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Integrating effects of hunting policy, catastrophic events, and inbreeding depression, in PVA simulation: the Scandinavian wolf population as an example

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Abstract

Focusing on the wolf *Canis lupus* in Scandinavia as an example, criteria are proposed and an analysis performed to assess the effect on extinction risk of various control policies, while accounting simultaneously for effects of inbreeding depression and potential catastrophic events. Each control policy is characterized by a hunting pressure (the increase caused by hunting of annual mortality rates) combined with a hunting threshold (the population size below which hunting is not permitted). Catastrophes are taken into account by including the persistence of a severe catastrophe in the criterion for population viability. Based on these criteria, the results suggest that only a very limited amount of hunting should be permitted at low population sizes. The results also illustrate the importance of including a long-term perspective in modelling threatened populations.
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1. Introduction

Can a certain amount of regulated hunting be acceptable, from a conservation point of view, although the population is smaller than a minimum viable population (MVP)? Intuitively, two alternative answers both sound sensible. Proponents of hunting argue that before a population goes extinct, it has to drop below a low threshold (e.g. 50, 100, 200), and hunting should be permitted above such a threshold as it should not pose a threat to the population. Opponents of hunting argue that the precautionary principle should lead us to let the population reach the size required for viability as fast as possible. In the present study, I demonstrate, using the wolf *Canis lupus* in Scandinavia as a case study, how criteria can be formulated and an analysis performed to search an answer based on more than sheer intuition.

In Scandinavia, i.e. Sweden and Norway, as in many other parts of the world (cf. Mech, 1995; Breitenmoser, 1998), the wolf is a controversial species. Although the wolf population is very small and the species is protected by law in both countries, hunters and farmers pressurise on authorities to permit hunting to reduce the number of wolves in certain areas. In Norway, in 2000 and 2001, respectively, 4 and 10 wolves were shot with permission, out of a total Scandinavian population of fewer than 100 animals (Aronson et al., 2000, 2001). In Sweden, the authorities have been more restrictive, but in 2002 a few permits to shoot wolves were given. Legislation in both countries is meant to implement the Bern Convention on the Conservation of European Wildlife and Natural Habitats (19.ix.1979), which gives a limited opportunity to permit hunting of protected species under certain conditions, but only provided that such control measures will not be detrimental to the survival of the population concerned (Bern Convention, Article 9).

Another controversial issue regarding the wolf is how large the population should be. So far, neither Sweden nor Norway has officially set a goal for what population size is desirable. By signing the the UN Convention on Biological Diversity (5.vi.1992), both countries have agreed to promote the maintenance of viable populations of species in their natural surroundings. In the

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1990s, the environmental authorities of the two countries discussed a stage goal of 8–10 reproducing family groups in Scandinavia, and in 1997 this stage goal was sanctioned by the Parliament of Norway. In 2001, the Parliament of Sweden decided on a stage goal of 20 annual reproductive events (i.e. litters born) within Sweden. This may seem like a striking difference between the two countries, but it is important to remember (although often forgotten in the public debate) that these figures are not definite goals but only stages on the way to a viable population.

Analysing which population size that will keep extinction risk at an acceptable level (the minimum viable population, MVP) is a classical subject for population viability analyses (PVAs), which for the Scandinavian wolf population has been addressed previously by Ebenhard and Johnsson (Johnsson and Ebenhard, 1996; Ebenhard, 1999; Ebenhard, 2000). Their analyses take into account demographic stochasticity, inbreeding depression, and moderate levels of environmental stochasticity, but they have not considered the possibility of catastrophic events that might strike the population.

In an important review, Young (1994) showed that catastrophic die-offs in wild mammal populations are so widespread in nature that such events must be taken into account in PVAs and in the practical management of endangered populations. Young summarized 96 reported instances of catastrophic die-offs among large and middle-sized mammals; and additional examples of catastrophic declines in carnivore populations are provided by Appel and Summers (1995), Osterhaus et al. (1998) and Murray et al. (1999). Among the cases compiled by Young, he found a relative overabundance of die-offs reducing the population by 70–90%, and an underabundance of die-offs greater than 90%. In reports concerning canids, reductions ranged from 50 to 87%.

