

MANAGEMENT STRATEGIES FOR THE WOLVERINE IN SCANDINAVIA

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Abstract: The use of Population Viability Analysis has recently been criticized mainly because uncertainties in population predictions are often ignored. We analyzed the viability of Scandinavian wolverine *Gulo gulo* populations that allow for the inclusion of uncertainties in parameter estimates and stochastic effects on population dynamics. We used the insight gained from analyses of stochastic population models to quantitatively analyze different management options for the wolverine. These management options were based on data from an individual-based demographic study in the Sarek National Park, Sweden, and data from monitoring schemes in Norway and Sweden. Stochastic components in population dynamics of the wolverine were large. Strong density regulation occurred around the carrying capacity. According to the World Conservation Union (2001), the carrying capacity of populations must exceed 46 sexually mature (≥ 3 -yr-old) females to be considered not vulnerable. Continuation of the current levels of offtake in Norway will lead to extinction of the wolverine over large parts of the country. Hence, current rates of mortality of female wolverine make the northern population endangered, whereas the southern population is classified as vulnerable. Management plans allowing harvest of individuals should be based on a proportional threshold harvest strategy. Only 40–60% of the surplus individuals exceeding a certain threshold for harvesting should be removed. Our analyses emphasized the importance of including estimates of precision in parameter estimates, including stochastic factors in recommendations based on Population Viability Analysis, and examining the robustness of the conclusions against variation in crucial parameters by sensitivity analyses.

JOURNAL OF WILDLIFE MANAGEMENT 69(3):1001–1014; 2005

Key words: density dependence, *Gulo gulo*, Population Viability Analysis, risk of extinction, Scandinavia, stochastic effects, wolverine.

Population Viability Analysis (PVA) has wide application in the management of threatened and vulnerable species (Beissinger and Westphal 1998, Groom and Pascual 1998, Sjøgren-Gulve and Ebenhard 2000, Beissinger and McCullough 2002). The predictions from such analysis have recently received severe criticism (Ludwig 1996, 1999; Fieberg and Ellner 2000; Ellner et al. 2002). There are 3 major problems with many PVAs: (1) For most threatened or vulnerable species few demographic data are often available. Even when 20–30 years of high-quality data are available, the uncertainties in the parameter estimates are still large (Sæther et al. 2000; Sæther and Engen 2002*a,b*). (2) In many cases, available data are inappropriate for estimating crucial parameters for describing dynamics and may even result in biased estimates. For instance, the specific growth rate at low densities is often difficult to estimate in many time series of population fluctuations because interpolation over a wide range of population sizes is often necessary (Taylor 1995, Aanes et al. 2002). (3) The

stochastic effects on the population dynamics are often not properly estimated and modeled (Sæther and Engen 2002*a*), resulting in biased estimates of the risk of extinction. As a consequence, the validity of predictions based on PVA has been seriously questioned (Ludwig 1999).

Recently, great advances have been made in our understanding of stochastic effects on the dynamics of fluctuating populations (Lande et al. 2003). An important step was the development of precise definitions of the stochastic components (Engen et al. 1998) that permitted estimation of demographic and environmental stochasticity from field data (Sæther et al. 2000, 2002*a*; Engen et al. 2001). Demographic stochasticity is due to random variation in individual fitness, whereas environmental stochasticity arises from random variation that affects the whole or parts of the population similarly. These methods allow us to separate stochastic effects on population dynamics from deterministic components (e.g., due to density dependence or life history variation).

In PVA, development of projections for future population fluctuations is necessary for calculating the risk of extinction or the probability of reaching

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some critical lower population size. Such analyses must model the deterministic influence and the stochastic effects on the population dynamics and take into account uncertainty in population parameters (Sæther and Engen 2002a). After the highly influential paper of Mace and Lande (1991), the World Conservation Union (2001) included criteria based on quantitative analyses into their risk classification of threatened or endangered species. Thus, according to World Conservation Union (2001), only populations with $\leq 10\%$ risk during 100 years will not be considered vulnerable to extinction.

Many large carnivores became vulnerable or threatened because of human persecution (Swenson et al. 1994). For instance, the Scandinavian wolverine population was persecuted from the mid-19th century when harvest increased due to the introduction of state bounties. The main reason for this intense persecution was predation by wolverines on domestic sheep and reindeer (*Rangifer tarandus tarandus*), a conflict still present today in many parts of Scandinavia. As a consequence, harvest of individuals is important to consider as an option in management plans and is often a prerequisite for local acceptance. In such cases, stochastic factors must be estimated and modeled to obtain a proper understanding of the effects on the viability of the population (Lande et al. 1995, 1997, 2001; Tufto et al. 1999).

Our objective was to use recent advances in the theory of stochastic population ecology to perform a PVA of the Scandinavian wolverine. We combined data from long-term population studies with data on individual variation in reproductive success and survival to obtain estimates of the stochastic components in the population dynamics. We then provided analyses of factors influencing the time to extinction. We used this insight to quantitatively analyze different management strategies. By means of sensitivity analysis, we focused on how uncertainty in parameter estimates and imprecise population estimates affect the choice of management actions.

Wolverines in Fennoscandia

Historically, the wolverine was found throughout mountainous and forested areas in Norway and from the south-central to the northern parts of Sweden (Johnsen 1929, Lönnberg 1936). From the mid 19th century the Scandinavian wolverine population decreased due to human persecution until the species became protected in Sweden in 1969, in southern Norway in 1973, and in the remaining parts of Norway in 1982 (Landa et al. 2000). In the beginning

of the 1980s, the distribution of wolverine was limited to the mountain range along the Swedish–Norwegian border. The population increased in both countries slowly during the first decades after protection. The estimates of total population size in 1998–2000 were 326 (± 45) individuals in Sweden and 269 (± 32) individuals in Norway (Landa et al. 2001). The Swedish population was protected, whereas in Norway offtake of individuals through regular harvest or killing of litters has become an important tool in wolverine population management.

