the analysis, with red circles (not recovered individuals), blue circles (recovered individuals) and green circles (both recovered and not recovered individuals).

2.2. Field methods

Between 2002 and 2007 fifteen adult females were captured at their secondary den sites during spring and fitted with GPS-collars (May et al. 2010). These females' puppies were ID-marked in their den (Fig. 1) from 2002 to 2007 by a small tissue sample from the puppies' ear. Altogether 37 wolverines from 15 adult females with 20 litters were used in the present analysis (Appendix 1).

Scat samples were collected on snow along wolverine tracks during the monitoring of natal dens in late winter-early spring from 2002-2012, by the Norwegian state Nature Inspectorate and field personnel of the County Boards in Sweden (Flagstad et al. 2008; van Dijk et al. 2008; Flagstad et al. 2012; Flagstad et al. 2013). Altogether, 10,866 scat and hair samples were collected across the entire wolverine distribution range in Scandinavia. The majority of samples (94 %) were collected during a three-month period from mid-February to mid-May after the end of the hunting season and before cubs of the year start moving around their mothers (Broseth et al. 2010). A small portion of each scat sample was used for DNA extraction. The extraction protocol, microsatellite genotyping and quality control are described by Broseth et al. (2010). 7,259 of the samples were of sufficiently high quality to generate a reliable DNA profile and subsequent individual identification (ID) of the sample. Given the large number of samples that were analysed over an extensive period, with a good coverage of the wolverines distributions range in Scandinavia, I assume that most, if not all, of the juvenile wolverines that established their own territory were identified from the scat sampling.

2.3. Statistical Analysis

To estimate the annual survival of wolverine’s migration from their birthplace, an uncounted history was constructed for each wolverine based on whether or not it was recovered from scat or hair samples during the sampling period 2002-2012. The wolverine cubs were divided in two groups, (1) wolverines that were identified after dispersal from the natal den locality and (2) those that were never identified after dispersal. We assumed that wolverines in the latter group had not survived the dispersal period. All wolverines that were harvested or suffered human-mediated mortality in their first year were removed from the analysis. A Kaplan-Meier estimate is according to Goel et al. (2010) the simplest way to analyse the survival over time, and involves analysing the probability of occurrence of an event at a certain point of time and multiplying these successive probabilities by an earlier calculated probability to get the final estimate (Goel et al. 2010). The analysis was used to compare the survival of male and female wolverines, and to compare wolverines born prior to or in a rodent peak year with wolverines born in other years. Rodent density was taken from Framstad (2013).

3. Results

3.1. Identification of established wolverines

A total of 45 wolverines (21 males and 24 females) were identified at the den sites, ID-marked by a tissue sample and subsequently monitored in the DNA-based monitoring programme of the Scandinavian wolverine's population. Eight individuals (2 males and 6 females) were legally harvested within their first year of age and omitted from the analyses, because they never got the chance to establish their own territory (Appendix 1).

Among the remaining 37 juvenile wolverines used in the further analyses (19 males and 18 females), 18 were recovered (13 males and 5 females) and given an identification (Appendix 3; Fig. 2-5), whereas 19 were not recovered (6 males and 13 females) and assumed to have died before one year of age (Appendix 2).

