Population Ecology of Scandinavian Wolverines

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Abstract

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In this thesis I examine reproductive patterns, test for effects of reproductive costs and winter food availability on female reproduction, estimate rates and causes of juvenile mortality, examine dispersal patterns and analyze population viability.

Wolverine (*Gulo gulo*) females reached the reproductive stage no earlier than 3 years of age and the minimum average age at first reproduction was 3.4 years. Each year about every second female reproduced and produced an average of 0.8 kits per female.

Reproduction incurred costs on females that affected reproduction the subsequent year. Experimental food-supplementation of females in early winter enhanced reproductive rates, even though all food-supplemented females had reproduced the preceding year. I therefore suggest that reproductive success of wolverine females is determined by the combined effect of reproductive costs and winter food availability.

The survival rate of radio-marked juveniles from May to February was about 70%. Intraspecific predation was the most important cause of juvenile mortality (50%), and occurred in May-June when juveniles are dependent on their mother and in August-September after independence.

Mean dispersal age was 13 (7-26) months for both sexes. All males (n = 11) and 69% of the females (n = 9) dispersed. Competition for resources apparently determined female dispersal pattern, while competition for mates seemed to explain male dispersal pattern.

Population dynamics of wolverines are largely influenced by stochastic components. A population viability analysis suggest that the carrying capacity of a Scandinavian population should exceed 46 adult (≥3 years old) females to not be considered vulnerable according to IUCN (2000). This should be seen as a preliminary guideline as parameter estimates in the model are uncertain. The Swedish population averaged 100 adult females during 1999-2001, which is far above the carrying capacity recommended for a population to not be considered "vulnerable".

The recruitment rate to the next generation is primarily influenced by adult female survival, effects of reproductive costs and winter food availability on female reproduction, and intraspecific predation on juveniles. The recruitment shows a large variation among individuals and years, suggesting that wolverine population dynamics is strongly characterized by stochastic components. Wildlife managers should especially consider the importance of adult female survival.

Key words: demography, dispersal, *Gulo gulo*, infanticide, intraspecific predation, juvenile survival, Norway, population viability, PVA, reproduction, reproductive costs, Sweden, wolverine

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Contents

Appendix

Papers I-V

I base my thesis on the following papers, which will be referred to by the corresponding Roman numerals in the text.

I. Persson, J., Landa, A., Andersen, R. and Segerström, P. Reproduction in Scandinavian wolverines. (Manuscript).

II. Persson, J. Effects of reproductive costs and winter food availability on wolverine female reproduction. (Manuscript).

III. Persson, J., Willebrand, T., Landa, A., Andersen, R. and Segerström, P. The role of intraspecific predation in the survival of juvenile wolverines. *Wildlife Biology* (In Press).

IV. Vangen, K.M., Persson, J., Landa, A., Andersen, R. and Segerström, P. 2001. Characteristics of wolverine dispersal. *Canadian Journal of Zoology* 79: 1641-1649.

V. Sæther, B.-E., Engen, S., Persson, J., Brøseth, H., Landa, A. and Willebrand, T. Management strategies for the Scandinavian wolverine: practical application of stochastic models in Population Viability Analysis. (Manuscript submitted to Ecological Applications).

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Introduction

"Picture a weasel - and most of us can do that, for we have met that little demon of destruction, that small atom of insensate courage, that symbol of slaughter, sleeplessness, and tireless, incredible activity - picture that scrap of demoniac fury, multiply that mite some fifty times, and you have the likeness of a wolverine" (Ernest Thompson Seton, 1953). This is a typical description of the wolverine (*Gulo gulo*) in early literature and northern folklore, where the wolverine often was described as a ferocious animal, with extraordinary strength, courage and excessive food habits.

These early descriptions of the wolverine were not dispelled until the second half of the 20th century, when several wolverine studies were initiated. Wright & Rausch (1955) analyzed reproductive tracts from harvested wolverines in Yukon and Alaska. Other early studies of wolverine biology were mainly based on snow-tracking in Fennoscandia (Krott, 1959; Pulliainen, 1963; Haglund, 1966; Myhre, 1967; Myrberget, Groven & Myhre, 1969). Thereafter, a number of short-term studies of wolverine biology based on radio-telemetry were conducted in Montana (Hornocker & Hash, 1981), Alaska (Magoun, 1985; Gardner, 1985; Whitman & Ballard 1983), Yukon (Banci 1987), Idaho (Copeland, 1996), and Norway (Landa, 1997). Some aspects of reproductive biology have been studied on captive wolverines (*e.g.* Mead *et al.*, 1991).

Although these studies contributed to basic information about wolverine biology, the species is still frequently characterised as one of the northern hemisphere's least known large carnivores. However, some aspects have been illuminated more than others. For instance, spatial patterns (home range size *etc.*), food habits in winter, and some aspects of reproduction, such as pregnancy rates from in utero studies, are relatively well described (*e.g.* Banci, 1994; Pasitschniak-Arts & Lariviere, 1995; Landa, Lindén & Kojola, 2000). In contrast, little information is available on demographic rates and what factors limit these parameters. This is primarily due to difficulties in studying an animal with large home ranges, low population densities, a solitary lifestyle, and a distribution restricted to remote and harsh environments in the north. As a consequence, available demographic data are based on small sample sizes from short-term studies, which make earlier estimates of demographic rates less precise.

The wolverine - current knowledge

The wolverine has a circumpolar distribution, inhabiting boreal coniferous forests and arctic tundra of the northern hemisphere (Pasitschniak-Arts & Larivière, 1995). Wolverines are generally described as generalist predators and scavengers, with a seasonal pattern of primarily scavenging in winter and using a variety of prey in summer, *e.g.* rodents, birds and carrion. Wolverines are probably dependent on the existence of ungulate populations in winter (Magoun, 1985; Gardner, 1985; Banci, 1987). They are capable of taking large ungulates as live prey (Haglund, 1966, 1968; Pulliainen, 1968; Magoun, 1985), but ungulate presence in the wolverine diet is often the result of scavenging (Banci, 1994). Yet, the wolverine in Fennoscandia is a frequent predator on reindeer (*Rangifer* *tarandus*), sheep (*Ovis aries*) and in rare cases on moose (*Alces alces*) (Haglund, 1966; Bjärvall *et al.*, 1990).

The mating system of the wolverine is polygamous (Rausch & Pearson, 1972). Females may attain sexual maturity at about 15 months, but previous studies report varying proportions of pregnant females at 2 years of age (Rausch & Pearson, 1972; Liskop, Sadleir & Saunders, 1981; Banci & Harestad, 1988). Mating occurs from May to August (Wright & Rausch, 1955; Rausch & Pearson, 1972; Magoun & Valkenburg, 1983). Wolverines exhibit delayed implantation, and implantation occurs from November to March (Banci & Harestad, 1988), with a subsequent gestation of about 30-50 days (Rausch & Pearson, 1972; Mead *et al.*, 1993). Most females give birth in February and early March (Pulliainen, 1968; Blomqvist, 2001). Juveniles are born in dens and females sometimes use multiple dens prior to weaning (Magoun & Copeland, 1998). Juveniles are weaned at 9-10 weeks (Iversen, 1972) and begin to travel with their mothers by late May to mid-June (Magoun, 1985). Information from reproductive tracts have shown that a high proportion of adult females (≥3 years) are pregnant each year (Rausch & Pearson, 1972; Liskop, Sadleir & Saunders, 1981; Banci & Harestad, 1988), indicating that most adult females mate every year. However, observations of radio-collared wolverines indicate that the proportion of females in the population that will reproduce successfully is much lower than the proportion of pregnant females (Banci & Harestad, 1988). Banci & Harestad suggested that the proportion of pregnant or postpartum females were highest in 4-6 years old animals, but mean number of corpora lutea increased with age to a maximum for 7-12-year-old females.

Estimates of age specific mortality causes and survival rates for wolverines are not available. Only single cases of juvenile mortality have been documented (starvation and probable wolf predation; Banci, 1987). Human harvest is an important cause of adult mortality in many North American wolverine studies (Hornocker & Hash, 1981; Whitman & Ballard, 1983; Magoun, 1985: Banci, 1987), while starvation and predation are the most common natural causes of adult mortality (Banci, 1994; Copeland, 1996).

In relation to their body size, wolverines have very large home ranges and they exhibit intra-sexual territoriality (Banci, 1994). Males have larger home ranges than females and females without kits have larger home ranges than females raising kits (*e.g.* Hornocker & Hash, 1981; Copeland, 1996). Home range use appears to vary with season (Whitman, Ballard & Gardner, 1986; Copeland, 1996). Previous studies suggest that males are more likely to disperse than females (Banci, 1994) and that young females sometimes establish residency next to or within the natal home range (Magoun, 1985).