Population Model

The dynamics of all populations have a deterministic (predictable) and a stochastic (unpredictable) component that operate simultaneously. The deterministic component can be mathematically defined as the expected change of the log population size during the next year, the mean value of $\Delta X_t = X_{t+1} - X_t$ conditioned on X_t , or alternatively, it can be defined as the mean change in population size, where N_t is the population size in year t and $X_t = \ln N_t$. The theta-logistic model is a very general class of models specifying the deterministic component (Gilpin and Ayala 1973; Gilpin et al. 1976; Sæther et al. 1996, 2000, 2002b; Lande et al. 2003):

$$\Delta N = rN[1 - (N/K)^\theta], \quad (1)$$

where the time index is omitted to simplify the notation. Here θ denotes the form of the density regulation. Large values of θ show strong density regulation around the K . For a positive value of the parameter θ , r is the specific growth rate at small population sizes, formally the growth rate obtained in the limit as N approaches zero. The carrying capacity for this model is K , which means that the expected change in population size when $N = K$ is zero. For small and moderate changes between 2 years, $\Delta N/N \approx \Delta \ln N = \Delta X$ giving:

$$\Delta X \approx r[1 - (N/K)^\theta]. \quad (2)$$

Because all methods for parameter estimation from data are based on the use of log population size, we prefer to use eq (2) rewritten as an exact equation as our basic model. If we define extinction to occur at $N = 1$, the smallest possible specific growth rate is actually the growth rate at $N = 1$, $r_1 = r[1 - K^{-\theta}]$. Using r_1 rather than r in eq (2), the model may be rewritten as:

$$\Delta X = r_1[1 - (N^\theta - 1)/(K^\theta - 1)] = r_1[1 - h(N, \theta)/h(K, \theta)], \quad (3)$$

where $h(N, \theta) = (N^\theta - 1)/\theta$. An advantage with this formulation of the theta-logistic model is that a well-defined model is obtained as θ approaches zero and even when θ is negative. Considering the limit as θ approaches zero, $h(N,0) = \ln N = X$. Hence, for $\theta = 0$, we obtain a form of density regulation that is linear on the log scale,

$$\Delta X = r_1(1 - X/k), \tag{4}$$

where $k = \ln K$ is the carrying capacity on the log scale. This is called the Gompertz type of density regulation. Alternatively, this may also be written as:

$$X_{t+1} = r_1 + (1 - r_1/k)X_t \tag{5}$$

a linear model frequently used in time series analysis of population fluctuations (Royama 1992). Another special case is the logistic model obtained as $\theta = 1$, giving a second-degree polynomial on the right side of eq (1) and a linear expression in N in eq (2).

When studying small fluctuations around the carrying capacity a simple linear approximation on the absolute scale a linearization of $E(\Delta N | N)$ is often used (Lande et al. 2002). Such a linear form is also a special case because if $\theta = -1$, then:

$$\Delta N = \frac{r_1 K}{K-1} \left[1 - \frac{N}{K} \right]. \tag{6}$$

Another special case of the theta-logistic model that is often used for territorial species is the ceiling model (Lande 1993) that has no density regulation (i.e., exponential growth) for population sizes smaller than K . The ceiling at $N = K$ is then a reflecting barrier preventing the population size from exceeding K . Equation (3) demonstrates that this is exactly the model we obtain in the limit as θ approaches infinity.

The expected time to extinction is computed by adopting the diffusion approximation to the process on the logarithmic scale (Lande et al. 2003). The infinitesimal mean and variance is then $\mu(N) = r_1 N [1 - h(N, \theta)/h(K, \theta)]$ and $v(N) = \sigma_e^2 N^2 + \sigma_d^2 N$. The expected time to extinction is calculated numerically by first calculating the Green function for the diffusion process (Karlin and Taylor 1981; Lande et al. 1995, 2003):

$$G(N, N_0) = \begin{cases} 2m(N)S(N) & \text{for } 1 \leq N \leq N_0 \\ 2m(N)S(N_0) & \text{for } 1 \leq N_0 \leq N \end{cases}, \tag{7}$$

where

$$S(N) = \int^N s(z)dz, \quad s(N) = \exp \left[-2 \int^N \frac{\mu(z)}{v(z)} dz \right]$$

and $m(N) = 1/v(N) \times s(N)$. We then integrate this function numerically from the extinction barrier at $N = 1$ to infinity. For the ceiling model of Lande (1993) we consider the limiting form as θ approaches infinity. This is equivalent to a model with reflecting barrier, a ceiling, at population size K , and exponential growth with stochastic growth rate r_1 below K . The Green function of eq (7) for this process must be equal to zero for $X > \ln K$. Expected time to extinction can then be written as:

$$ET = \int_1^K G(N, K) dN.$$

for $N_0 = K$. Because the Green function does not depend on K except that $G(N, K) = 0$ for $N > K$, we find that

$$dET/dK = G(N, K), \tag{8}$$

which then takes the form

$$dET/dK = 1/r_0 K \left[\left(\frac{K + \delta}{1 + \delta} \right)^\gamma - 1 \right], \tag{9}$$

where $r_0 = r_1 - \sigma_e^2/2r_0 / \sigma_e^2 - 1$ and $\delta = \sigma_d^2 / \sigma_e^2$ (Lande et al. 2003). This expression can easily be integrated numerically to give ET .

In Scandinavia, wolverines kill domestic, free-ranging sheep and semidomestic reindeer that graze in mountain ranges. As a consequence, there is a strong demand for the reduction of wolverine population size through individual offtake. A central aim of offtake is to minimize its effect on the expected time to extinction. We suggest, based on theoretical studies (Engen et al. 1997, Tufto et al. 1999, Aanes et al. 2002, Lande et al. 2003), that 2 types of harvest strategies be considered: proportional harvesting and proportional threshold harvesting.

Proportional harvesting means removing a fixed proportion of the population each year, giving the annual yield:

$$y = b N, \tag{10}$$

where b is the proportion harvested. In fisheries, this strategy is often carried out by assuming that a given harvesting effort leads to harvesting a given proportion of the population (Quinn and

Deriso 1999). The optimal proportion to harvest depends on the dynamics of the populations (e.g., the form of the density regulation; Beddington and May 1977, May et al. 1978, Jonzén et al. 2002). Unfortunately, this commonly employed harvesting strategy leads to higher risk of extinction than threshold harvesting (Lande et al. 1995, 1997); i.e., harvesting occurring only when the population size exceeds a certain threshold c .

The wolverine population size is difficult to assess, so uncertainty in population estimates should be considered when choosing a harvest strategy (Engen et al. 1997, Quinn and Deriso 1999). If \hat{N} is the estimated population size and q is the proportion of the estimated surplus, individuals above the threshold c that can be removed. Engen et al. (1997) proposed that proportional threshold harvesting that is defined as:

$$y(\hat{N}, q, c) = \begin{cases} q(\hat{N} - c) & \text{for } \hat{N} > c \\ 0 & \text{otherwise} \end{cases}, \quad (11)$$

will reduce the effect on population viability by overestimating the actual population size and thereby causing animal offtake to be too high.

A reasonable assumption about the sampling variance in the estimated population size \hat{N} is that it is proportional to the expected population size:

$$\text{var}\hat{N} = \varepsilon^2 EN, \quad (12)$$

where ε determines the sampling error. The coefficient of variation in \hat{N} $CV = \varepsilon / \sqrt{E/\hat{N}}$ then becomes dependent on N . If we assume binomial sampling (Seber 1982) with probability p of detecting an animal, $\varepsilon = \sqrt{(1-p)/p}$. Thus, $p = 0.5$ corresponds to $\varepsilon = 1$.