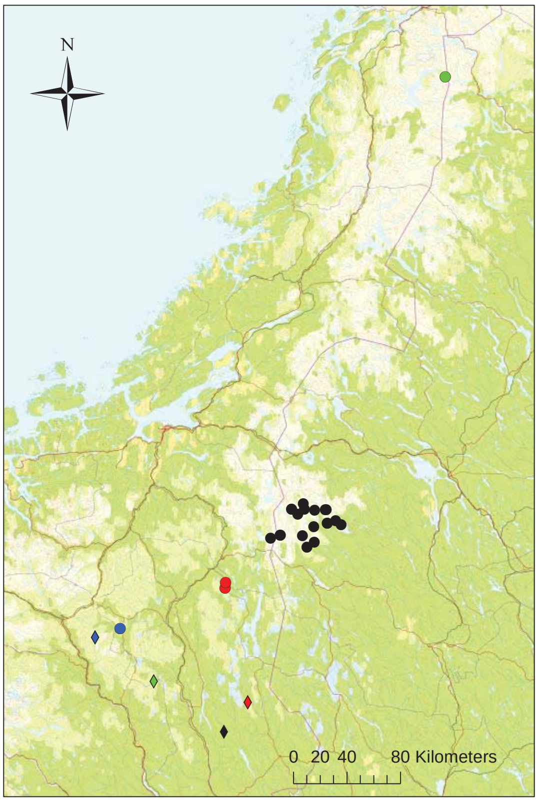

Figure 2. Location of den sites (diamonds) and recoveries (circles) for wolverines' born in 2003, two males (Ind222; black, Ind1086; green) and two females (Ind249; red, Ind5519; blue).

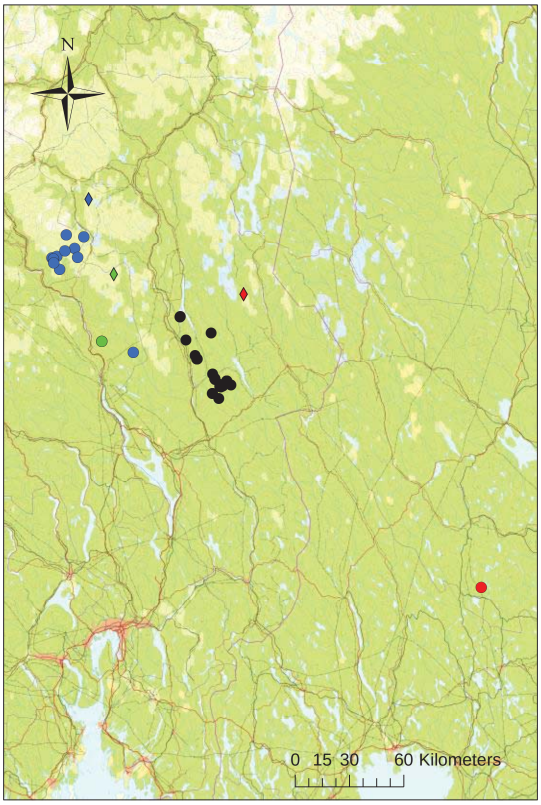

Figure 3. Location of den sites (diamonds) and recoveries (circles) for wolverines' born in 2004, three males (Ind223; black, Ind224; green, Ind225; blue) and one female (Ind793; black). Ind223 and Ind793 were born in the same den (red diamond).

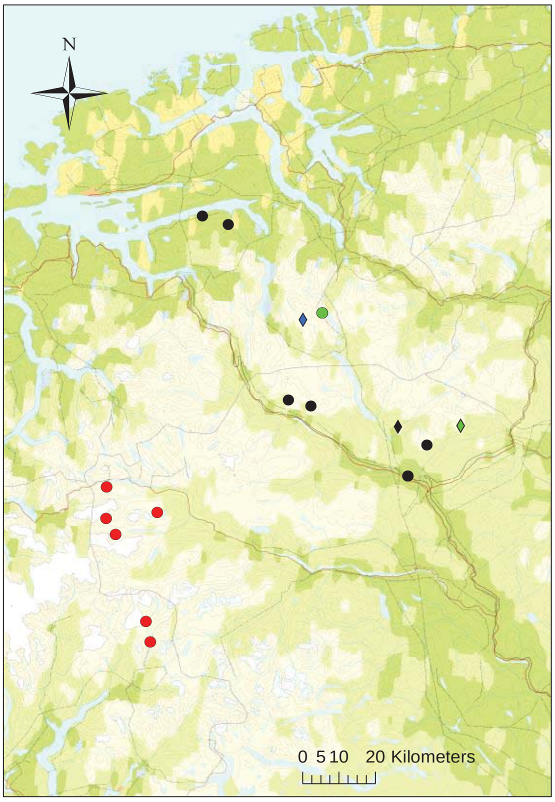

Figure 4. Location of den sites (diamonds) and recoveries (circles) for four wolverine' males born in 2005 (Ind227; black, Ind250; red, Ind307; green, Ind308; blue). Ind307 and Ind250 were born in the same den (green diamond), and Ind307 and Ind308 were recovered at the same location (green circle).