In summary, current information is mostly based on North American studies which indicate that wolverine ecology is characterized by a dependency on availability of ungulates as carrion and/or prey, low reproductive rates, intrasexual territoriality and male biased dispersal.

Distribution in Scandinavia

Historically, wolverines were found throughout mountainous and forested areas in Norway and in south central to northern Sweden (Johnsen, 1929; Lönnberg, 1936). The Scandinavian wolverine population followed the same path of human persecution as most large carnivore populations around the world (*e.g.* Johnson, Eizirik & Lento, 2001) when state bounties were introduced in the mid 19th century. Hunting statistics indicate that the population declined from about 1870 until they became protected 1969 in Sweden, 1973 in southern Norway and 1982 in remainder of Norway (Landa *et al*., 2000). At that time, wolverines were limited to a small population in the mountain range along the Swedish-Norwegian border and the population increased slowly the first decades after protection.

The current distribution of the Scandinavian wolverine is largely sympatric with reindeer and mainly restricted to mountainous areas and associated forests (Fig. 1). The distribution is patchy, with large areas of unoccupied but presumably suitable habitat. Highest densities are found in the northernmost part of Sweden and in mountainous areas of Norway along the Norwegian-Swedish border and in south-central Norway. The latter is a subpopulation, isolated by about 100-200 km from the main population in northern Norway and central Sweden (Landa, Lindén & Kojola, 2000). The subpopulation is genetically differentiated from the main population, and the overall genetic variation in the Scandinavian population is lower than reported for other mustelids (Walker *et al.*, 2001). Today, the wolverine is protected in Sweden while lethal control is widely used in Norway. The latest population estimates based on records of natal dens was 326 (S.E. = 45) in Sweden and 269 (S.E. = 32) in Norway (Landa *et al.*, 2001).

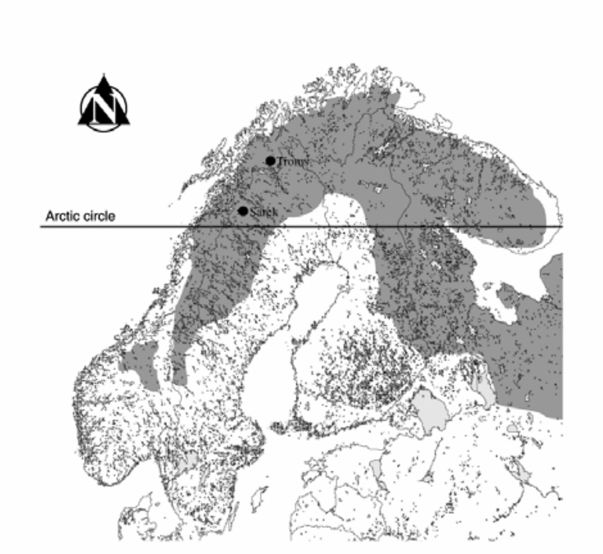

Figure 1. Present distribution of wolverines (*Gulo gulo*) in northern Europe. The solid circles in the north indicate the study areas Sarek and Troms (redrawn from Landa, Lindén & Kojola, 2000)

Concerns for management

Wolverines are ecologically similar to large carnivores such as wolves (*Canis lupus*), bears (*Ursus arctos*) and lynx (*Lynx lynx*). They have large home ranges, occur at low densities and frequently prey upon larger prey such as reindeer. This predatory behaviour puts the wolverine in conflict with human interests. The main problem for management in Scandinavia is that the wolverine is a predator on semi-domesticated reindeer throughout the year in northern Sweden and Norway, and prey upon free-ranging domestic sheep in the summer in Norway (Bjärvall *et al*., 1990; Landa & Tømmerås, 1996; Aanes, Swenson & Linnell, 1996). Herding of semi-domesticated reindeer is deeply tied to the Sámi culture of central and northern Scandinavia. Reindeer husbandry should be considered as both an economic activity and a part of the identity of an ethnic minority (Landa *et al*., 2000). Reindeer husbandry is based on extensive herding of reindeer ranging over large areas of pastures, including mountain, tundra, and boreal forests, often with distinct seasonal patterns (Bjärvall *et al*., 1990). The herds are often left unattended for long periods but reindeer migration patterns are largely influenced by active herding. At least locally, reindeer husbandry suffers from heavy predation by wolverines and other predators (Bjärvall *et al*., 1990; Kvam *et al.,* 1995). The conflict between reindeer husbandry and wolverine predation represents a unique problem of compromising between sustainability of an indigenous culture and conservation of predators. In most parts of Norway, wolverine conservation is further complicated by depredation upon free-ranging and unattended sheep that graze on mountain and forest pastures during the summer (*e.g*. Aanes, Swenson & Linnell*,* 1996). These conflicts continually lead to demands for increased hunting quotas and illegal harvest of wolverines (Anonymous, 1999). Therefore, managers are forced to compromise between sustaining viable wolverine populations and supporting the livelihoods of those involved in animal husbandry. Current attempts to manage these conflicts are mainly based on compensation systems in both countries and lethal control of wolverines in Norway.

Wolverine management is different in North America where depredation by wolverines on domestic livestock is seldom reported, presumably because the distribution of wolverines rarely overlaps that of domestic sheep (Banci, 1994). Instead, wolverine management issues in North America include regulating trapper harvest, preventing human disturbance at natal denning sites, and mitigating for habitat loss and fragmentation (Paquet & Hackman, 1995; Copeland, 1996). Habitat loss and fragmentation is currently not of great concern in Scandinavia, because large areas of sparsely populated and continuous mountains and forests are presumed to be suitable wolverine habitat (Landa *et al.,* 2000).

Sound management of wolverines in Scandinavia and other large carnivore populations primarily involves political decisions in which managers have to consider socio-economic consequences of their management plans. However, the most relevant questions in current management of carnivore populations cannot be answered without reliable biological information. In particular, we need data on demographic rates and their spatial and temporal variation to estimate sustainable harvest levels and population persistence in Population Viability Analyses. We also need to understand what factors affect demographic rates; *e.g.* why a population is decreasing or how we can make it increase, and to understand dispersal pattern and individual capacity for functional dispersal in order to predict re-colonization of vacant habitat and connectivity between subpopulations.

Objectives

In this thesis I address general patterns of wolverine population ecology in Scandinavia. More specifically; reproductive ecology, life-history from birth to dispersal and the effects of management strategies on viability. My main objectives in paper I-V are the following:

1. To describe reproductive aspects of wolverine population ecology. This includes examination of age at first reproduction, and estimation of reproductive parameters in adult female wolverines (Paper I).

2. To test the effect of reproductive costs and winter food availability on reproductive success of wolverine females (Paper II).

3. To estimate juvenile survival rate and assess the importance of factors affecting juvenile survival (Paper III).

4. To describe patterns of dispersal in wolverines and examine sex-specific age, rate and distance of dispersal (Paper IV).

5. To analyze wolverine population vulnerability and effects of different management options on vulnerability by using insight gained from stochastic population models (Paper V).

Material and Methods

Study area

I conducted the main part of my thesis work in and around Sarek National Park in Norrbotten County, northern Sweden (Kvikkjokk: 67°00'N, 17°40'E) (Fig 1.). In addition, the thesis is partly based on data from the south-eastern part of Troms County in northern Norway (Dividalen: 68°50'N, 19°35'E). The climate is continental with average temperatures of -10 to -13°C in January and 13 to 14°C in July. The annual precipitation is 500-1000 mm in both areas, but higher in the western part of Sarek (around 2500 mm) (Påhlson, 1984; Ryvarden, 1997). The ground is usually snow-covered from October to May. Both areas are characterised by deep valleys, glaciers and high plateaus with peaks ranging from 1 700 to 2 000 m a.s.l. The valleys are dominated by mountain birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*), and also Norway spruce (*Picea abies*) in Sarek (Grundsten, 1997). Mountain birch forms the tree-line in both areas and occurs at a maximum elevation of 600-700 m a.s.l. (Grundsten, 1997; Ryvarden, 1997). Semi-domesticated reindeer are managed extensively by indigenous Sámi in both study areas, and sheep graze during the summer in the western part of the study area in

Troms. Reproducing populations of brown bear and lynx occur in both areas although brown bears are less common in Troms. Moose is the only wild ungulate occurring in significant numbers in both study areas. The study area in Sarek is approximately 6 000 km^2 and in Troms approximately 2 500 km^2. The approximate density of wolverines is 1.4/100 km^2 and 1/100 km^2 in Sarek and Troms, respectively.