The expressions for the infinitesimal mean and variance to be applied in the diffusion approximation for this process are given by Engen et al. (1997). The derivation of these functions was based on the assumption that the estimate of the population size is unbiased and normally distributed. When the population size is not known exactly, harvesting also introduces an additional term in the infinitesimal variance that must be incorporated (Engen et al. 1997).

STUDY AREA

We studied individual variation in reproductive success and survival in Sarek National Park and surrounding areas in Norrbotten County (hereafter referred to as Sarek) in northern Sweden (67°00'N 17°40'E; Fig. 1). The climate was continental with cold winters (-10 to -13°C in Jan), and

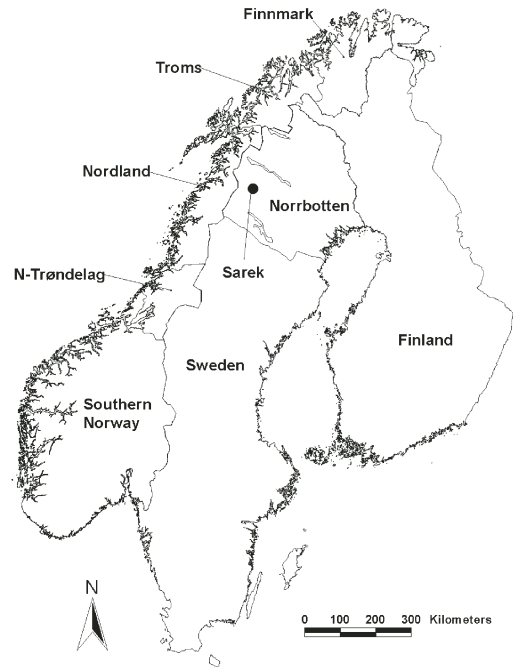


Fig. 1. The location of study areas in Fennoscandia to examine wolverine ecology.

the annual precipitation was 500–1,000 mm. Snow usually covered the ground from October to May. The area is characterized by deep valleys, glaciers, and mountain plateaus with peaks reaching above 2,000 m above sea level. The valleys forests were dominated by mountain birch (*Betula pubescens*) and scots pine (*Pinus sylvestris*). The tree line was formed by mountain birch and reached a maximum of 600–700 m above sea level. Semidomesticated reindeer managed by the indigenous Sámi were numerous in Sarek.

METHODS

Our analysis was based on data from 37 radiocollared, adult females. The females were equipped with an intraperitoneally implanted transmitter. We radiotracked individuals from the ground or air approximately once every 2 weeks. In this way we determined whether the female and her offspring survived to the following reproductive season that was assumed to start on 1 March.

We also used helicopters and snowmobiles to search an area of approximately 6,000 km² in Sarek from 1995 to 2002 for dens during winter and spring. We assumed that this extensive fieldwork and the numerous radiocollared individuals allowed us to accurately estimate the annual variation in the Sarek breeding population. During

Table 1. The number of active dens and the number of age-determined adult (>1-yr-old) females harvested in different parts of Fennoscandia, 1979–2002.

Year	Norway								Sweden		
	Southern Norway ^a		N-Trøndelag and Norrland County		Troms County		Finnmark County		Sarek		Norrbottn County
	Dens	Harvest	Dens	Harvest	Dens	Harvest	Dens	Harvest	Dens	Harvest	Dens
1992	4		9		1	0	7				
1993	4		5	0	7	1	3				
1994	5		7	1	17	5	3	0			
1995	8	0	11	1	13	2	9	1	11	0	
1996	5	2	11	1	11	5	6	0	16	0	50
1997	5	0	7	1	6	5	9	1	9	2	47
1998	8	3	12	3	10	2	9	0	13	1	40
1999	8	1	10	4	9	0	10	2	14	1	37
2000	10	2	8	4	15	4	7	9	12	0	28
2001	12	8	13	1	7	1	5	0	15	0	38
2002	8		12		7		3		19		37

^a In southern Norway, the number of recorded dens each year was (dens/year): 3/1979, 2/1980, 3/1981, 3/1982, 2/1983, 3/1984, 3/1985, 2/1986, 4/1987, 3/1988, 4/1989, 4/1990, and 2/1991.

the study period, the number of dens fluctuated between 9 and 19 active dens (Table 1).

Population Censuses

In Scandinavia, annual censuses of wolverine breeding population were conducted over larger parts of its distributional range (Fig. 1; Table 1). Likely den localities were visited several times during late winter and early spring by experienced persons who searched for typical characteristics of a natal den (for a more detailed description of the den characteristics, see Magoun and Copeland 1998 and Andersen et al. 2001). In addition, established routes were driven by snowmobiles to search for wolverine tracks in many areas. When a track was detected, it was followed to see if it led to a denning area. In this way, an estimate of the minimum number of reproductive females was obtained.

In Sarek, the mean proportion of the radiocolared adult females that bred each year was 0.57 ($n = 6$ yr). Thus, the number of active dens (Table 1) represents an underestimate of the actual number of sexually mature females in the population.

In southern Norway (Fig. 1), an increase in numbers occurred during the last years (Table 1). In the northern parts of the country, no clear trend was present in population fluctuations. In contrast, we recorded a decline in the number of dens in Sweden during the study (Table 1). This decline was mainly due to a decline in Norrbotten County, which had the largest number of wolverines.

Since 1990, female wolverines (≥ 1 yr old) were killed by humans over larger parts of their distributional range (Table 1). In Norway, the wolverine population was managed by 2 regional manage-

ment boards: 1 covering the 4 northernmost counties (Nord-Trøndelag, Nordland, Troms, Finnmark; Fig. 1) and 1 for southern Norway. These 2 boards had heavy representation from various user groups. The annual quota was determined by the boards.

Estimation of Parameters

We estimated the demographic variance (σ_d^2) and the environmental variance (σ_e^2) from individual-based data from Sarek. We let $R_{i,j}$, $i = 1 \dots n_j$, $j = 1, 2, \dots, t$, denote observations of the contribution by the females to the following generation, where j was the year and n_j was the number of females for which data were available in a given year. The total contribution of female i in year j ($R_{i,j}$) was the number of female offspring born during the year that survived for 1 year plus 1 if the female survived to the next year (Sæther et al. 1998a). If \mathbf{Z} was a stochastic vector describing the environment influencing R , the variance in R could be partitioned into 2 components (Engen et al. 1998):

$$\text{var}(R) = \text{Evar}(R|\mathbf{Z}) + \text{var}(ER|\mathbf{Z}), \quad (13)$$

where $\text{Evar}(R|\mathbf{Z}) = \sigma_d^2$ and $\text{var}(ER|\mathbf{Z}) = \sigma_e^2$ is the demographic and the environmental variance, respectively. For a given population size N , the variance in the change in population size to the next year will then be:

$$\text{var}(\Delta N|N) = \sigma_d^2 N + \sigma_e^2 N^2. \quad (14)$$

We let \bar{R}_j denote the mean value of the contributions in year j , and let \bar{R} be the mean of all recorded contributions. The major part of the information in