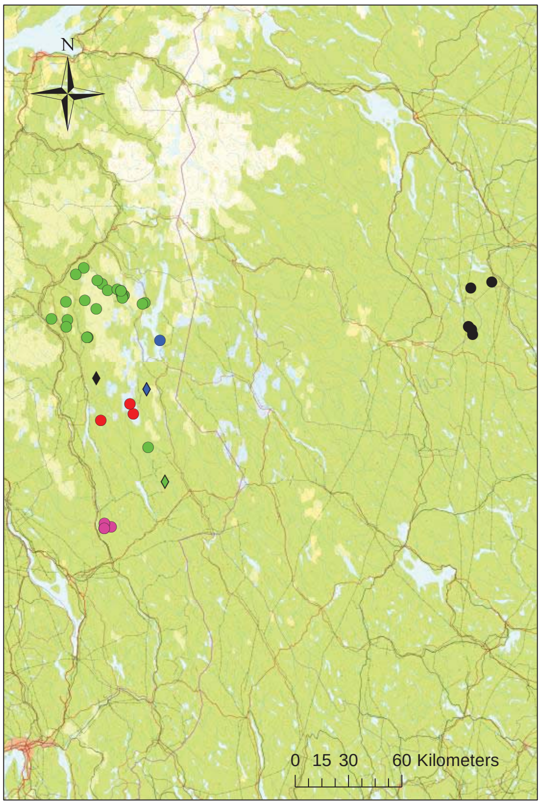

Figure 5. Location of den sites (diamonds) and recoveries (circles) for wolverines' born in 2006, four males (Ind244; green, Ind252; red, Ind333; pink, Ind867; black) and one female (Ind3551; blue), and one female born in 2007 (Ind382; yellow). Ind244 and Ind252, and Ind333 and Ind3551, were born in the same den (green and blue diamond, respectively).

3.2. Survival in relation to sex

The average first-year survival of juvenile wolverines was 0.53 for all (Table 1) and 0.68 and 0.28 for males and females respectively (Table 2 and 3). The highest age recorded was 7 years for males (Table 2) and 6 years for females (Table 3). Cumulative survival (Table 1, Fig. 6) shows that 49% of the wolverines survived their first year, and thereafter the survival decreased slightly until the 7'th year of age. The cumulative survival of males was significantly higher than of females (Fig. 6) (F = 3.94, P = 0.047). Wolverines that survived through their first year also lived through their second (Table 2 and 3). Five wolverines were legally shot after one year of age, but are not corrected for in the analysis for cumulative survival. Four other wolverines, which in this analysis are estimated as dead, were recovered as late as in 2012 (the last year of study).

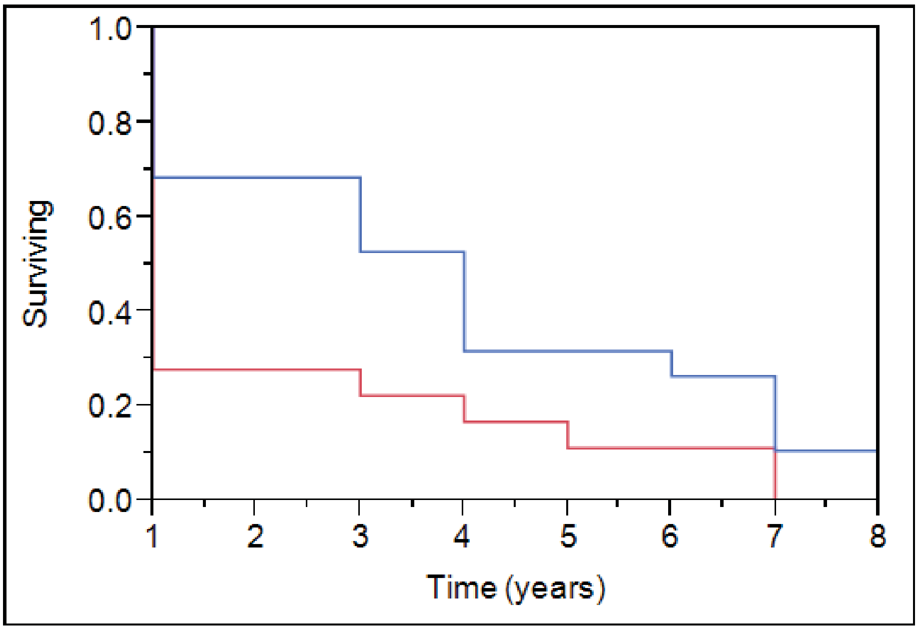

Figure 6. Cumulative survival curves in female (red) and male (blue) wolverines in Norway/Sweden 2003-2012.