Methods

The basis for my thesis is data from individually marked wolverines of different ages. Wolverines were radio-marked and monitored during 1993-2002 in Sarek and during 1996-2002 in Troms. We monitored 55 radio-marked female wolverines older than 1 year of age (37 in Sarek and 18 in Troms). Eighty juvenile wolverines (52 in Sarek and 28 in Troms) were monitored for survival and dispersal analyses. We captured juveniles by hand and equipped them with transmitters at maternal dens or rendezvous sites (*i.e.* dens used after weaning; Magoun & Copeland, 1998) mainly in late April to early June (*i.e.* when the kits were 2-3 months old). We located juveniles either by locating a transmitter-equipped mother or by snow-tracking non-marked females. Adult females were captured in maternal dens or at rendezvous sites, or were darted from helicopters. Most adult males were darted from helicopters. The wolverines were immobilised with Xylazin and Ketamin until 1999 in Sarek and thereafter Medetomidin and Ketamin in both Sarek and Troms (see Arnemo *et al*., 1998). During 1993-1995 we equipped juveniles in Sarek with transmitters glued to the fur (Telonics® Mod 055, Arizona, USA, 31-34 g, n = 15) and then later in the summer relocated and equipped them with collar-mounted radio transmitters (Telonics® Mod 315, Arizona, USA, 150-200 g). From 1996 we equipped juveniles with intraperitoneally implanted transmitters (Telonics® Imp/210/L, Imp/300/L or Imp/400/L, Arizona, USA, 30-90 g, n = 74). Adult wolverines were equipped with intraperitoneally implanted transmitters only (Telonics® Imp/210/L, Imp/300/L or Imp/400/L, Arizona, USA, 30-90 g) or collar-mounted radio transmitters (Telonics® Mod 315, Arizona, USA, 150-200g). At capture, we took morphological measurements, retrieved the 1st premolar for aging, sampled tissue and hair for genetic analyses, and took blood samples for veterinary medicinal analysis. The study was approved by the Animal Ethics Committee for northern Sweden, Umeå.

We determined positions for home range and dispersal analyses (Paper IV) and detected death of wolverines during bi-weekly radio-tracking from fixed-wing aircraft or from the ground (Paper III). When a mortality signal was detected, we investigated the site as soon as possible to determine the cause of death (see details in Paper III). Sometimes we lost contact with marked wolverines due to radio-failure, long-distance dispersal, or illegal killing and destruction of the transmitter.

Reproduction of radio-marked wolverines was determined during the denning season primarily by intensive radio-tracking of >24-month-old females (Paper I and II). Radio-tracking was supplemented with visits on the ground to investigate the site of a suspected den in search of typical characteristics of a den site. Presence of kits and litter size was determined from early May to early June, either by snow tracking of the female with kits or while marking family groups. To experimentally investigate the effect of food availability in early winter on reproductive success, some females were provided with carcasses (road-killed reindeer and moose) in early December 1998-2001. Subsequently, the reproductive success of food-supplemented females was compared with reproductive success of non-supplemented females.

A stochastic population model was used to analyze the effect of different management strategies on viability of wolverine populations (Paper V). In the analysis, data on individual variation in reproductive success and survival from Sarek were combined with data from long-term population monitoring to obtain estimates of the stochastic components in wolverine population dynamics.

Results and discussion

Reproduction (I, II)

Age at first reproduction

Age at first reproduction is an important parameter of reproduction because of its relatively large influence on population growth rate (Stearns, 1992). In paper I, we showed that none of ten known-aged 2-year-old wolverine females reproduced. Moreover, the average age at first reproduction was 3.4 years, and possibly higher, among females monitored to their first reproduction. These results contrast with predictions from in utero studies that the proportion of 2-year-old females that reproduce is variable (*e.g*. Rausch & Pearson 1972; Liskop, Sadleir & Saunders, 1981; Banci & Harestad, 1988), and that some 2-year-old females have reproduced in captivity (Blomqvist, 2001). Our results should therefore not be considered as evidence that no wolverine females reproduce at the age of 2 years in wild populations, but that the proportion of 2-year-old females reproducing in the wild most likely is very low. Considering the relatively low number of known-aged females monitored in our study, one might find reproducing females at this age if a larger number of females were monitored. Furthermore, age at maturity is generally assumed to be influenced by food availability (Sadleir, 1969; Bronson, 1989) and nutrition has been shown to affect age at first reproduction in several carnivore species (Kirkpatrick, 1988). Hence, age at first reproduction might be lower in areas with higher food availability, but our results clearly show that the reproduction of 2-year-old wolverine females is very low and that the reproductive onset is late in our study area; even later than for larger sized carnivores like wolf (Mech, 1970) and lynx (Andren *et al.*, in press). This is important, as reproduction of females in younger age-classes has a greater effect on population growth than reproduction of older age-classes (Stearns, 1992). Although this new data on reproductive onset is important, the general relationship between age and reproduction in wolverines needs further investigation.

Annual reproduction

The rate of reproduction after first reproduction is an important determinant of population growth rate. Paper I show that Scandinavian wolverine females have a low reproductive rate compared to other large carnivores (*e.g.* Weaver, Paquet & Ruggiero, 1996). In particular, the proportion of adult females reproducing each year was 0.54, and the average annual birth rate was 0.80. The annual recruitment of juveniles to the age of one year was 0.5 kits per female (0.3 females and 0.2 males) and is highly variable between individuals and years (Paper V). The rate of reproduction in Scandinavian wolverines is in the range of previous studies in North America (proportion of females reproducing = 0.38-0.57; birth rate = 0.43-0.89; Magoun, 1985; Copeland, 1996; Krebs & Lewis, 1999).

The annual recruitment to next generation (1 year) was about 0.3 female kits per adult female. Therefore, an average wolverine female must live more than two years after first reproduction to replace herself, *i.e.* about 5-7 years. This suggests that wolverine females may have a low lifetime reproduction or a long lifespan. A long reproductive lifespan can compensate for low annual reproduction (Stearns, 1992). Unfortunately, little is known about the life-span and reproductive senescence of wolverines. In captivity, 12 and 13 year old females have reproduced (Blomqvist, 2001), but according to earlier assumptions few females in the wild reproduce past the age of 8 years (Rausch *&* Pearson, 1972; Hash, 1987). Nevertheless, two females at least 7 years old and one at least 8 years old reproduced during our study, even though we monitored most females a relatively short time. It is clear that we need better data on lifespan and senescence in wolverine females to fully estimate reproductive lifespan. Although the lifetime reproduction of wolverine females is unknown, the low annual productivity and relatively late onset of reproduction indicate that Scandinavian wolverines have a low potential population growth rate. Note however that this study, as well as previous field studies that have estimated reproductive rates (Magoun, 1985; Copeland, 1996), was conducted in an area where reproduction possibly was food limited (Paper II). Hence, reproduction could be higher in harvested or colonizing populations with higher food availability.

Reproductive costs and food availability

I showed in paper II that current reproduction in wolverine females is influenced by the combined effects of reproductive costs from the preceding year and food availability in winter of the current year.

The effects of costs from reproduction in the preceding year on current reproduction were illustrated by a higher productivity in females that did not reproduce the preceding year. For instance, females that did not reproduce the preceding year produced on average 3.2 times more offspring than females that did reproduce the preceding year. This is consistent with studies on other large mammals (*e.g*. Clutton-Brock, Guiness & Albon, 1983; Berger, 1989; Ruusila, Ermala & Hyvärinen, 2000).

Previous studies have shown that costs of lactation and provisioning young are much larger than those of pregnancy in mammals (*e.g*. Sadleir, 1969; Bronson, 1989; Clutton-Brock, Albon & Guinness, 1989; Oftedal & Gittleman, 1989). Low litter weight and low litter energy values (Oftedal & Gittleman, 1989) should lead to relatively low costs of pregnancy for wolverines. In contrast, high energy output during lactation in mammals, presumably enhanced by a very high basal metabolic rate during the first months of life in wolverines (Iversen, 1972), should lead to high costs for wolverine females from lactation and provisioning of young and it would be expected that subsequent reproduction in wolverines should be affected by the duration of these expenditures. In accordance with this, paper II provided support for a relation between the duration of parental care and subsequent reproductive success in female wolverines (Fig. 2); a larger effect of reproductive costs was seen when females that reproduced but lost kits the previous year were included in the non-reproductive category, because they had the same reproductive success as females that did not reproduce the previous year.

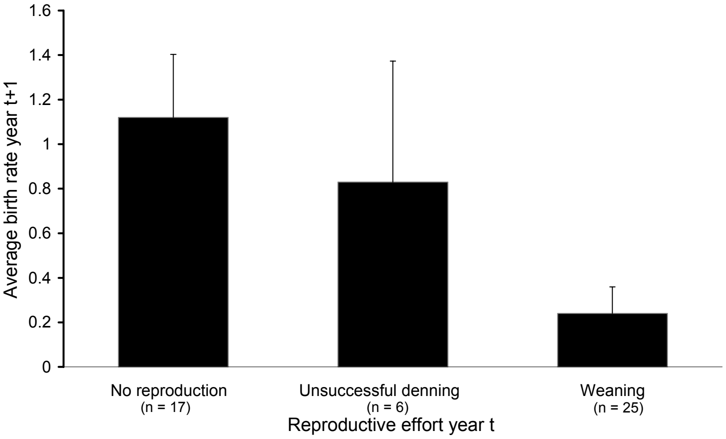

Figure 2. Average (+S.E.) birth rate for wolverine females in year t+1 in relation to reproductive effort in year t.