the environmental variance came from the variation between years, whereas the variation in R_{ij} within years contained information about the demographic variance. Sæther et al. (1998a) showed that:

$$\hat{\sigma}d^2 = \frac{1}{n-t} \sum_{j=1}^t \sum_{i=1}^{n_j} (R_{ij} - \bar{R}_j)^2 \tag{15}$$

was an unbiased estimator for the demographic variance, where

$$n = \sum_{j=1}^t n_j .$$

Usually, σ_e^2 was estimated from time series of fluctuations in ΔN (Sæther et al. 1998a, 2000, 2002a). A problem with this approach is that the environmental stochasticity is extremely difficult to separate from the effects of sampling errors in the population estimates (De Valpine and Hastings 2002). Thus, in many cases it is better to estimate σ_e^2 from the individual variation in fitness. Engen et al. (1998) showed that the fitness contributions can be written in the form $R_{ij} = ER + e_j + d_{ij}$, where e_j and d_{ij} are independent, $\sigma_e^2 = \text{var}(e_j)$ and $\sigma_d^2 = \text{var}(d_{ij})$. In general, we have the relationship:

$$\text{var}(\bar{R}_j - \bar{R}) = \text{var}(\bar{R}_j) + \text{var}(\bar{R}) - 2\text{cov}(\bar{R}_j, \bar{R}). \tag{16}$$

From eq (13), it then follows:

$$\text{var}(\bar{R}_j) = \sigma_e^2 + \sigma_d^2/n_j, \tag{17a}$$

$$\text{var}(\bar{R}) = \sigma_d^2/n + \sigma_e^2 \sum n_j^2/n^2 \tag{17b}$$

and:

$$2\text{cov}(\bar{R}_j, \bar{R}) = 2(\sigma_d^2 + n_j\sigma_e^2)/n. \tag{17c}$$

This gives:

$$E \sum_{j=1}^t (\bar{R}_j - \bar{R})^2 = \sigma_e^2(t-2 + t\sum n_j^2/n^2) + \sigma_d^2[\sum(1/n_j) - t/n],$$

which leads to the estimation equation:

$$\sum_{j=1}^t (\bar{R}_j - \bar{R})^2 = \hat{\sigma}_e^2(t-2 + t\sum n_j^2/n^2) + \hat{\sigma}_d^2[\sum(1/n_j) - t/n], \tag{18}$$

that combined by eq (15) determines $\hat{\sigma}_e^2$. We used equal weights in eq (18) on $(\bar{R}_j - \bar{R})^2$ because this was optimal for large values of n_j that gave $\bar{R}_j \approx e_j$.

Estimation of the variance components for wolverine in Sarek was also complicated because

radiocollared females did not represent a random sample of the population because only females that had a den were captured in the first year. We, therefore, did not include the results from the year of capture in the analyses. In this way we obtained data from 28 females from 1995 to 2001.

The Specific Population Growth Rate r_1

The specific population growth rate was a problematic parameter for us to estimate because the population must spend periods at low population sizes to avoid interpolation over a large range of population sizes (Taylor 1995, Sæther and Engen 2002a, Aanes et al. 2002). Thus, we followed Sæther et al. (2002b) and used demographic data to get information about this parameter. Female wolverines may attain sexual maturity at about 15 months, but previous studies reported varying proportions of pregnant, 2-year-old females (Rausch and Pearson 1972, Liskop et al. 1981, Banci and Harestad 1988). Information from reproductive tracts showed that a very high proportion of adult females (≥ 3 years old) were pregnant each year, but observations of radiocollared wolverines indicated that the proportion of females actually reproducing was much lower (Banci and Harestad 1988). However, in an area where females were given supplemental food, 83% of the females gave birth to a litter (Persson 2003). The mean litter size of litters dug out soon after birth was 2.77 (Pulliainen 1968), which was significantly higher than the litter size at the time of radiomarking in Sarek ($\bar{x} = 1.9$; Persson 2003) and than sizes recorded in North America (Magoun 1985, Copeland 1996). This reduction was probably due to losses from infanticide, starvation, predation, or disease (Persson et al. 2003). At low population densities we assumed these losses were reduced by 25%, giving a litter size of 2.12 at weaning. Assuming a slightly female-biased sex ratio at birth (55% females; Persson et al. 2003) and a juvenile survival rate of 0.81, this represents an annual recruitment rate of 0.78 juvenile females to the next generation. If we assumed reproductive onset at 3 years and an adult survival rate of 0.92 (Willebrand et al. 1999), the specific population growth rate at low density was $r_1 = 0.27$.

The Form of Density Regulation θ

We estimated the form of density regulation for the population in Sarek, where the population estimates were assumed to be reasonably accurate. We estimated by maximum likelihood, assuming the population process was a Markov process and ΔN normally distributed with mean $\mu(N) = r_1 N [1 - h(N, \theta)]/h(K, \theta)$ and variance $v(N) = \sigma_e^2 + \sigma_d^2/N$.

We estimated a large value of θ for the Sarek population ($\hat{\theta} = 12.5$) that indicated a strong density regulation around the carrying capacity K and weak regulation below K . However, as expected from the short study duration, the estimate of θ was very uncertain with a relatively high proportion of the bootstrap-replicates at very large values ($q > 25$) (Sæther et al. 2003). In relation to their body size, wolverines have

very large home ranges, and the females occupy distinct home ranges that overlap to a small extent (Powell 1979, Magoun 1985, Copeland 1996), whereas adult males occupy larger home ranges than females and can encompass several female home ranges (Banci 1994). This suggests that the ceiling model of Lande (1993) describes the form of the density regulation of the wolverine reasonably well. Hence, we used this model of density regulation in the following analyses.

Time to Extinction

When we assumed that the ceiling model of Lande (1993) was valid and used the transformation formulas for diffusion (Karlín and Taylor 1981), the infinitesimal mean and variance for the process $X = \ln N$ was $r_1 - 1/2 \sigma_e^2 - 1/2 \sigma_d^2 e^{-X}$ and $\sigma_e^2 + \sigma_d^2 e^{-X}$ for $X \leq \ln K$, respectively. We estimated the risk of extinction by simulating this model using 1,000 sample paths (Sæther et al. 2003).

RESULTS

The range of variation in the individual contributions of females R was from zero to 4 (Sæther et al. 2003) with 1 as the modal value. The estimated demographic variance was $\sigma_d^2 = 0.571$, whereas the environmental variance was $\sigma_e^2 = 0.154$. A problem with this approach using eqs (16–18) is that variation in R will also be dependent on fluctuations in population size through the effects of density regulation. Thus, our estimate of σ_e^2 may represent an upper level for the environmental variance in Sarek.