Hence, although we are still far from being able to estimate the probability of such a catastrophe for a specific population, there is a reasonably good basis for assessing the severity of a severe catastrophe on a wild mammal population. This study demonstrates how this knowledge can be taken into account in PVA simulations.

2. Material and methods

2.1. PVA software

The simulations were performed with the VORTEX program (Miller and Lacy, 1999), version 8.41.

2.2. History of the study population

Culling statistics (summarized in Persson and Sand, 1998) indicate that in the early nineteenth century there must have been at least 1500 wolves in Sweden, suggesting that the number in the entire Scandinavian peninsula may have been 2000–3000 or even more. A hundred years later the species had been exterminated throughout most of the area and persisted only in sparsely populated regions in the north, and in the early 1970s, the wolf was officially considered extinct in both Sweden and Norway (Wabakken et al., 2001). Some years later, however, the presence of a few wolves in mid-Scandinavia was confirmed. These reproduced and during the 1980s and 1990s their descendants managed to persist and achieve an impressing increase in numbers.

The core of the area inhabited by the population covers a few counties on each side of the Swedish–Norwegian border. Several of the family groups have territories crossing the country border, and distances between Swedish and Norwegian territories are fairly short relative to the distances often moved by young wolves before they establish a territory. Hence, biologically, the wolves in Scandinavia are clearly one population, rather than one Swedish and one Norwegian population (cf. Wabakken et al., 2001).

Previous simulation studies have assumed that around 1980 the population consisted of only two individuals (Johnsson and Ebenhard, 1996; Angerbjörn et al., 1999). However, Ellegren et al. (1996) found five alleles at a single locus among wild Scandinavian wolves, showing that most probably at least three individuals have contributed genes to the present population.

Aronson et al. (2000), having evaluated a huge amount of reported observations of wolves or their tracks during the winter 1999/2000, concluded that the Scandinavian population in early 2000 (before reproduction) consisted of 61–75 individuals.

2.3. Demography and inbreeding depression

An important conclusion of Johnsson and Ebenhard (1996) was that while population size and intrinsic growth rate were of overriding importance in determining extinction risk, within parameter ranges plausible for wolves, the demographic details of how a certain growth rate was produced caused only minor variation around the overall relationship between growth rate and extinction risk. Therefore, in the present study, rather than performing a sensitivity analysis regarding each demographic parameter, I handle the uncertainty about the true demography of the population by modelling two alternative scenarios with different intrinsic growth rates. Scenario A is intended to represent the most likely case, given current knowledge, while scenario B is intended to err on the cautious side with regard to the intrinsic growth rate of the population. In addition, a third scenario C is included, which is intended to err on the cautious side with respect to the wolves' sensitivity to inbreeding depression. The input data and empirical estimates for comparison are summarized in Table 1.

Table 1
Input data for the three scenarios of this study, compared with data used in previous PVAs of the Scandinavian wolf population and to empirical data

	Empirical estimates		Previous PVAs[e,f]	This study		
	Comparable populations range/mean	Scandinavian population/ Fennoscandic zoo population		Scenario A	Scenario B	Scenario C
Mean litter size	2.83[m]–6.9[c]/5.15[b,c,d,i,k,l,m,n]	4.94[e]	4.94	4.94	4.44	4.94
Proportion of adult females reproducing (%)		29[e]	29	29	29	29
EV (%)			7	9.67	9.67	9.67
Pup mortality (%)	26[i,l]–63[d]/36[d,i,j,k,l]	30.4[a]	22–28	24	27	24
EV (%)			5–7	8	9	8
Yearling mortality (%)	26[i,l]–36[d]/31[d,i,j,k,l]		25–38	17.5	20.5	17.5
EV (%)			6–9	5.83	6.83	5.83
Adult mortality (%)	20[l]–36[d]/30[d,i,j,k,l]		10–14	11	14	11
EV (%)			5	3.67	4.67	3.67
Sensitivity to inbreeding		Effect on survival to age 660 days: 1.57 lethal equivalents[h], plus effect on litter size and several other fitness measures: 6–7% reduction per 10% increase of inbreeding[g]	1.57–3.0 lethal equivalents	3.0 lethal equivalents	3.0 lethal equivalents	6.1 lethal equivalents