In paper II, I experimentally showed that females that were supplied with carrion in early winter were more productive than non-supplemented females, as illustrated by a higher proportion of food-supplemented females reproducing and weaning kits, as well as a strong tendency for higher birth rates (Fig. 3). This strongly indicates that the amount of food available for feeding and caching at this time, coinciding with the timing of implantation and parturition, affects the reproductive success of wolverine females. Moreover, food-supplemented females were more productive than non-supplemented females despite the fact that they reproduced the previous year. This suggests that the reproductive costs incurred on wolverine females can be compensated for by high food availability. My findings support previous assumptions that costs of reproduction in mammals may depend on resource availability (Ruusila, Ermala & Hyvärinen, 2000), and previous observations that the effects of reproductive costs vary with density (Clutton-Brock, Guiness & Albon, 1983; Festa-Bianchet *et al.*, 1995; Berube, Festa-Bianchet & Jorgenson, 1996; Festa-Bianchet, Gaillard & Jorgenson, 1998).

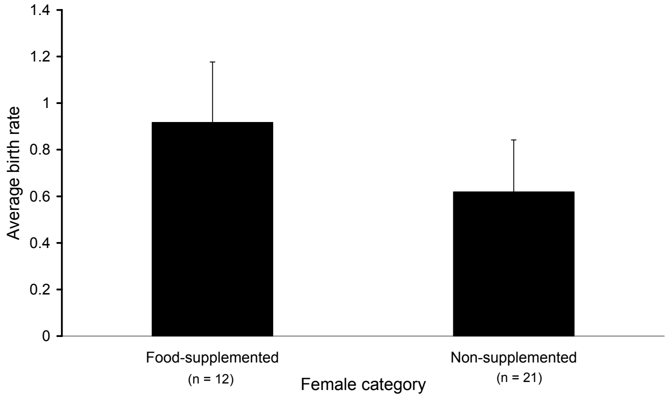

Figure 3. Average (+S.E.) birth rate for food supplemented females versus non-supplemented females in the control group.

Based on the results in paper II, I suggest that the reproduction of wolverine females in a given year is ultimately determined by their physiological condition at the time of gestation and lactation. Further, I propose that the condition of females at this time is determined by the interacting effects of reproductive costs from the previous year and the availability of food in the current winter. It has been hypothesized for fishers (*Martes pennanti*) that a physiological threshold exists that determine whether pregnancy or lactation will be terminated (Arthur *&* Krohn, 1991). Possibly, such a physiological threshold also exist in wolverines, where costs of reproduction from the preceding year and winter food availability determine a female's relation to the threshold, and hence the reproductive success of individual females.

Reproduction in populations

The observed effects of reproductive costs on reproduction are primarily observed on the individual level, but the effect of winter food availability could be conveyed into the population level. Considering the effect of food on individual reproductive performance seen in Paper II, it seems obvious that the overall availability of food in winter can have a strong influence on reproduction in wolverine populations. Furthermore, it indicates that reproduction in the Sarek population is at least partly food limited and that reproductive rates could be higher in populations that are far below carrying capacity than estimated in previous studies (Magoun, 1985; Copeland, 1996; Paper I). Note that the Sarek area presumably have the highest density of wolverines in Scandinavia, therefore reproduction might not be food-limited in other parts of the Scandinavian wolverine distribution.

To propose that food is the ultimate factor limiting reproduction in a mammal population is far from controversial and food availability has been shown to affect reproduction in many carnivore species (*e.g.* Kirkpatrick, 1988; Fuller *&* Sievert, 2001). In American marten (*Martes americana*), another mustelid, reduced reproduction has been correlated with declining prey populations (Mead, 1994) and food shortage affects ovulation rate and pregnancy rate in this species (Thompson & Colgan, 1987). Myrberget & Sörumgård (1979) found a positive correlation between small rodent abundance and litter size for wolverines in northern Norway. However, it is probably rare that small rodents constitute an important part of the wolverine diet in winter (Myhre & Myrberget, 1975; J. Persson, pers obs.), and wolverines are probably too large to survive on small prey only (Banci, 1994). Still, feeding on rodents could have a positive influence on the condition of wolverine females during peak years when rodents are numerous enough to make up a major part of the diet. Nevertheless, I believe that the most important factor by far influencing reproduction in the Scandinavian wolverine population is the availability of reindeer and moose carrion in winter, as indicated in paper II. The availability of reindeer is affected by reindeer migration patterns, which in turn are affected by herding by humans. The density of other large predators can affect the availability of carrion. For example, lynx is an efficient predator on reindeer in most parts of the wolverine distribution in Scandinavia, and the observed pattern of carcass use by lynx leads to a large number of partially consumed reindeer carcasses available for wolverines (Pedersen *et al.*, 1999). It appears that the food availability in terms of ungulate carrion in most areas is quite variable and unpredictable for the territorial wolverine. I suggest therefore that wolverine density influences reproduction primarily by affecting the potential for spatial adaptation to changing food availability, *e.g.* increasing or changing territories according to spatial variation in food availability. Thus, costs of reproduction are more likely to be compensated for by high food availability at low wolverine densities than at high densities, in relation to carrying capacity.

Juvenile survival and intraspecific predation (III)

In paper III, we estimated survival rates and evaluated the relative importance of different mortality causes among juvenile wolverines. The survival rate for juveniles was 0.68 (May-March) in Sarek, and 0.77 (May-December) in Troms (Fig. 4). The average first-year survival rate when the 2 areas were pooled together was 0.68.

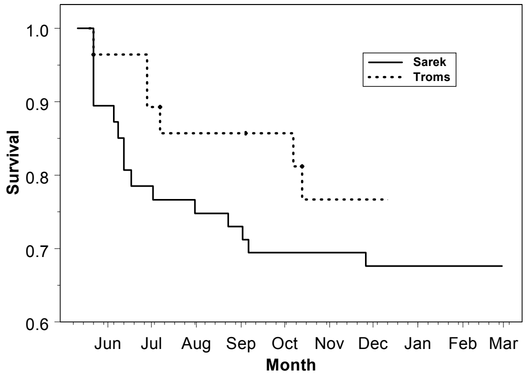

Figure 4. Survival curves for radio-marked juvenile wolverines in Sarek (May- 28 February) and Troms (May-December), respectively, 1993-2000.

Intraspecific predation was the most important cause of juvenile mortality, responsible for at least 50% of the mortality (n = 22), and human caused mortality accounted for 27% (n = 6). This is the first time that intraspecific predation on juvenile wolverines has been documented, although others have suggested it as a possible cause of juvenile mortality (Banci, 1994; Bjärvall *et al.*, 1996). We separated the intraspecific predation into two categories, based on the timing and location of the event. Seven kits were killed between May 10 and July 7 when juveniles are still dependent on their mother. Killing of dependent offspring is defined as infanticide (van Schaik & Janson, 2000). In addition, four kits were killed between August 10 and September 28, coinciding with the time of independence (Paper IV). This leads me to propose that the two categories could be separated also referring to underlying causes for the killing.

Who killed the juveniles in August-September? They were killed during the time of independence, they were all females, and they were all killed outside their mother's home range. Wolverine spacing pattern is generally characterized by intrasexual territoriality (Banci, 1994). Furthermore, one adult female in Sarek was killed by another wolverine (J. Persson, unpublished data), possibly in territorial strife with another female. This leads me to hypothesize that the juvenile females were killed in territorial defence by resident females.

It is more difficult to explain the infanticide in May-July and currently we can only discuss ecological conditions for potential explanations of infanticide in wolverines, to formulate ideas for further studies.

Infanticide could be non-adaptive, *i.e.* the result of selection for some other behaviour. For instance, infanticide could result from general aggressiveness in males during mating time (van Schaik 2000b) or opportunistic predation on vulnerable kits. On the other hand, infanticide could be adaptive as both males and females could gain selective advantage by killing non-related dependent juveniles; unrelated males by increasing their reproductive benefit (sexual selection hypothesis) and intruding females by decreasing competition for resources (*i.e.* territories or denning areas).