We examined the dynamic characteristics of the population in Sarek by simulating 1,000 sample paths from this population model (eq 6). We assumed that the number of active dens recorded represented only 50% of the sexually mature fe-

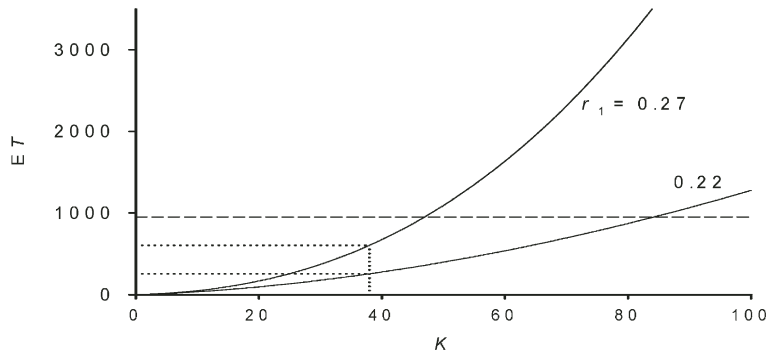


Fig. 2. Expected time to extinction ($E T$) in relation to the carrying capacity (K) in the ceiling model of Lande (1993) for different values of the specific growth rate r_1 for the wolverine population in Sarek, northern Sweden (see Fig. 1). The dashed line indicates the expected time to extinction for a population that is considered vulnerable according to World Conservation Union's (2001) classification. The dotted line indicates the estimates for the Sarek population

males actually present in the population (see Methods). We found that a population at an initial population size of $N = K = 38$ adult (≥ 3 -yr-old) females had a 10% probability of becoming extinct after 137 years, and there was only a 50% probability that the population would be present after 898 years. These results were very sensitive to the estimate of the environmental variance σ_e^2 . If we assume $\sigma_e^2 = 0.075$, the population would not be considered vulnerable according to World Conservation Union's (2001) classification.

The distribution of the time to extinction of the Sarek population, using the ceiling model (eq 6) and assuming an initial population size of $K = 38$ (≥ 3 -yr-old) females, closely resembles an exponential distribution. Thus, the probability of extinction will be highest during the first years. Assuming the population parameters as estimated for the Sarek population, we found that the expected time to extinction increased curvilinearly with carrying capacity K (Fig. 2). The expected time to extinction of the Sarek population was 604 years (Fig. 2) when assuming a ceiling model with K equal to twice the highest number of dens we recorded ($K = 38$ [≥ 3 -yr-old] females) with $r_1 = 0.27$. This means that the wolverine population in Sarek must be recorded as vulnerable according to World Conservation Union's (2001) classification if no individuals immigrate. Only populations with a carrying capacity > 46 adult (≥ 3 -yr-old) females can be considered not vulnerable according to this classification (Fig. 2). As expected (Lande 1993, Sæther et al. 1998a), this critical population size is strongly influenced by the value of r_1 (Fig. 2). A decrease in r_1 by 0.05 increased the necessary carrying capacity for the population not to be considered vulnerable to $K = 85$. In contrast, if $\sigma_e^2 = 0.075$ this critical carrying capacity was reduced to only $K = 18$.

We used the ceiling model to examine the different harvest strategies and assumed an initial population $N_0 = K = 60$ sexually mature (≥ 3 -yr-old) females. Furthermore, we required that the harvest strategy give an expected lifetime of the population > 952.3 years; thus, this satisfied the criteria of World Conservation Union (2001) for populations that are not considered vulnerable when the time to extinction is approximately exponentially distributed. No offtake is permitted when $E T < 952.3$ years. If $T > 952.3$ without harvesting, we consider harvesting strategies (c, q) that keep T constant equal to 952.3 years. When the population surveys are accurate, but environmental stochasticity is large, only small values of q can be permitted for relative thresholds c/K up to approximately 0.8, resulting in a very low annual offtake of individuals (Fig. 3). When c/K approaches 1, about half of the individuals in excess of the threshold can be removed, giving a low expected population size after the hunt but with harvest only permitted for a few years (Fig. 3). When the precision in the population estimates is improved, q increases for larger values of c/K (Fig. 3).

These patterns were extremely sensitive to the estimates of the environmental variance σ_e^2 , as expected from theoretical analysis of harvesting models (Sæther et al. 1996, Lande et al. 1997, 2001). When we assume a lower estimate of σ_e^2 , all individuals above the threshold can be removed for $c/K > 0.37$. With reduced bias in the population estimates, this critical threshold can be reduced (Fig. 3). The number of animals that can be removed and the expected population size after the hunt depend on the particular combinations of c/K and q chosen (Fig. 3). Lowest expected population size after the hunt was found for values of c/K between 0.3 and 0.4, dependent on the census accuracy. In contrast, the highest offtake of animals occurred at $c/K = 0.59$. We also found that population dynamics were strongly influenced when all excess individuals were removed (Fig. 3).

We then applied the insight gained by analysis of the Sarek population to the development of management strategies of the Norwegian wolverine. However, the application of the ceiling model of Lande (1993) requires an estimate of the carrying capacity for the different regions in Fig. 1. We assumed that continuous areas > 50 km² situated 600 m above sea level (or 300 m above sea level in the 2 northernmost counties) represented suitable wolverine habitat. Scandinavian home range studies have shown that the mean size of a female's annual home range varies from 274 km² in Snøhetta in southern Norway (Landa et al.

1998) to 322 km² in Sarek (J. Persson, University of Umeå, unpublished data). Because these estimates were obtained in areas likely to represent very suitable habitats for wolverine, we assumed that an average Norwegian female wolverine requires an area of 400 km². Dividing the total area of available wolverine habitat with the mean home range size, the rough estimate of K is 166, 48, 26, and 46 sexually mature (≥ 3 -yr-old) females in southern Norway, Nordland (including Nord-Trøndelag), Troms, and Finnmark, respectively (Fig. 1). These estimates are based on that nonreproductive territorial 2-year-old females (Vangen et al. 2001) comprise 30.5% of the adult (≥ 2 -yr-old) females in the population (Landa et al. 2001).

In all parts of Norway, adult (> 1 -yr-old) female wolverine were killed almost every year (Table 1) due to different forms of human activities such as legal hunting, illegal killing, and control of individuals that kill semidomestic reindeer or sheep.

We examined the consequences of this mortality on future wolverine population dynamics by assuming that removal of individuals during a period could be approximated by a constant harvest strategy where the number of animals removed each year has a constant mean and variance. We assumed that the future harvest in southern and northern Norway would be equal to the harvest during past years (Table 1). We also assumed that the number of active dens represented only 50% of the sexually mature females present. In both regions, our simulations showed that continuation of the current level of harvest of females will, with 10% probability, cause extinction of the wolverine within 20 years (Fig. 4). The probability of absence of the wolverine in northern Norway in 243 years is higher than the probability of its presence. Our simulations also showed that time to extinction was relatively independent of the estimates of the carrying capacity. For instance, an increase in K by reducing the required home range size from 400 km² to 200 km² in all regions had $< 5\%$ influence on the expected time to extinction. Thus, prolonging the current harvest of wolverine in Norway is likely to cause extinction of the species in the near future. Hence, if the current rate of killing female wolverines continues, the northern population will be classified according to World Conservation Union's (2001) criteria as endangered, whereas the southern population will be considered vulnerable (Fig. 4). The classification of the southern population is sensitive to the estimate of N_0 . For instance, for $N_0 = 20$ the southern population will also be considered endangered.