Table 1. Cumulative survival of 37 individuals of wolverines in Norway/Sweden 2003-2012.

Time in year	Number at risk	Deaths	Proportion of survival	Cumulative survival[a]	Cumulative mortality (1 - cumulative survival)
1	37	19	0.4865	0.4865	0.5135
2	18	0	1.0000	0.4865	0.5135
3	18	4	0.7778	0.3784	0.6216
4	14	5	0.6429	0.2432	0.7568
5	9	1	0.8889	0.2162	0.7838
6	8	1	0.8750	0.1892	0.8108
7	7	5	0.2857	0.0541	0.9459
8	2	2	0.0000	0.0000	1.0000
9	0				

[a] Cumulative survival is calculated as the proportion of survival in year x multiplied by the cumulative survival in year x-1

Table 2. Cumulative survival of 19 individuals of wolverine males in Norway/Sweden 2003-2012

Time in year	Number at risk	Deaths	Proportion of survival	Cumulative survival[a]	Cumulative mortality (1 - cumulative survival)
1	19	6	0.6842	0.6842	0.3158
2	13	0	1.0000	0.6842	0.3158
3	13	3	0.7692	0.5263	0.4737
4	10	4	0.6000	0.3158	0.6842
5	6	0	1.0000	0.3158	0.6842
6	6	1	0.8333	0.2632	0.7368
7	5	3	0.4000	0.1053	0.8947
8	2	2	0.0000	0.0000	1.0000
9	0				

[a] Cumulative survival is calculated as the proportion of survival in year x multiplied by the cumulative survival in year x-1

Table 3. Cumulative survival of 18 individuals of wolverine females in Norway/Sweden 2003-2012.

Time in year	Number at risk	Deaths	Proportion of survival	Cumulative survival[a]	Cumulative mortality (1 - cumulative survival)
1	18	13	0.2778	0.2778	0.7222
2	5	0	1.0000	0.2778	0.7222
3	5	1	0.8000	0.2222	0.7778
4	4	1	0.7500	0.1667	0.8333
5	3	1	0.6667	0.1111	0.8889
6	2	0	1.0000	0.1111	0.8889
7	2	2	0.0000	0.0000	1.0000
8	0				

[a] Cumulative survival is calculated as the proportion of survival in year x multiplied by the cumulative survival in year x-1

3.3. Survival in relation to small rodents abundances

In Central Norway, small rodent populations peaked in autumn 2004 and 2007. Cumulative survival was calculated separately for the wolverines that were born one year prior to or in a rodent peak year (24 wolverines) and for those that were born other years (13 wolverines) (Table 4 and 5). The difference in survival was significant (F = 4.83, P = 0.030), with a higher survival of wolverines born prior to or in a rodent peak year (Fig. 7).