Sexually selected male infanticide typically functions by shortening the interval until next ovulation in the mother (Hrdy, 1979) and is predicted to be rare among seasonal breeders (Hrdy & Hausfater, 1984). As the wolverine is a seasonal breeder and most females mate every year, one has to identify factors that could promote a fitness benefit for infanticidal males. First, even in strictly seasonal breeders males could gain a limited reproductive advantage if loss of part or all of the litter will increase the size or survival of the subsequent litter (Hrdy *&* Hausfater, 1984) or if reproductive effort one year affects the effort in subsequent year (van Schaik, 2000a and male infanticide has been shown in other seasonal breeders (Bartoš & Madlafousek, 1994; van Schaik, 2000b). Secondly, only about 50% of wolverine females reproduce each year (Paper I) and the reproductive success of wolverine females is influenced by the reproductive effort in the previous year (Paper II). Thus, a wolverine male could decrease a female's reproductive effort by killing her offspring and thereby gain a reproductive advantage by improving the female's physiological condition for the next reproductive season. However, it is unclear whether it would significantly affect a female's condition to loose infants after weaning, when the observed infanticide occurred. Instead, infants should be killed earlier during the period of maximal parental investment (Hrdy 1979). Nevertheless, feeding of fast-growing young after weaning might incur high enough costs on females to affect her condition the subsequent winter, thereby making infanticide a tenable strategy even some time after weaning. In conclusion; the earlier the kits are killed, the larger the potential benefit would be for an infanticidal male.

Females could also gain from infanticide by eliminating non-related progeny to decrease future competition for territories or denning areas for her and her progeny. In addition, the death of an unrelated infant could also reduce the net reproductive success of a competitor (Hrdy & Hausfater, 1984). Competition for territories determine dispersal behaviour in female wolverines (Paper IV), suggesting that there is strong competition for territories among female wolverines.

Wolff and Peterson (1998) hypothesized that a primary function of female territoriality in solitary mammals could be to protect vulnerable young from infanticidal conspecific females. Four predictions can be deduced from their offspring-defence hypothesis: 1) Female territoriality should be associated with young that are vulnerable to infanticide. 2) Female territoriality should be associated with defence of offspring, and therefore most pronounced during the offspring-rearing season. 3) Defence will be greatest against the segment of the population that commits infanticide and against those individuals that females can dominate. 4) Optimal territory size should be a function of intruder pressure, intruder detectability, female response distances and offspring vulnerability, and changes in food abundance and distribution should not affect territory size directly unless they are correlated with the other factors. In concordance with predictions 1-3, wolverines have altricial young that are vulnerable from late winter until late summer (March – August) and female territoriality seem to be strongest during this period (Magoun, 1985; Landa, Lindén & Kojola, 2000). We lack data to evaluate prediction 4. However, in contrast to prediction 4, I believe that food actually is an important determinant of territory size in wolverine females (see Banci, 1994).

There are substantial losses of young from pregnancy and birth to weaning (Paper I). Females have been observed aggressively chasing males from the vicinity of dens (Magoun, 1985; Bjärvall *et al*., 1996) and wolverine females take care to provide secure dens for their kits (Magoun & Copeland, 1998). This could indicate that the observed infanticide represents the late part of more frequent but rarely observed infanticide in March to May.

Obviously a number of questions remain unanswered and current information is too limited to fully explain infanticide in wolverines. Instead, I put forward three, not mutually exclusive, hypotheses for further investigation of this phenomenon: 1) Males kill non-related juveniles to increase their fitness, 2) Females kill non-related juveniles to reduce competition for resources, 3) Infanticide in wolverines is non-adaptive, *e.g.* a by-product of male aggression during mating time or opportunistic predation.

Dispersal (IV)

In paper IV, we found that the mean dispersal age for both males and females was 13 months. This implies that most wolverines disperse before or at the age of sexual maturity which is similar to what is found in most mammalian species (Krebs & Davies, 1997).

We observed a male-bias in the dispersal pattern, *i.e.* all males (n = 11) dispersed, while 69% of females (n = 13) dispersed. When discussing explanations for sex-specific dispersal in wolverines, one should consider that wolverines are polygamous and demonstrate intrasexual territoriality (Banci, 1994), like many other mustelids (*e.g.* Powell, 1979). Such a spacing mechanism implies that young of both sexes must leave their natal range (Arthur, Paragi & Krohn, 1993). Even if intrasexual competition and territoriality are the ultimate cause for dispersal in both sexes, proximate factors could be different between the sexes.

Why do some, but not all females disperse? Sandell (1989) suggested that spacing of solitary female carnivores is determined by the distribution of food resources, therefore, food should be the main object of competition between females. All wolverine females that stayed in the natal area did so after the natal territory became vacant with the retirement of the mother. Mothers retired by either dying or shifting to a neighbouring territory. All dispersing females left territories that were still occupied by the mother at the age of (7-26 months). Accordingly, we suggest that competition for resources, *i.e.* good quality territories, is the main factor determining female dispersal

What forces all males to disperse? Sandell (1989) assumed that spacing in solitary male carnivores is determined primarily by the distribution of females, at least during the mating season. Such male spacing pattern is proposed for several other mustelids (Powell, 1994). It is further predicted that in polygamous species, mate competition would be greater among males than females, leading to increased dispersal of young males (Dobson, 1982). Young male wolverines are probably not able to defend territories in competition with adult males, which should force them to disperse and search for vacant territories outside the natal range. Previous studies have suggested that reproductive competition influenced dispersal in wolverines (Magoun, 1985), and that the appearance of adult males influences the dispersal of immature males and their establishment of home ranges (Gardner, 1985; Banci, 1987). Based on the observations in Paper IV and theoretical predictions, we suggest that competition for mates is the main factor determining male dispersal in wolverines.

Density dependence in dispersal has important implications for both individual fitness and for population ecology (Sutherland, Gill & Norris, 2002). Assuming that competition for territories and mates determines female and male dispersal, respectively, I would expect dispersal to be influenced by density as competition for both resources should be affected by density.

Whether the mother is still in the territory or not determine female dispersal. The question is how long a young female should wait before she leaves the natal range. I would expect that the availability of vacant territories in the surrounding affects the time a female should wait. A female should wait longer if the surrounding density is high than if it is low. Female dispersal rate could therefore be inversely density dependent which is consistent with predictions for territorial mammals (Wolff, 1997). On the other hand, female dispersal distance could be density dependent as those who actually disperse should have to disperse further away in dense populations.

The result in Paper IV confirm previous observations (see review in Banci, 1994) that most young wolverine males disperse, which indicate that males disperse independent of density. Yet, the amount of data from different areas is too scarce to draw any such conclusions. Assuming there were male territory vacancies, no effect was seen on male dispersal in our study areas, possibly because of stronger competition for male territories than female territories. Still, it can not be excluded that male dispersal is influenced also by the presence of the mother and therefore both the mother and the resident male has to disappear to allow young males to stay in the territory. It has been suggested that juvenile dispersal in many mammals is correlated with the presence of opposite-sex relatives at natal sites, presumably as a function of inbreeding avoidance (Wolff, 1997). I hypothesize that the rate of male dispersal is density independent, but that dispersal distance is related to density (*i.e.* availability of vacant territories in the surrounding).

Dispersal distance

I prefer to define movements of dispersing individuals as maximum movement observed rather than dispersal distances, because individuals that died or disappeared outside their natal area were considered dispersing in Paper IV. There was no difference in the maximum distance moved between males (51 km; 11-101 km; n = 11), and females (60 km; 15-178 km; n = 9). However, maximum movements observed in paper IV were in most cases not distance to establishment and therefore were conservative “dispersal” distances. Still, this result is different from dispersal in many polygamous species in which males often disperse longer distances than females (Greenwood, 1980) but similar to dispersal patterns in fishers (another mustelid in which males and females seem to disperse similar distances; Arthur, Paragi & Krohn, 1993). Note that females moved further away than males if we account for sex-specific home range radii, as males have much larger home ranges than females.

The most important management implications of dispersal stem from rates of long-distance movements and dispersal between rather than within populations (Waser, Strobeck & Paetkau, 2001). Wolverines clearly have the potential for long distance dispersal as shown by maximum movements of 170 to 380 km (Gardner, 1985; Magoun, 1985; Copeland, 1996; paper IV). This implies that lack of capacity for long distance dispersal does not account for the gaps in the present distribution of the wolverine in Scandinavia. More important is rate and success of long distance dispersal, for which we have little knowledge. Even if females have the capacity for long distance dispersal, factors influencing rates of female dispersal should also influence rate and capacity for recolonization. The most important factor is probably competition for territories. Therefore, I suggest that turnover rate in the female population affect the flux of new females into distribution gaps and between populations

A Population Viability Analysis (V)

Sound management in situations where society have strong opposing interests to satisfy will primarily involve political decisions in which one has to consider socio-economic as well as biological consequences of their decisions (Decker, Brown & Siemer, 2001). In such a situation wildlife managers will need biological goals to assure viability of populations, especially if those are harvested. To assure population viability and prevent harvest from negatively influencing viability, different factors that influence dynamics of small populations have to be considered.

The dynamics of small populations is affected by demographic and environmental stochasticity (variance). Demographic variance is random variation in survival and reproduction of individuals within a year and is strongly dependent on population size, *i.e.* affects only small populations (Lande, 1993; Morris & Doak, 2002). Environmental variance is random variation in survival and reproduction due to unpredictable changes in the environment. Environmental variance affects the whole or parts of a population similarly and differs from demographic variance as it is mainly independent of population size (Lande, 1993; Morris & Doak, 2002).