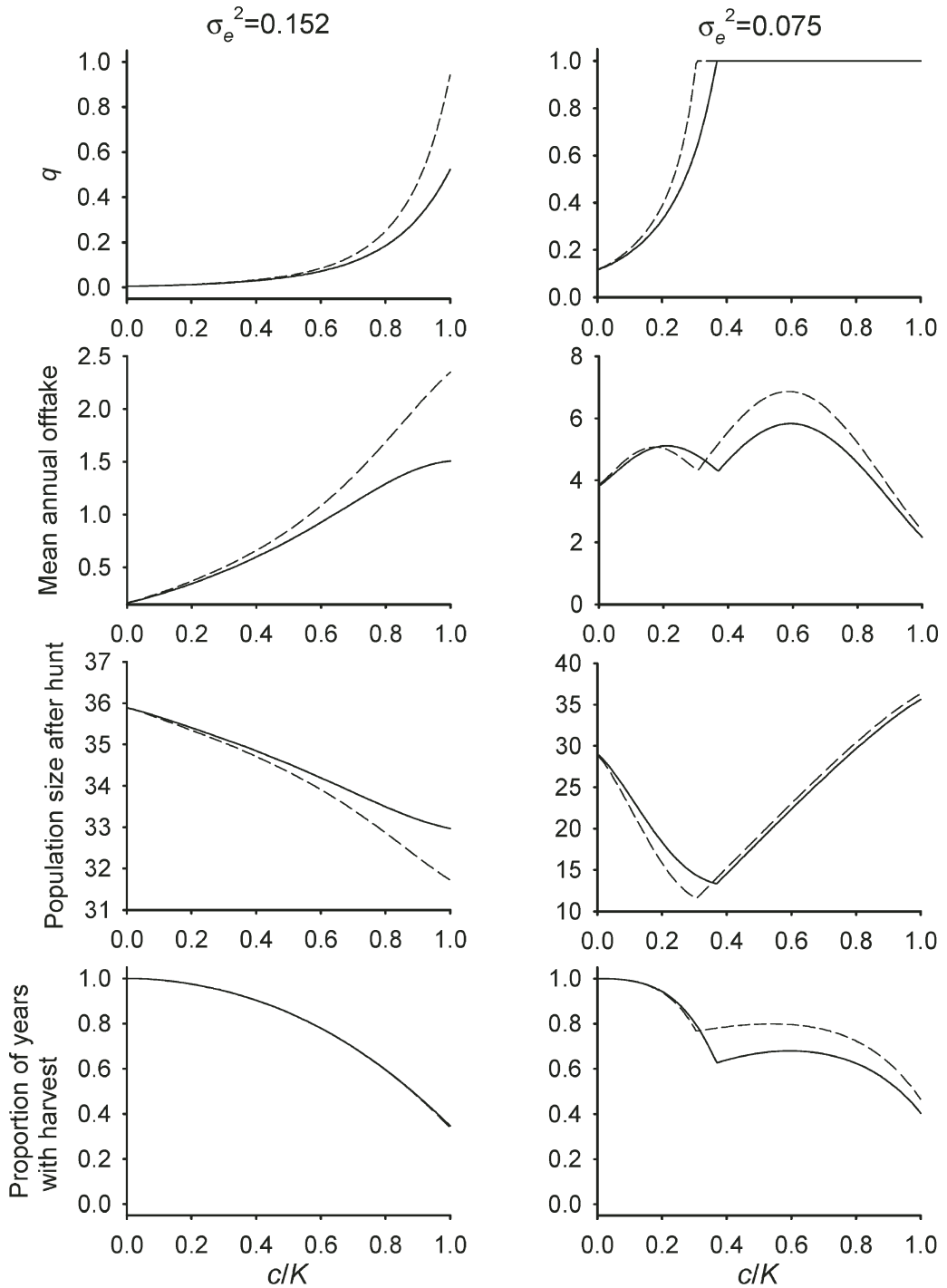


Fig. 3. The proportion of wolverines in excess above the threshold c that can be removed (q), the mean annual harvest of individuals, the expected population size after the hunt, and the proportion of years when harvest is allowed in relation to the threshold c/K for different levels of uncertainty in the population estimates (dashed line: $\epsilon = 0.01$, solid line: $\epsilon = 1$, see (12) in the text) for 2 values of environmental stochasticity under the constraint of an expected time to extinction of 952.3 years, thus satisfying the criteria that the population would not be classified as vulnerable according to World Conservation Union (2001). The population model is the ceiling model of Lande (1993). Other parameters were $r_1 = 0.27$, $\sigma_d^2 = 0.571$, and initial population size was $N_0 = K = 60$.

To determine a sustainable strategy for offtake of wolverine, we examined the threshold c/K in the different regions of Norway, under the constraints that the expected time to extinction

should be 952.3 years. Thus, the population should not be considered vulnerable according to the criteria of World Conservation Union (2001). We used $q = 0.4$, representing a strategy to mini-