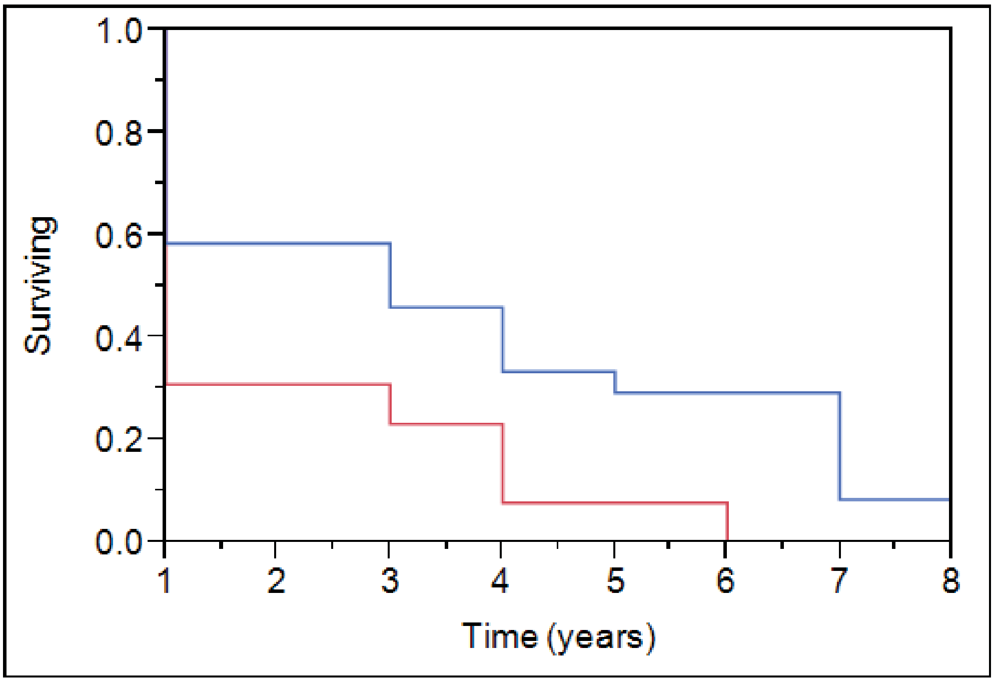

Figure 7. Survival in wolverines born prior to or in a rodent peak year (blue) compared to those born in other years (red).

Table 4. Cumulative survival of 24 individuals of wolverine born prior to or in a rodent peak year in Norway/Sweden 2003-2012.

Time in year	Number at risk	Deaths	Proportion of survival	Cumulative survival[a]	Cumulative mortality (1 - cumulative survival)
1	24	10	0.5652	0.5652	0.4348
2	14	0	1.0000	0.5652	0.4348
3	14	3	0.7692	0.4348	0.5652
4	11	3	0.7000	0.3043	0.6957
5	8	1	0.8571	0.2609	0.7391
6	7	0	1.0000	0.2609	0.7391
7	7	5	0.1667	0.0435	0.9565
8	2	2	0.0000	0.0000	1.0000
9	0				

[a] Cumulative survival is calculated as the proportion of survival in year x multiplied by the cumulative survival in year x-1

Table 5. Cumulative survival of 13 individuals of wolverine not born prior to or in a rodent peak year in Norway/Sweden 2003-2012.

Time in year	Number at risk	Deaths	Proportion of survival	Cumulative survival[a]	Cumulative mortality (1 - cumulative survival)
1	13	9	0.3077	0.3077	0.6923
2	4	0	1.0000	0.3077	0.6923
3	4	1	0.7500	0.2308	0.7692
4	3	2	0.3333	0.0769	0.9231
5	1	0	1.0000	0.0769	0.9231
6	1	1	0.0000	0.0000	1.0000
7	0				

[a] Cumulative survival is calculated as the proportion of survival in year x multiplied by the cumulative survival in year x-1

4. Discussion

4.1. Survival in relation to sex

The average first year survival rate for juvenile wolverines was 0.49 for all and 0.68 and 0.28 for males and females respectively. Persson et al. (2003) found that the juvenile survival from May to February, before dispersal, was 0.68 (95% CI: 0.56-0.80) for all and 0.81 (95% CI: 0.63-0.99) and 0.62 (955% CI: 0.46-0.77) for males and females respectively. This could indicate that the mortality is 0.13 for males and 0.34 for females during the dispersal. However, the study of Persson et al. (2003) was carried out in an area with higher wolverine density, which may have caused more intraspecific competition and associated infanticide. According to Persson et al. (2003), intraspecific predation is the most important cause of juvenile mortality and is accoutred during two periods, from May to early June when the juveniles are still dependent, i.e. infanticide, and in August-September, after they have reached independency (Persson et al. 2003). Banci et al. (1994) suggested that very young and old individuals are less successful foragers, even if food resources are abundant. This is in accordance with my study where the mortality was highest during the first year of age and for the old age classes. However, some individuals considered as dead may still have been alive or at least have reached a higher age than recorded. If so, the survival of individuals from the old age classes would have been higher than estimated in this study.