We estimated and modelled stochastic factors in a Population Viability Analysis (PVA) to estimate viability and effects of harvest on wolverine populations. We combined data from long-term population studies with data on individual variation in reproductive success and survival of wolverines in Sarek to 1) estimate stochastic components in the population dynamics of Scandinavian wolverines, 2) analyze what factors affect the time to extinction. Insights from these analyses were used to quantitatively analyze different management strategies for different types of populations, especially focusing on, by means of sensitivity analysis, how uncertainty in parameter estimates and imprecise population estimates should affect the choice of management actions. We based the classification of population vulnerability on IUCN's criteria (IUCN 2000).

Components in wolverine population dynamics

We estimated both demographic and environmental variance in wolverine populations from adult females' fitness contribution (R), based on their own survival and their contribution of female offspring that survived to the age of 1 year. The demographic variance was estimated from the variation in R within years, and the environmental variance was estimated from variation in R among years. The estimated demographic variance was 0.57 and the environmental variance was 0.15. These values are both high. For instance, the estimated demographic variance is more than 3 times higher than for Scandinavian brown bears (Sæther *et al*., 1998). Although a high environmental variance would be expected for the Scandinavian wolverine because of the influence of a high variability in food availability on recruitment (Paper II, Landa *et al.,* 1997) our estimate of environmental variance probably represents an overestimate. Therefore, we performed all analyses using 2 values of environmental variance (0.08 and 0.15). Moreover, a lower environmental variance could be expected in areas with a more stable food source. The high demographic and environmental variances in wolverine populations are very important as both influences the extinction risk in small populations (Lande, 1993; Lande, Sæther & Engen, 2003).

In addition to information about stochastic components of wolverine population dynamics, we need to estimate the form of density regulation and the specific growth rate at low population size to model population viability. Our estimated value for density regulation in the Sarek population appeared to be large. A large value for the density dependence means that the population is strongly regulated around carrying capacity (K), whereas there is little regulation below K. However, because of the short study period this estimate is very uncertain. Still, the estimated strong density regulation indicates that a ceiling model (Lande, 1993) is the most appropriate to use for simulating the dynamical characteristics of a wolverine population. Such dynamics seem to be typical for solitary and territorial vertebrates (Sæther, Engen & Matthysen, 2002). We used demographic data (see Sæther & Engen, 2002) to estimate the specific growth rate at low density

Time to extinction

When we used population parameters estimated for the Sarek population, we found that the expected time to extinction increased curvilinearily with carrying capacity. The conclusion was that the carrying capacity of a population must exceed 46 sexually mature (≥3 years old) females not to be considered as vulnerable according to the IUCN criteria. However, time to extinction was very sensitive to the estimate of the environmental variance and, as expected (Lande, 1993; Sæther *et al.*, 1998), also strongly influenced by the level of the specific growth rate (Fig. 5). In this context, we acknowledge that the analyses are based on several simplifying conditions. First, the estimate of specific growth rate at very low densities is based on positive assumptions regarding reproduction and losses of juveniles and is therefore likely to be an overestimation. Second, too short time series of precise population estimates were available to reliably estimate density dependence. Therefore, we used a simplified description of density regulation (see Lande, 1993). Together these simplifying assumptions suggest that our analyses overestimate the time to extinction (*i.e.* underestimate vulnerability). For instance, when specific growth rate was decreased by 0.05 the necessary carrying capacity for a population to be considered not vulnerable increased to 85 (≥3 years old) females (Fig. 5). On the other hand, our estimated environmental variance is likely to represent the upper limit of this variance. Consequently, the necessary carrying capacity was reduced to only 18 females (≥3 years old) when environmental variance was decreased by half (0.075). Importantly, these estimates highlight the large influence of the level of r and environmental variance on time to extinction. The possible overestimation of environmental variance suggests that our estimate of time to extinction is an underestimation. Still, our results are more likely to overestimate rather than underestimate time to extinction because r is based on positive assumptions while the environmental variance is estimated.

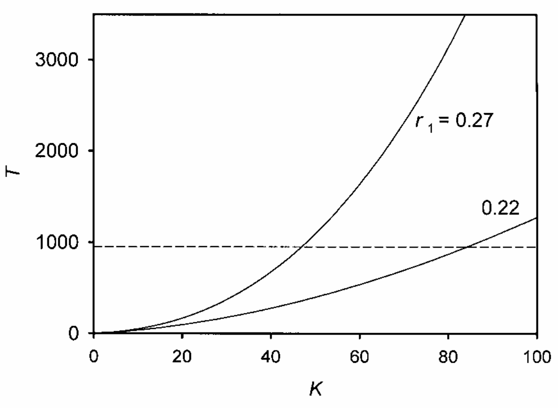

Figure 5. Expected time to extinction (T), in relation to the carrying capacity (K) for different values of the specific growth rate r^1 in the ceiling model. The dashed line indicates the expected time to extinction for a population that is 'vulnerable' according to IUCN's (2000) classification.

In conclusion, our estimation of a carrying capacity of 46 females (≥3 years old) necessary for a population to not be considered vulnerable should be seen as a preliminary guideline based on present available data. Nevertheless, the average annual number of denning females during 1999-2001 in the Swedish population was 49 (Östergren *et al.*, 2001). Therefore, assuming that denning females represent 50% of adult females in the population the Swedish population is far above the carrying capacity necessary for a population to not be considered vulnerable.

Harvesting strategies

When harvesting from small populations it is crucial to minimize the effect of harvest on viability and use the most appropriate harvest strategy. In paper V, we initially considered proportional harvest and threshold harvest. Proportional harvest means that the same proportion of the population is removed regardless of population size. Threshold harvest means that harvest of the population is only allowed above a certain threshold (c). Lande, Sæther & Engen (1997) showed that proportional harvest leads to a higher risk of extinction than threshold harvesting. Furthermore, if population estimates are uncertain and environmental variance is large, proportional threshold harvesting should be adopted, where only a certain proportion of the population above the threshold is removed (Engen, Lande & Sæther, 1997).

Consequently, as both the environmental variance and uncertainty in population estimates are large for the Scandinavian wolverine, we suggest proportional threshold harvest as the strategy for harvest of Scandinavian wolverines. We analyzed the effect of environmental variance and uncertainties in population estimates, as well as determined the threshold and the proportion of individuals above the threshold that can be removed (q). In these analyses, we required that the harvest strategy should give an expected lifetime of the population larger than 952.3 years, according to IUCN criteria for populations that are not considered vulnerable when the time to extinction is approximately exponentially distributed. No harvest was permitted when time to extinction was less than 952.3 years. We also separated two optimization criteria; optimization of the annual harvest and minimization of the population size after harvest. Both these criteria depend on the chosen combination of threshold (c) and the fraction of individuals above c that are removed annually (q). Note also that all estimations of harvest are based on the assumption that no illegal killing occurs.

We found that the environmental variance had large influence on the effect of different harvest strategies (Fig. 6), in consistence with previous theoretical analyses (Sæther, Engen & Lande, 1996; Lande, Sæther & Engen, 1997). Harvest could be allowed at much lower population sizes and lower thresholds could be chosen for a given q with lower environmental variance. Moreover, the threshold could be lowered with increasing K (Fig. 6). Harvest could only be allowed on populations with a carrying capacity above 47 adult females. However, harvest can be permitted on populations exceeding 22 adult females if the carrying capacity is far above this threshold.

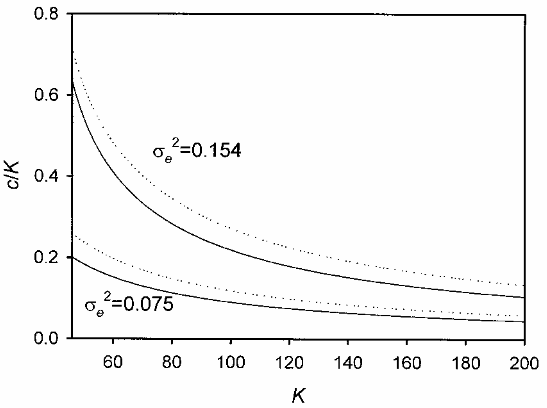

Figure 6. The threshold c/K in relation to the carrying capacity for different choice of q and environmental variance that gives an expected time to extinction of 952.3 years; thus, satisfying the criteria that the population would not be classified as vulnerable according to IUCN (2000). The solid lines represents q = 0.4 and the dotted line q = 0.6. Other parameters were specific growth rate = 0.27, demographic variance = 0.571 and initial population size was 40 (adult females).