[a] Calculated from number of produced yearlings per litter in Angerbjörn et al., 1999, and litter size in Johnsson and Ebenhard, 1996.
[b] Bjorge and Gunson, 1989.
[c] Period of high ungulate biomass per wolf in Boertje and Stephenson, 1992.
[d] Fuller, 1989.
[e] Johnsson and Ebenhard, 1996.
[f] Ebenhard, 2000.
[g] Laikre, 1999.
[h] Laikre and Ryman, 1991.
[i] Mean of estimates for years 1973–1975 in Mech, 1977.
[j] Area of high prey availability in Messier, 1985.
[k] Peterson et al., 1984.
[l] Pletscher et al., 1997.
[m] Pulliainen, 1965.
[n] Rausch, 1967.

Scenario A was based as far as possible on published empirical data for the Scandinavian population. Comparisons were also made with nine other studies of wolf populations experiencing a boreal climate, high food abundance, and some exposure to conflicts with humans, but not intensive control programs (Pulliainen, 1965; Rausch, 1967; Mech, 1977; Pletscher et al., 1997; Peterson et al., 1984; Messier, 1985; Bjorge and Gunson, 1989; Fuller, 1989; Boertje and Stephenson, 1992). Sensitivity to inbreeding depression, measured as number of lethal equivalents, was based on empirical data for wolves in captivity (Laikre and Ryman, 1991; Laikre, 1999), which are descendants from a few wolves captured in Sweden and Finland. Inbreeding depression in the simulations affects pup mortality, so to avoid 'double dipping' (Brook, 2000) pup mortality prior to inbreeding was set somewhat lower than the empirical estimate. Parameters for which no empirical estimates for the Scandinavian population have been published, i.e. adult and yearling mortality, were iteratively tuned so that starting from three individuals, the surviving populations after 20 years would have a mean size of 61–75 individuals, similar to the observed increase of the population. The adult and yearling mortality rates used were low relative to other comparable populations, but this was inevitable to achieve the rapid growth shown by the population, and this population growth is very well documented (cf. Wabakken et al., 2001).

In scenario B, litter size was reduced and mortality rates increased so that among populations starting with three individuals and surviving after 20 years the probability of reaching 61 individuals or more was ca. 5%. Inbreeding depression was the same as in scenario A.

In scenario C, demography was kept as in scenario A while the strength of inbreeding depression was increased so that the probability of reaching 61 individuals or more was ca. 5%.

In all three scenarios, mating system was monogamous with long-term pair bonding, sex ratio at birth was 50:50, age of first reproduction was 2 years and maximum breeding age 16 years, and all adult males were potential breeders. Environmental variation of proportion of females reproducing and of mortality rates were correlated, and were given a standard deviation of one third of their respective mean. Inbreeding depression was modelled purely as heterozygote advantage, i.e. with no part of it attributed to single lethal alleles.

2.4. Accounting for previous inbreeding

To model the future prospects of the population it is convenient to start with a population size within the range calculated for the actual population in early 2000, i.e. 61–75 individuals. However, starting the simulations with around 70 individuals would mean implicitly assuming that these were genetically unrelated, which is certainly not the case, and would result in an over-optimistic picture (cf. Frankham, 1995, about past inbreeding). To account for the previous inbreeding history of the population, all simulations were started with three individuals. At year 20, all populations were 'killed' that were not within the range 61–75 individuals, and only those within this range were allowed to continue. Hence, in all simulations the first 20 years represent the time between 1980 and 2000, and all results presented are based only on the subset of simulation runs that resembled the likely development of the true population by growing from a few animals to 61–75 individuals in 20 years.

2.5. Catastrophes

The approach taken here to account for potential catastrophic events without knowing their frequency was to include the survival of a catastrophe in the criterion for viability. Hence, the population was considered viable if its risk of extinction in a period of 100 years was below 5% even though a severe catastrophe was simulated within that century.