Although the results from my study and that of Persson et al. (2003) are not directly comparable, there was a higher survival of males than of females in both studies, indicating that females are more exposed to intraspecific predation after independence (Persson et al. 2003). However, there is a higher chance to recapture males than females by scat sampling in early spring, 76% and 52%, respectively (Broseth et al. 2010), since breeding females at that time are in or close to their den with their offspring (Broseth et al. 2010). The survival of females may therefore be underestimated compared to that of males. Nevertheless, the sampling of scats in my study was comprehensive, and continued for several years, which means that most, if not all, females that managed to establish a territory before they died, were recovered.

The survival may also be affected by the habitat quality and impacts associated with infrastructure. Reproducing female wolverines prefer the den site locations near the tree line for shelter, and moves downhill for more food as the cubs grow more mobile and independent (Landa et al. 1997; May et al. 2010; May et al. 2012). Juvenile wolverines travel more on unknown locations and do not have the same benefit from hunting on familiar home ranges as wolverines with a territory (Branci et al. 1994).

The wolverines that were shot legally were not included in the cumulative survival analysis, which means that the survival of adult wolverines are a bit underestimated, since they probably would have lived longer. The same concerns adult wolverines recovered in the latest year of the study, since they were estimated dead in this analysis, but were shown to still be alive.

4.2. Survival in relation to small rodents abundances

This study revealed a significantly higher survival of wolverines born prior to or in a rodent peak year compared to wolverines born in other years. The survival was almost twice as high for wolverines born prior or in a rodent peak year (S = 0.57 vs. 0.31), indicating that rodents were an important food source for wolverines in their first year of age.

Landa et al. (1997) found that wolverine juveniles in Snøhetta had a significant higher survival if they were born in a rodent peak year, and suggested that the lack of other large predators could make wolverines more dependent on peaks in the rodent cycles than would be expected in a more intact system. Landa et al. (1997) analysed scats from den sites in June when the female wolverines had left the dens with the cubs, and found a significant higher rodent content in scats from wolverines with surviving cubs (51%) than the average (34%). Van Dijk et al. (2008) reported that rodents were the third most important food source for wolverines, and that they tended to eat 4% less rodents and scavenge more when they were living in the presence of wolves. The females' diet consisted of more rodents than the diet of the males (van Dijk et al. 2008). This may indicate that the mortality of females is higher because of their dependence on rodents, while males find other food sources easier, either from hunting or perhaps more likely by being superior competitors for carrions, as starvation is a significant natural cause of wolverine mortality in some populations (Inman et al. 2012).

It is well known that other species lining in the arctic tundra are extremely dependent on the rodent cycles. The arctic fox is probably the most extreme example (Henden et al. 2008), where most of the puppies die before dispersal if they are born in years where the populations of small rodents crash (Meijer et al. 2013). They have a higher survival during years where rodent populations increase again, both because they have more food in the important first weeks and months of their lives, and because they are provided with higher abundances of rodents during dispersal (Meijer et al. 2013). For the wolverine, the potential dependency on rodents has never been established, although some studies indicate that rodents may be an important food supplement (Landa et al. 1997; van Dijk et al. 2008; Persson 2009). My study demonstrates that the rodent cycles have a substantial impact on the juvenile survival in wolverines, and adds important data to this discussion.

The dependence of juvenile survival on rodent peaks can be used as an aid for management implications in a harvested wolverine population. The Norwegian government takes out the access of wolverines each year, but by taking into account the population level of small rodents, they could vary the annual hunting effort, and obtain a more efficient hunt for population control.

For further analyses of relationships between juvenile survival and rodent peaks, the rodent abundance could be divided into different groups, ranging 1 (lowest) to 3 (highest) as Landa et al. (1997) did. The scat samples from their first and second year of age could also be analysed according to the food sources. Continuing this study would not only increase the sample size, but also corroborate the results by including more rodent peak years.