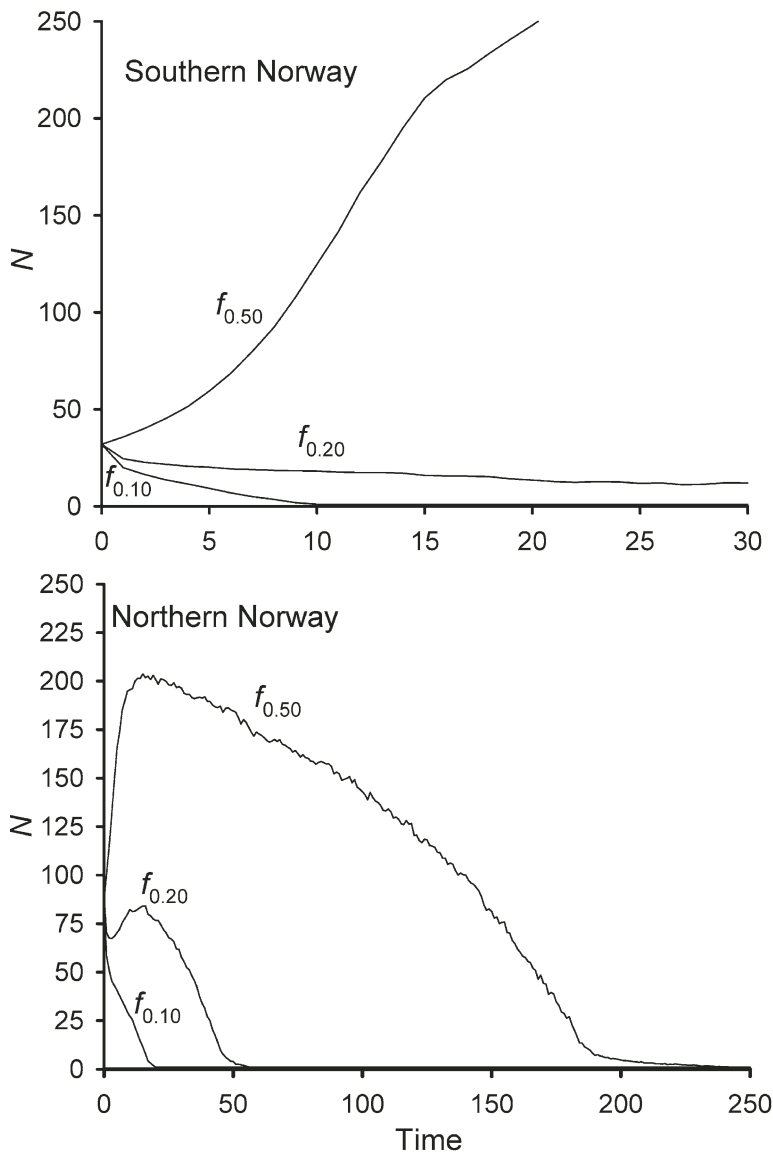


Fig. 4. Simulation of the effects of harvesting on wolverine populations in the southern and northern Norway (counties N-Trøndelag, Nordland, Troms, Finnmark; Fig. 1) with parameters estimated for the Sarek population (solid line) for $\sigma_e^2 = 0.154$. In the distribution of the simulated population sizes resulting from 1,000 sample paths, the 50%, 20%, and 10% quantiles are denoted by $f_{0.5}$, $f_{0.20}$, and $f_{0.10}$, respectively. The population size of sexually mature (≥ 3 -yr-old) females was set to twice the estimated number of active dens in 2002, assuming no sampling errors in the estimates. Because many killed females were not age-determined, we included the complete adult (≥ 1 -yr-old) female segment of the population in the analyses. We assumed that 1- and 2-year-old individuals comprised 50.5% of the population (Landa et al. 2001). This gave $N_0 = 32$ and $K = 332$ in southern Norway and $N_0 = 88$ and $K = 240$ in northern Norway. A constant harvest was assumed, specified by the mean and variance in the number of adult females harvested in the region over the past years (Table 1). The carrying capacity was determined from an assessment of the areas with available wolverine habitat. Other parameters were $r_1 = 0.27$ and $\sigma_d^2 = 0.571$.

imize expected population size after hunt, and $q = 0.6$, a strategy aimed to maximize the mean annual offtake of animals (Fig. 3). Using the parameter estimates from the Sarek population and an initial population size of $N_0 = K$, harvest could only be allowed in populations with $K > 47$ sexually mature females if the expected time to extinction was long enough to consider the population as nonvulnerable. For increasing values of K , the threshold could decrease, reaching 10–15% of K in very large populations (Fig. 5). These patterns were very sensitive to environmental stochasticity. For lower estimates of σ_e^2 , harvesting could start at much lower population sizes, and lower thresholds could be selected for a given q (Fig. 5).

DISCUSSION

We demonstrated that the carrying capacity K of wolverines in Scandinavia must be >46 sexually mature (≥ 3 -yr-old) females (Fig. 2) for a population to be considered not vulnerable by the World Conservation Union (2001), assuming that the demographic characteristics of the Sarek population were typical for most populations in Scandinavia. This implies that the current population in Sarek is not viable (Fig. 2) with-

out immigration from surrounding areas. Furthermore, we demonstrated that the rate of loss of wolverines in Norway due to various kinds of human activities will likely lead to rapid wolverine extinction (Fig. 4), provided that no immigration occurs from neighboring countries.

Our analyses were based on several simplifying assumptions. Our estimate of the specific growth rate $r_1 = 0.27$ was based on all females being mature at age 3. In general, this is not the situation in Scandinavian populations where only 33% of 3-year-old females reproduce. The average age at first re-

production among females monitored to their first reproduction was 3.4 years (Persson 2003). Similarly, we assumed very small losses of offspring before weaning (see Methods). A problem with these estimates is that the demographic study was undertaken in an area with a high density of animals that is likely to represent a favorable habitat for the wolverine. Thus, our choice of parameter values for calculating the mean growth rate at small population sizes was likely to overestimate r_1 in other areas. In general, a reduction in r_1 will have a strong influence on time to extinction (Lande 1993; Sæther et al. 1998a,b; Lande et al. 2003; Sæther and Engen 2003), as was the case for the wolverine population in Sarek (Fig. 2). Furthermore, we assumed that the recorded number of active dens represented only half of the number of sexually mature females present in the population. However, there was large annual variation in the proportion of females breeding. If the large number of dens recorded in Sarek in 2002 (Table 1) was due to a high breeding propensity among the females that particular year, we may have overestimated the carrying capacity for the area. This suggests that our estimates of the time to extinction of the Sarek population (Figs. 2, 3) are likely to represent overestimates.

Reliable estimates of density regulation require long-time series of precise population estimates (Sæther et al. 1998b, 2000, 2002a,b), far longer

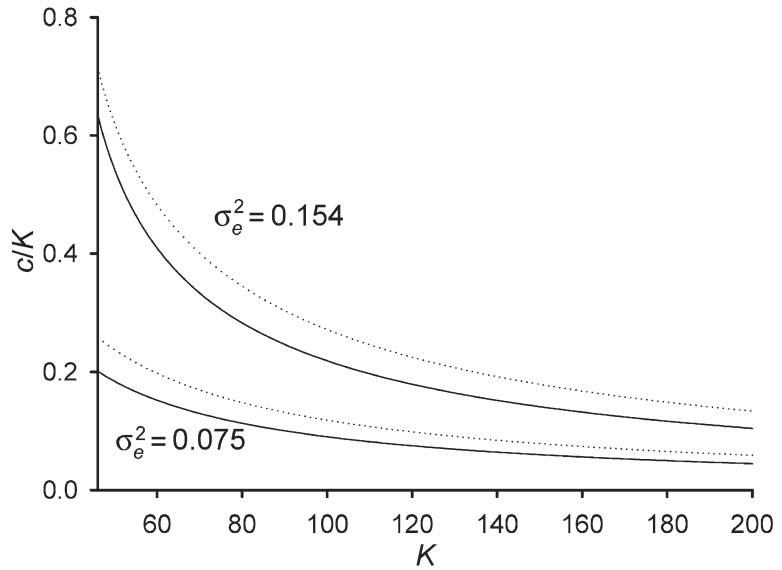


Fig. 5. The threshold c/K in relation to the carrying capacity K for different choice of q and environmental variance σ_e^2 that gives an expected time to extinction of 952.3 years and thus satisfies the criteria that the wolverine population would not be classified as vulnerable according to World Conservation Union (2001). The solid lines represents $q = 0.4$, and the dotted line represents $q = 0.6$. Other parameters were $r_1 = 0.27$, $\sigma_d^2 = 0.571$, and initial population size was $N_0 = 40$.

than available for any Scandinavian wolverine population. Thus, in most of the analysis, we assumed the ceiling model of Lande (1993) with a very simplified description of the density regulation. The uncertain estimates of θ in the Sarek population (Sæther et al. 2003) do indicate strong density regulation around K , which supports the choice of this model. This type of population dynamic seems typical for many solitary vertebrates that defend territories (Lande 1987, Sæther et al. 2002b).