The catastrophes simulated here meant that in a single year mortality rate was raised to 90% for the yearlings and 85% for the adults, and no reproduction succeeded in that year. The normal environmental variation was turned off in that year so that the catastrophe would have approximately the same severity in all simulation runs. This caused an immediate reduction of population size by ca. 86%, with some variation due to demographic stochasticity. Hence the severity of the catastrophes was in the upper range, but not unrealistically severe, compared with the data of Young (1994).

2.6. Hunting

VORTEX allows two alternative ways to include hunting: either as an increase of annual mortality rate, or as removal of a specified number of individuals per time period. In the present study, hunting was modelled as an increase of annual mortality rate occurring when the population reached a certain threshold size. The increase in mortality due to hunting was equal across sexes and age categories. Environmental variation in mortality was not increased, but was kept at one third of the background mortality rate. If the population dropped below the threshold, hunting was stopped until the population reached or exceeded the threshold again. No hunting took place in the year of a catastrophe.

The extent of poaching cannot be controlled, and therefore poaching is best modelled as part of the background mortality. Since the mortality rates were estimated from the population growth that has occurred in spite of some amount of poaching, the effect of pre-

vious rates of poaching is accounted for in these estimated mortality rates.

To evaluate the analysis with respect to permitted hunting, a quantitative criterion is needed to identifying acceptable increases in extinction risk from unacceptable increases. As long as the extinction risk is low, it is reasonable to accept some hunting providing it does not cause the extinction risk to exceed the 5% criterion (as defined earlier in Section 2.5). However, if the extinction risk without hunting already exceeds 5%, the question becomes more controversial. If extinction risk is very high, or if the population in question is important for the global persistence of its species, then the precautionary principle suggests that no deliberate killing is acceptable. However, considering that the 5% criterion here is sharpened by including the persistence of a catastrophe in the criterion, and considering that the wolf is a widespread species with large populations in some countries, it may be sensible to propose that an increase of extinction risk by one percentage point is acceptable, as long as extinction risk without hunting is not extremely high. Hence, in the present study the following criteria were used to delimit what is an acceptable effect of hunting:

- If without hunting the risk of extinction in 100 years, given that a severe catastrophe occurs, is at most 4%, then a control policy is acceptable if it does not increase this risk to more than 5%.
- If without hunting the risk of extinction in 100 years, given that a severe catastrophe occurs, is more than 4%, then a control policy is acceptable if it does not increase the risk by more than one percentage point.

2.7. Preliminary analyses

Initially, various combinations of the population ceiling ('K') and simulation time span were tested with a low number of simulation runs, to explore which combinations were feasible, with regard to computation time, to investigate further. Note, the ceiling termed 'K' in VORTEX is a population size above which all individuals are killed; hence, it does not act like we usually imagine an environmental carrying capacity would act, but it may well represent a situation where the human society decides a maximum number for a population.

2.8. Population size for long-term viability

The simulations aiming at estimating the size of a viable population were run for 1000 years and the extinction risk was calculated for the last 100 years, i.e. between year 900 and year 1000 of each simulation. A catastrophe struck each population in year 910. To find

out which population size would keep this extinction risk below 5%, simulations were run with varying values of the population ceiling 'K'. Each estimated extinction risk was based on > 1500 simulation runs surviving through year 900 for scenario A, > 1000 runs for scenario B, and > 300 runs for scenario C.

2.9. Effect of hunting on short-term extinction risk

The simulations aiming at assessing the effect of hunting on short-term extinction risk were run for 120 years, and extinction risk was calculated between year 20 and 120 of the simulations. A catastrophe struck each population in either year 30, 50, 70, 90 or 110, with equal probability for these five alternative years. The population ceiling ('K') was 600, chosen to represent a fairly probable (from the social and political point of view) compromise between the size of a MVP estimated under scenario A and the higher values estimated under the other scenarios.