5. Conclusion

I found that the survival was significantly higher for wolverine males than for females. The probability of recovery may be lower for females, but because of extensive field work for several years, I assume that most, if not all, females that succeeded in establishing a territory was recovered. Wolverines born prior to or in a rodent peak year had a higher survival than those born in other years, indicating that rodents are one of the most important food sources during their first year of life. This insight may be used by the game authorities to achieve the goal of keeping the wolverine population at a stable level.

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Appendix 1. Locations of the wolverines den and identification (ID) of the adult females and their offspring. Juvenile wolverines that were legally shot before they had the chance to establish their own territory were omitted from the analyses and are marked with an asterisk.

Offspring (ID)	Birth year	Den location	Location, municipality	Adult female (ID)	Sex
S1402	2002	J-NOP-003 Grøndalen	Skredahøin, Lesja	S1602	F
S1502	2002	J-NOP-003 Grøndalen	Skredahøin, Lesja	S1602	M
S5105	2005	J-NOP-003 Grøndalen	Grøndalen 2, Lesja	S1602	M
S5005	2005	J-NOP-003 Grøndalen	Grøndalen 2, Lesja	S1602	M
S2503	2003	J-NHE-004 Gråfjellet	Kvannbekken, Åmot	S2203	M
S2303	2003	J-NHE-004 Gråfjellet	Kvannbekken, Åmot	S2203	F
S2403	2003	J-NHE-004 Gråfjellet	Kvannbekken, Åmot	S2203	M
S3003	2003	J-NST-003 Lindalen-Dindalen	Fiskbekklia, Oppdal	S2903	F
S3103*	2003	J-NST-003 Lindalen-Dindalen	Fiskbekklia, Oppdal	S2903	M
S2003*	2003	J-NST-004 Knutshø Vest	Breidslågan, Oppdal	S1903	M
S2103*	2003	J-NST-004 Knutshø Vest	Breidslågan, Oppdal	S1903	F
S3303	2003	J-NOP-005 Haverdalen	Djupdalen, Dovre	Not marked	F
S3203	2003	J-NOP-005 Haverdalen	Djupdalen, Dovre	Not marked	F
S1803	2003	J-NHE-006 Rømundfjell	Skjærbekkdalen, Engerdal	S1703	F
S3504	2004	J-NHE-006 Rømundfjell	Skjærbekkdalen, Engerdal	S1703	M
S3604	2004	J-NHE-006 Rømundfjell	Skjærbekkdalen,	S1703	F

			Engerdal		
S2803	2003	J-NOP-009 Storfjellet	Storfjellet Nord, Stor-Elvdal	S2603	M
S2703*	2003	J-NOP-009 Storfjellet	Storfjellet Nord, Stor-Elvdal	S2603	F
S3703*	2003	J-NOP-009 Storfjellet	Storfjellet Sør, Ringebu	S2603	F
S3804	2004	J-NOP-009 Storfjellet	Storfjellet Sør, Ringebu	S2603	M
S4104	2004	J-NHE-008 Mjovassdalen	Mjovasskletten, Folldal	S3904	M
S4004*	2004	J-NHE-008 Mjovassdalen	Mjovasskletten, Folldal	S3904	F
S4204	2004	J-NOP-006 Einbuggdalen	Einøvlingseggen, Dovre	Not marked	F
S4304	2004	J-NOP-006 Einbuggdalen	Einøvlingseggen, Dovre	Not marked	M
S5905*	2005	J-NHE-013 Magnhildalen	Trolldalen, Tynset	S5805	F
S4405	2005	J-NHE-014 Tylldalen	Svartberget, Tynset	Not marked	F
S4505	2005	J-NHE-014 Tylldalen	Svartberget, Tynset	Not marked	F
S6005	2005	J-NMR-001 Gravdalsområdet	Røyra, Nesset	Not marked	M
S6105	2005	J-NMR-001 Gravdalsområdet	Røyra, Nesset	Not marked	M
S5705	2005	J-NOP-001 Skamsdalen	Svalie, Lesja	S5505	M