Stochastic factors strongly influence the population dynamics of the wolverine. Our estimate of the demographic variance σ_d^2 in the wolverine population in Sarek was higher than those previously estimated in most vertebrate populations (Lande et al. 2003). Similar values have only been recorded in some small passerine birds (Lande et al. 2003). This is related to the combination of relatively high survival rate of the adult females but highly variable recruitment success (Sæther et al. 2003). Previous studies have indicated high losses of offspring after the denning period that were probably related to intra-specific predation (Persson et al. 2003). However, these estimates of recruitment could also be an artifact of the sampling procedure because, during the first year, only breeding females were radiocollared. Accordingly, we included only females that already had been followed 1 year in the estimates of recruitment success. However, including

all adult females or selecting only females followed over 2 years gave a small change (<5%) in $\hat{\sigma}_d^2$. This suggests that large demographic stochasticity is an important characteristic of wolverine population dynamics. Theoretical analyses have shown that the demographic stochasticity strongly influences the time to extinction of small populations (Lande 1993; Lande et al. 1998, 2003; Sæther and Engen 2003). Thus, the results of our calculations of the expected time to extinction (Fig. 2), the simulations of future population trajectories (Fig. 4), and our analysis of different harvest strategies (Figs. 3, 5) are all likely to be influenced by such a high estimate of σ_d^2 . This illustrates the importance of incorporating analysis of demographic stochasticity, especially when considering management options for small populations (Sæther and Engen 2002a).

Environmental stochasticity is another important component of the population dynamics of the wolverine. Usually, we estimate this from time series of population fluctuations (Dennis and Otten 2000; Sæther and Engen 2002b; Sæther et al. 2000, 2002b). In the Sarek population, we used the among-year variation in the individual fitness contributions, using the method of variance partitioning described in Engen et al. (1998). We then assumed that the annual fluctuations in population size were only due to stochastic fluctuations around K and were not related to density dependence. Thus, $\hat{\sigma}_e^2$ probably represented an upper limit for the environmental variance σ_e^2 . However, large environmental stochasticity was expected in the population dynamics of the wolverine because the demography was presumably influenced by highly variable food availability, such as the abundance of ungulate carrion (Persson 2003) and rodents (Landa et al. 1997). Therefore, we performed all analyses using $\hat{\sigma}_e^2 = 0.154$ and $\sigma_e^2 = 0.075$. As expected from theoretical analysis (Lande 1993, 1998; Lande et al. 2003; Sæther and Engen 2003), variation in this parameter strongly influenced the expected time to extinction and the choice of harvest strategy for larger populations (Fig. 3). However, predictions of the future development of wolverine populations in Norway were relatively independent of the estimates of σ_e^2 (Fig. 4); this was probably because the harvest of individuals (Fig. 3) affected the deterministic dynamics by reducing r_1 . It is therefore important to continue long-term individual-based population studies of the wolverine to improve precision in the estimates of r_1 and σ_e^2 .

Theoretical analysis of harvesting models has shown that proportional threshold harvesting has some useful properties in reducing the variance in

the annual yield, compared to a pure threshold strategy (Engen et al. 1997; Lande et al. 1997, 2001). We are then left with 2 options, determining the threshold and determining the proportion of individuals above the threshold that can be removed, q . When we kept the expected time to extinction constant, we found that, for large values of the environmental stochasticity, the annual yield was maximized and the expected population size after the hunt was minimized for high thresholds c/K (Figs. 3, 5). In contrast, when environmental stochasticity was smaller, the chosen values c and q depend on the optimization criteria. If the expected population size after the hunt should be minimized, a smaller threshold c/K should be chosen than for maximization of the annual off-take as optimization criterion. Irrespective of the value of σ_e^2 , higher values of q could occur when the precision in the population estimates is improved (Fig. 3). Thus, larger off-takes were permitted for small sampling errors than for larger sampling errors (Tufto et al. 1999); this strongly emphasized the need for the investment in precise population censuses for a sustainable harvest strategy for wolverine. A central focus for such schemes should be to obtain estimates of the nonbreeding part of the population (i.e., by using modern DNA techniques to obtain individual identification from samples of feces or urine samples collected from tracks [Flagstad et al. 2004]). Such data can be analyzed by capture-recapture techniques to provide information on the precision in the censuses (Seber 1982, Mills et al. 2000) and estimates of important demographic variables (Lebreton et al. 1992).

MANAGEMENT IMPLICATIONS

Our analyses have shown that the Norwegian management boards have given quotas that are too high to secure viable wolverine populations in Norway according to the World Conservation Union's (2001) criteria (Fig. 4). Thus, if the current practice is continued, this is likely to lead to extinction of the wolverine over the larger parts of Norway within a relatively short period (Fig. 4). Assuming the demographic characteristics of the Sarek population are typical of most Norwegian populations, our estimates of K , though admittedly very rough, suggest that harvest should not be permitted before the populations exceed 22 sexually mature females in both northern and southern Norway. This calculation is based on $q = 0.4$ and the initial population size of sexually mature (≥ 3 -yr-old) females; that is twice the number of active dens in the 2 regions in 2002 (Table 1). When the estimated population size exceeds this value,

40–60% of the excess individuals can be removed (Fig. 3). Thus, the current population size must be increased before harvesting should be permitted in the southern Norwegian management region. In northern Norway, a limited offtake can be permitted. However, this assumes strong regulation of the offtake with no harvest below the threshold.

A central element in a management strategy would be to reduce the number of animals killed illegally that is likely to occur even in the protected Sarek area (Table 1). A consequence of this will be an increase in the specific growth rate and a reduction in the stochastic influences on the population. This will strongly increase the expected time to extinction (Fig. 2) and improve viability of the species.

ACKNOWLEDGMENTS

This study was financially supported by grants from the Norwegian Directorate for Nature Management. The field study of wolverines in Sarek was financed by the Swedish Environmental Protection Agency, World-Wide Fund for Nature, and Norwegian Directorate for Nature Management. P. Segerström and T. Wiklund conducted the fieldwork in Sarek.

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