Each control policy was characterized by a hunting pressure (the increase caused by hunting of annual mortality rates) combined with a hunting threshold (the population size below which hunting was not permitted). Under scenario A, hunting pressure increasing mortality by 2, 5, 10, 20 and 30 percentage points were combined with hunting thresholds of 50, 100, 150 and 200 individuals. Each combination was tested by > 2500 simulation runs surviving through year 20, and those combinations giving an extinction risk below 8% were run > 5000 times to improve precision around the limit between acceptable and unacceptable risk levels. Under scenarios B and C, hunting pressure increasing mortality by 1, 2, 5 and 10 percentage points were combined with hunting thresholds of 50, 100, 150, 200, 250, 300, 400 and 500 individuals. Each tested combination was simulated for > 1000 runs, and those combinations giving an extinction risk below 17% or below 31%, for scenario B and C, respectively, were run > 5000 times to improve precision. Each of the three scenarios was also run > 5000 times without additional mortality due to hunting.

2.10. Effect of hunting on long-term extinction risk

Among the combinations of hunting pressure and hunting threshold tested in short-term simulations under scenario A, eight combinations which all appeared acceptable in the short-term perspective were chosen for long-term evaluation. These were run for 1000 years, and a catastrophe struck the population in year 910. Extinction risk was calculated between years 800 and 900 (long-term extinction risk without catastrophe) and between years 900 and 1000 (long-term extinction risk with catastrophe). The population ceiling ('K') used was 600, for the sake of comparability with

the short-term results. Each estimated extinction risk was based on >1000 simulation runs surviving through year 900.

3. Results

3.1. Preliminary analyses

Apart for advising on the combinations of population ceiling and simulation time span to investigate further, the preliminary analyses showed that with rather low levels of the ceiling (e.g. 100) although extinction risk was very low during the first century (between year 20 and year 120 of the simulations) it rose sharply some hundred years later (Fig. 1).

3.2. Estimation of population size for long-term viability

Under scenario A, a population ceiling of 400 individuals was high enough to maintain the extinction risk in the last 100 years of the simulation below 5%. Under scenarios B and C, the population ceiling required was 1300 and 3000 individuals, respectively (Fig. 2).

3.3. Effect of hunting on the short-term extinction risk

Without hunting, but with a catastrophe striking the population once per simulation, the extinction risk between simulation years 20 and 120 under each of sce-

narios A, B and C was estimated at 0.96, 13.95 and 27.85%, so the limit for acceptable risk with hunting included was set to 5, 14.95 and 28.85%, respectively.

Under scenario A, a hunting pressure causing an increase of mortality by two percentage points above population threshold 50, five percentage points above 100, twenty percentage points above 150, or thirty percentage points above 200, did not increase extinction risk above the limit (Fig. 3). Under scenario B, raising mortality by two percentage points above population size 200, or ten percentage points above 400, did not cause an unacceptable increase in extinction risk (Fig. 4). Under scenario C, increasing mortality by two percentage points above population threshold 250, five percentage points above 300, or ten percentage points above 400, did not increase extinction risk above the limit (Fig. 5).