S5605	2005	J-NOP-001 Skamsdalen	Svalie, Lesja	S5505	F
S5405	2005	J-NMR-005 Vikebotn	Inste Gråhøsnyta, Nesset	S5205	M
S5305*	2005	J-NMR-005 Vikebotn	Inste Gråhøsnyta, Nesset	S5205	F
S7107	2007	J-NMR-005 Vikebotn	Vikebotn B, Nesset	S5205	F
S7007	2007	J-NMR-005 Vikebotn	Vikebotn B, Nesset	S5205	F
S7207	2007	J-NMR-005 Vikebotn	Vikebotn B, Nesset	S5205	M
S6306	2006	J-NHE-015 Kvitvola	Kvitvola, Engerdal	S6206	F
S6406	2006	J-NHE-015 Kvitvola	Kvitvola, Engerdal	S6206	M
S6706	2006	J-NHE-011 Trysilfjellet	Fjellslifjellet, Trysil	Not marked	M
S6606	2006	J-NHE-011 Trysilfjellet	Fjellslifjellet, Trysil	Not marked	M
S6506	2006	J-NHE-011 Trysilfjellet	Fjellslifjellet, Trysil	Not marked	F
S6806	2006	J-NHE-001 Sølen	Steinfjellet 2, Rendalen	S4605	M
S6906	2006	J-NHE-001 Sølen	Steinfjellet 2, Rendalen	S4605	F
S4705	2007	J-NHE-001 Sølen	Steinfjellet 2, Rendalen	S4605	F
S4805	2007	J-NHE-001 Sølen	Steinfjellet 2, Rendalen	S4605	F

Appendix 2. Wolverines that were recovered (Yes) and not recovered (No) and times of recovery in this study in Norway/Sweden 2003-20012.

Identification (ID)	**Year of birth**	**Sex**	**Times recovered**	**Times recovered**
S1402	2002	F	No	-
S1502	2002	M	No	-
S1803	2003	F	yes	2
S2303	2003	F	No	-
S2403	2003	M	No	-
S2503	2003	M	Yes	19
S2803	2003	M	Yes	1
S3003	2003	F	No	-
S3203	2003	F	No	-
S3303	2003	F	Yes	1
S3504	2004	M	Yes	23
S3604	2004	F	Yes	1
S3804	2004	M	Yes	2
S4104	2004	M	Yes	11
S4204	2004	F	No	-
S4304	2004	M	No	-
S4405	2005	F	No	-
S4505	2005	F	No	-
S4705	2007	F	No	-
S4805	2007	F	No	-
S5005	2005	M	Yes	1
S5105	2005	M	Yes	6
S5405	2005	M	Yes	1
S5605	2005	F	No	-
S5705	2005	M	Yes	7
S6005	2005	M	No	-
S6105	2005	M	No	-
S6306	2006	F	Yes	1
S6406	2006	M	Yes	4

S6506	2006	F	No	-
S6606	2006	M	Yes	24
S6706	2006	M	Yes	3
S6806	2006	M	Yes	6
S6906	2006	F	No	-
S7007	2007	F	No	-
S7107	2007	F	Yes	2
S7207	2007	M	No	-

Appendix 3. Identification on the 18 wolverines that was recovered (13 males and 5 females) and number of samples and period identified in Norway (N) and Sweden(S) 2003-2012

Wolverine ID	**Sex**	**Number of samples**	**Period identified**
S1803 Ind249	F	2	March 2007 - March 2009
S2503 Ind222	M	19	March 2005 - March 2010
S2803 Ind1086	M	1	April 2005
S3303 Ind5519	F	1	January 2005
S3504 Ind223	M	23	March 2006 - March 2011
S3604 Ind793	F	1	February 2007
S3804 Ind224	M	2	February 2006
S4104 Ind225	M	11	March 2006 - April 2007
S5005 Ind307	M	1	April 2008
S5105 Ind250	M	6	March 2007 - March 2010
S5405 Ind308	M	1	April 2008
S5705 Ind227	M	7	April 2006 - April 2007
S6306 Ind3551	F	1	January 2012
S6406 Ind333	M	4	April 2009
S6606 Ind244	M	24	April 2007 - April 2012
S6706 Ind252	M	3	April 2008 - March 2012
S6806 Ind867	M	6	April 2009 - February 2012
S7107 Ind382	F	2	March 2011

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