We examined harvest strategies in the ceiling model (initial population size = K = 60 females). When population estimates are accurate but environmental variance is large, only a small proportion of the surplus individuals above the threshold can be removed (q) unless the threshold was close to K (approximately above c/K = 0.8). For higher thresholds q can be higher. With a large environmental variance the annual harvest was maximized and expected population size after harvest was minimized when the threshold was kept high. A lower threshold is allowed and a much higher proportion of individuals above this threshold could be removed when environmental variance is lower. However, with low environmental variance, the chosen values of threshold and proportion of individuals that could be removed depends on which optimization criterion is used. Then, the highest possible harvest level was found at a higher threshold than if the criterion was to minimize the population size after harvest. Thus, managers have to choose the threshold depending on their goal for management.

Importantly, the proportion of the population above the threshold that can be harvested is largely dependent on the precision in population estimates, irrespective of the level of environmental variance. The smaller the error in population estimate is, the larger the possible proportion of individuals that can be harvested, and vice versa (see Tufto *et al*., 1999). This highlights the importance of precise census methods for wolverine populations that are harvested.

Conclusions

My main conclusions are:

1) I found that wolverine females reached the reproductive stage no earlier than 3 years of age. The minimum average age at first reproduction was 3.4 years among females monitored to their first reproduction. I also showed that the productivity of females after the first reproduction is rather low, *e.g.* the average annual birth rate was 0.8 kits per female. The late onset of reproduction and low productivity after the reproductive start indicate that wolverines have a low potential population growth rate as compared to for instance lynx and wolf, which are the subject of similar management concerns. Note however that this study was conducted in areas with some of the highest densities of wolverines in Scandinavia, and wolverine reproduction could therefore be higher in other areas.

2) Reproductive rates in females were higher in years preceded by a non-reproductive year than in years preceded by reproduction. This shows that current reproduction in wolverine females is influenced by reproductive costs from the preceding year. I further provided support for a relationship between the duration of parental care and the effect of reproductive costs. Food supplemented females were more productive than non-supplemented females which illustrates how winter food availability affects reproduction in wolverine females. Moreover, food-supplemented females were more productive than non-supplemented females despite the fact that the supplemented females all had reproduced the previous year, demonstrating that high food availability can compensate for reproductive costs. I therefore propose that the combined effect of reproductive costs and winter food availability determine the condition of wolverine females during gestation and lactation, and thus their reproductive success.

3) The average survival of juvenile wolverines from May to March (to 1 year of age) was about 70%. I found that there were two peaks in the timing of juvenile mortality, one in mid-May to early July and one in August to September. The two mortality peaks were attributed to intraspecific predation. Circumstantial evidence indicates that the independent female juveniles that were killed outside their mother's home ranges in late summer were killed by adult females in territorial defence. The infanticide in early summer is harder to explain; therefore I propose that further research primarily should investigate whether infanticide is explained by 1) sexually selected male infanticide, 2) females committing infanticide to decrease resource competition or 3) non-adaptive behaviours.

4) Dispersal age varied considerably but most wolverines of both sexes dispersed at an age of about 13 months, *i.e.* before or at the age of sexual maturity. There was no difference in dispersal distance between males and females, but all males dispersed while only 69% of females dispersed. I suggest that competition for territories determine female dispersal pattern, as all females that stayed did so only when they inherited their mother's territory while females with the mother still in the territory dispersed when they were 7-26 months old. For males I suggest that competition for mates is the most likely explanation for dispersal.

5) A population viability analysis showed that the dynamics of the Scandinavian wolverine population is strongly influenced by stochastic components. This includes first, a large demographic variance due a very variable success in recruitment of juveniles to the next generation. Second, it includes a high environmental variance, presumably due to variations in food availability. Assuming that the demography of the Sarek population is typical for most populations in Scandinavia, the carrying capacity of a Scandinavian wolverine population should exceed 46 sexually mature (≥3 years old) females to not be considered vulnerable according to the IUCN criteria. Please note that uncertainties in estimations of specific growth rate at low population size and environmental variance suggest that our estimate should be considered as a preliminary guideline based on present available data. Yet, the average annual number of denning females during 1999-2001 in Sweden was about 50. Therefore, assuming that denning females represent 50% of all adult females, the Swedish population numbered about 100 adult females which is far above our guideline for the carrying capacity that is necessary for a population to not be considered vulnerable.

Management implications

1) Survival rate of adult females is generally the most important parameter for population growth of long-lived mammals, especially for species with late reproductive onset and low productivity like the wolverine. Survival of resident female wolverines appears to determine rate of female dispersal. Therefore, it should be the highest priority to secure survival of reproductive females if the management goal is to increase the wolverine population and facilitate colonization by emigration from core areas, as well as dispersal between subpopulations.

2) The results and guidelines from the population viability analysis have several important management implications:

- The level of sustainable harvest depends on precision in population estimates. Therefore, precise population census methods and/or knowledge of the precision in population estimates should be prioritized to allow for a sustainable harvest strategy of wolverines in small populations. Long-term monitoring programs will also increase our understanding of density regulation in wolverine populations and thereby improve future viability analyses.
- As a preliminary guideline, harvest should only be allowed in populations with carrying capacity exceeding 47 sexually mature females if the expected time to extinction should be long enough to consider the population as non-vulnerable.

However, harvest could be permitted on populations exceeding 22 sexually mature females if the carrying capacity is far above this threshold.

- Considering the large stochastic components of wolverine population dynamics and uncertainty in population estimates, management plans including harvest of wolverines should be based on proportional threshold harvesting.
- Illegal killing is potentially important for the management of small wolverine populations. Occurrence of illegal killing could decrease the specific growth rate and increase demographic variance, and thereby affect the vulnerability of small wolverine populations and sustainable levels of legal harvest.

3) Reproductive onset at 3 years of age or even later should be used when modelling wolverine populations and when using number of recorded natal dens to calculate total populations size (*cf.* Landa *et al.,* 1998).

4) It is important to secure connectivity by means of dispersal between populations. This is especially important for populations if they are currently genetically separated (Walker *et al.* 2001), as loss of genetic variation could decrease population viability (Allendorf & Ryman, 2002).

5) Increased availability of carrion in winter enhances female reproduction which suggests that food supplementation could be used to increase reproduction in strategically chosen areas where it is especially desirable to promote reproduction, for example in colonization areas with few females. However, such management actions need local acceptance. Food availability for wolverines could also be considered when managing populations of other large carnivores (*e.g.* lynx) that could act as providers of carrion. For instance, it might affect wolverine reproduction if lynx are eliminated from critical wolverine areas.

Future research

1) Population models should be used to better understand the dynamics of wolverine populations and to help direct future research. To better model wolverine population dynamics and to perform more precise viability analyses in the future it is important to continue long-term individual based studies of wolverine populations. This will improve the data on stochastic components and demography to estimate growth rates. More reliable data is especially needed on age-dependent reproduction, reproductive senescence and adult female survival in wild wolverines to estimate their lifetime reproduction. This can only be achieved by long-term studies of known-aged females. This requires marking of juveniles because of the low reliability of current aging methods.

2) Future studies should focus on explaining what constitutes a good wolverine territory by analyzing female productivity in relation to habitat. This approach could be applied on a larger scale to explain spatial differences in wolverine density and predict availability of suitable habitat. This can then be used to estimate the carrying capacity of populations and be related to the viability analyses in Paper V.

3) Paper II indicated that reproduction is food-limited in the Sarek area. That is presumably true also for previous field studies that have provided data on

reproductive rates (Magoun, 1985; Copeland, 1996). It would therefore be valuable to achieve demographic data from wolverine populations that are known to be far below carrying capacity. This will give insight into density dependence in dispersal patterns.

4) Rate and success of long-distance dispersal is poorly known. Future studies should improve our understanding of how and to what extents subpopulations are connected and how new areas are or could be colonized. Increased use of modern techniques (*i.e.* satellite and GPS transmitters) and genetic analyses should be applied.

5) We need to learn more about the relation between wolverines and other large carnivores, especially the role of other carnivores as providers of carrion for wolverines, but also the potential effects of their predation on wolverine survival.

6) By studying predation by wolverines and other carnivores on reindeer we will better understand the relationship among those species. As the current knowledge of predation rates on reindeer is non-existing such study would gain useful information to wildlife managers handling conflicts between predators and reindeer herding.

7) There is a great interest in understanding what individuals are the perpetrators of wolverine infanticide and what the evolutionary context of infanticide is. If the infanticide we have observed in this study is sexually selected male infanticide, it might have consequences for management, as human harvest of resident adult males may affect levels of sexually selected male infanticide (Swenson, in press). Wolverine infanticide could be better understood by a combination of intensive monitoring, genetic fingerprinting and information on life-history that could indicate if and how different sex categories of wolverines might benefit from infanticide.

8) Lack of information on hard-to-study species like the wolverine could at least partly and temporarily be compensated for by information from other species. In that context I believe that wolverines are most similar to other mustelids when considering autecology, while they are more similar to most large carnivores when considering their role in ecosystems and management issues. Therefore, I recommend that information from other mustelids and large carnivores could be applied on wolverines, but it should be used according to the questions addressed.

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Den skandinaviska järvens populationsekologi

När vi har att göra med små djurpopulationer som lever i konflikt med mänskliga intressen är det viktigt att förstå hur och varför antalet djur varierar. Det är viktigt att öka vår kunskap om vad som påverkar järvpopulationens tillväxt eftersom vi saknar väsentlig information om järvens populationsekologi. Järven i Skandinavien är i konflikt med rennäringen (Sverige/Norge) och fårskötseln (Norge).

Min avhandling beskriver järvens populationsekologi. Jag har särskilt behandlat 1) järvars reproduktion, 2) vad som påverkar om och hur många ungar järvhonor får (reproduktionsframgång), 3) överlevnad och dödsorsaker hos ungar, 4) hur och varför järvar utvandrar och 5) hur järvpopulationens livskraft påverkas av populationsstorleken och jakt. Resultaten i avhandlingen bygger huvudsakligen på information från radiomärkta järvar i och omkring Sareks nationalpark i Norrbotten, men även från radiomärkta järvar i Troms, Nordnorge.

Reproduktion

Inga honor födde ungar som 2-åringar, en tredjedel av 3-åriga honor födde och vid 4 års ålder hade 85% av honorna fött ungar minst en gång. De var då i medeltal 3.4 år gamla. Årligen födde drygt hälften av de vuxna järvhonorna ungar och antalet ungar per hona i populationen var i medeltal 0.8 ungar i maj. Den genomsnittliga kullstorleken var 1.9 ungar och varierade mellan 1 och 4 ungar. Järvar i norra Skandinavien har en sen reproduktiv start och låg reproduktionstakt i jämförelse med exempelvis lodjur och varg. Det har betydelse för förvaltningen då det pekar på att järvar är känsligare för ökad dödlighet än lodjur och varg.

Faktorer som påverkar järvhonors reproduktionsframgång

Järvhonor som inte fött ungar det föregående året fick 3.2 gånger fler ungar än honor som födde ungar året innan. Det visar att honors reproduktion påverkas av föregående årets reproduktionsansträngning, vilket visar att honors kondition under vintern troligen är avgörande för om och hur många ungar de föder nästa år.

För att bekräfta att födotillgången under vintern påverkar honors kondition, och därmed om och hur många ungar de får, utförde jag ett experiment där jag försåg ett antal honor med ren- och älgkadaver under förvintern. De honor som fick extra föda födde ungar oftare än honor som inte fick extra föda. Det stödjer slutsatsen att järvhonors reproduktion påverkas av deras kondition under vintern. Honor som fick extra föda hade större reproduktionsframgång trots att de hade reproducerat sig föregående år och borde ha påverkats av den ansträngningen. Det visar att en god födotillgång kan kompensera för den ansträngning som det innebär att föda ungar året innan. Min slutsats är att föregående års reproduktionsansträngning och tillgången på föda under vintern tillsammans påverkar järvhonors reproduktion.

Att honor som fick kadaver födde ungar oftare tyder på att tillgången på föda begränsar reproduktionen hos järvhonor i delar av Sarekområdet. Detta område hyser troligen den tätaste järvstammen i Skandinavien och det är därför troligt att födotillgången inte har samma betydelse för järvars reproduktion i andra områden. Det är också viktigt att notera att andra faktorer, som exempelvis hög dödlighet, kan vara begränsande för järvstammens tillväxt i Skandinavien.

Ungdödlighet

Den årliga överlevnaden hos järvungar var omkring 70%. Dödande av vuxna järvar var den viktigaste dödsorsaken bland årsungar och stod för hälften av dödligheten.

Järvungar dödades av andra järvar under två tidsperioder. Sju ungar dödades från mitten av maj till början av juli när ungarna är beroende av modern. Vi vet inte vilka järvar som dödar ungarna under denna period. Det kan vara hanar som dödar ungarna för att öka sin reproduktionsframgång genom att minska honans reproduktiva ansträgning så att hon är i bättre kondition nästa vinter och med större sannolikhet föder hans ungar följande år. Men det kan också vara honor som dödar andra honors ungar för att minska konkurrensen för sig själv och sin avkomma. Slutligen kan det vara förbipasserande hanar eller honor som utan särskilt syfte dödar ungarna. Fyra ungar dödades i augusti och september. De var alla honor som var oberoende av modern och de dödades utanför moderns revir. Eftersom vuxna honor är revirhävdande kan dessa honungar ha dödats i revirförsvar av andra vuxna honor.

Spridning och utvandring

Åldern för utvandring varierade men både hanar och honor utvandrade i genomsnitt vid 13 månaders ålder vilket sammanfaller med könsmognaden. Utvandringsavståndet för hanar var 51 (11-101) km och för honor 60 (15-178) km. Det är sannolikt en underskattning av utvandringsavståndet eftersom det är störst risk att tappa kontakten med djur som vandrar långt och flera av de inräknade utvandringarna har endast följts till djuret tappats bort eller dött.

Alla hanar och två tredjedelar av honorna som följts från födsel utvandrade. Honorna som stannade kunde ta över moderns revir efter att hon antingen dött eller skiftat revir. Det tyder på att honors utvandring styrs av konkurrens om revir. Det antas vara stark konkurrensen mellan hanar om honor i järvpopulationer och alla hanar utvandrade, vilket antyder att hanars utvandring styrs av konkurrens om honor.

Utdöenderisk

Överlevnad och reproduktion i små populationer varierar slumpmässigt mellan individer (demografisk varians). Miljöförhållanden varierar också slumpmässigt, vilket påverkar alla individer lika i en population och har betydelse både för stora och små populationer. Vi använde en populationsmodell för att beräkna hur dessa slumpmässiga variationer påverkar livskraften hos järvstammens. Vi fann att de slumpmässida variationerna var stora i den skandinaviska järvpopulationen.

Beräkninar av risker i en modell skall ses som prognoser och inte definitiva sanningar. Våra beräkningar visar att bärförmågan (den nivån där populations-tillväxten är noll) för en skandinavisk järvpopulation bör överstiga 46 vuxna (3 år och äldre) honor för att inte betraktas som sårbar enligt IUCN's kriterier. Det innebär att en mindre population som har möjlighet att öka till en nivå över 46 vuxna honor har relativt liten risk att försvinna. Risken visade sig vara starkt beroende av nivån på tillväxttakten vid låga tätheter och miljövariationen. På grund av osäkerhetsmoment i våra beräkningar bör resultaten betraktas som preliminära riktlinjer baserade på befintliga men relativt osäkra data. För att kunna göra en säkrare beräkning av stammens långsiktiga risk för försvinnande behöver vi samla in mer data på hur överlevnad och reproduktion varierar i järvpopulationen.

Slumpmässiga miljövariationer har stor effekt på den skandinaviska järvpopulationen och det finns stor osäkerhet i beräkningarna av populationsstorleken. Det har stor betydelse för effekten av olika förvaltningsstrategier. Om man väljer att jaga järv rekommenderar vi en försiktig jaktstrategi där en andel av djuren över ett visst tröskelvärde får skjutas.

Slutsatser

Rekryteringen av unga järvar till ett års ålder påverkas av vuxna honors överlevnad och reproduktion samt överlevnaden av ungar. Honornas reproduktion påverkas av ansträngningen från tidigare reproduktion och tillgången på föda under vintern. Ungöverlevnaden påverkas främst av hur stor andel av ungarna som dödas av andra järvar.

Honors reproduktion i Sarek tycks vara födobegränsad och det är möjligt att reproduktionstakten är högre i andra delar av Skandinavien med mindre födokonkurrens. Innan det är bekräftat bör vi utgå ifrån att Skandinaviska järvar har en låg reproduktion, en relativt sen reproduktiv start och att varje hona i genomsnitt föder få ungar. Överlevnaden hos vuxna etablerade honor tycks påverka utvandringen av unga honor. Tillsammans pekar det på betydelsen av vuxna honors överlevnad för populationers tillväxt och kolonisering av nya områden.

Möjligheterna för en jakt som inte riskerar små järvpopulationers livskraft är beroende av god precison i inventeringar. Därför bör tillförlitliga inventeringar vara en prioriterad del i förvaltningen av små järvpopulationer som påverkas av människan.

Enligt våra preliminära riktlinjer bör en skandinavisk järvpopulation ha en bärförmåga på minst 46 vuxna honor för att inte betraktas som sårbar enligt IUCN's kriterier. Vid de senaste tre årens inventeringar har man funnit omkring 50 järvlyor årligen. Detta motsvarar ca 100 vuxna järvhonor. Enligt våra beräkningar är den svenska järvstammen följaktligen inte sårbar enligt IUCN's kriterier.

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