3.4. Effect of hunting on long-term extinction risk

Under scenario A, without hunting but with a catastrophe striking the population in simulation year 910, extinction risk between years 900 and 1000 was very close to 0 (in >1500 simulation runs the population never went extinct). Hence, the limit for acceptable risk with hunting was set at 5%. Permitting a hunting pressure increasing mortality by two percentage points, when the population was at or above a size of 50 animals, did not raise extinction risk above this limit. However, higher hunting pressure (increasing mortality
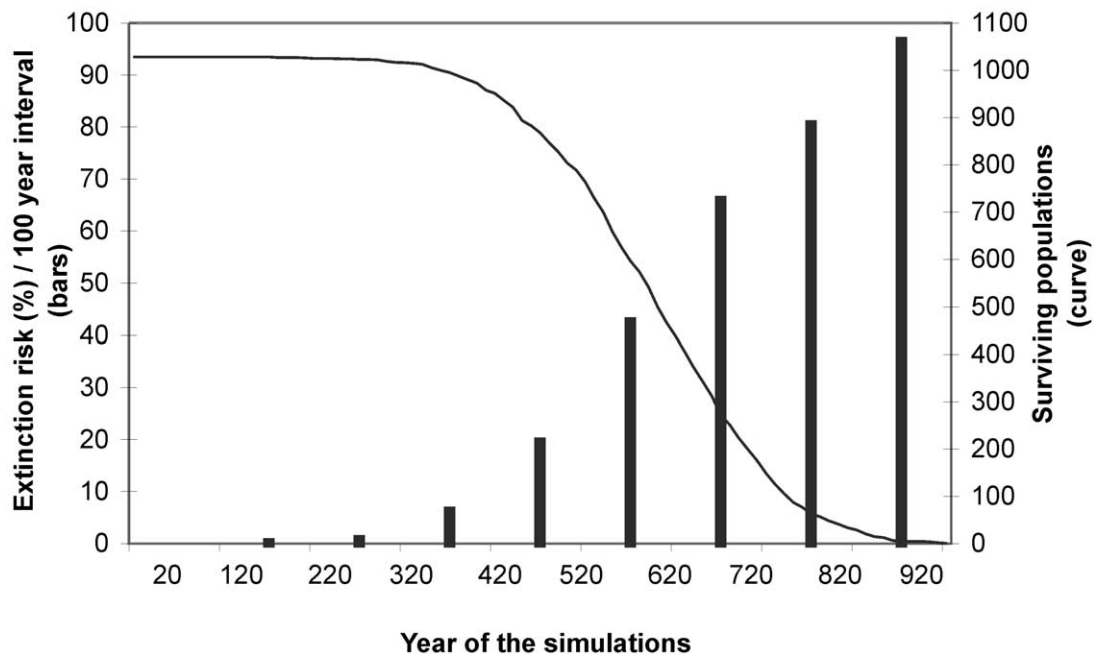

Fig. 1. Result of simulating scenario A for 1000 years with a population ceiling ('K') of 100 animals. The descending curve shows for every 10th year the number of populations still surviving out of 1028 populations having survived year 20. The ascending bars show the percentage extinction risk within each 100-year interval of the simulation, i.e. between year 20 and 120, between year 120 and 220, etc. The extinction risk per 100-year interval was first negligible, but then increased drastically. Only in two simulation runs out of 1028 did the population survive until it was struck by a catastrophe in year 910.
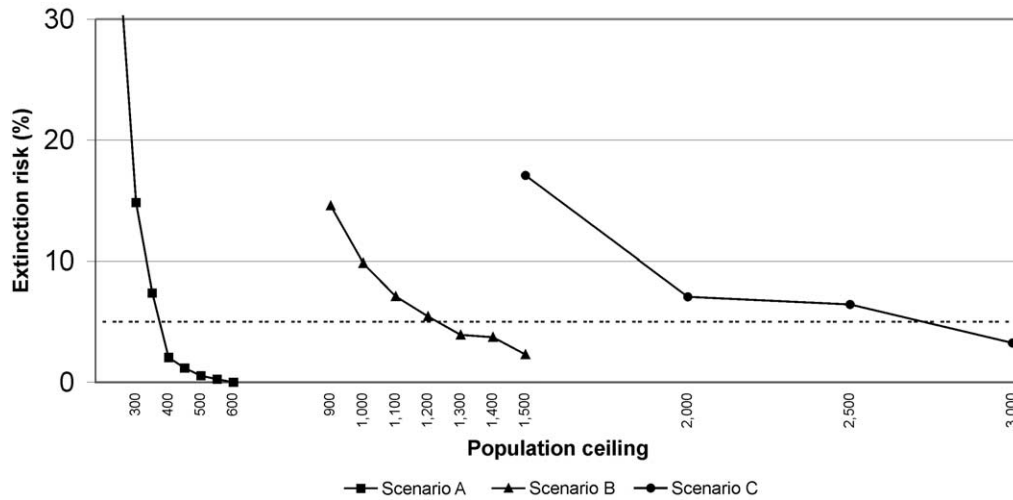
Fig. 2. Extinction risk between year 900 and 1000 of the simulations, without hunting but with a catastrophe striking the population in year 910, estimated for various levels of the ceiling size to which the population is allowed to grow, under scenarios A, B and C. The broken line represents 5% extinction risk.
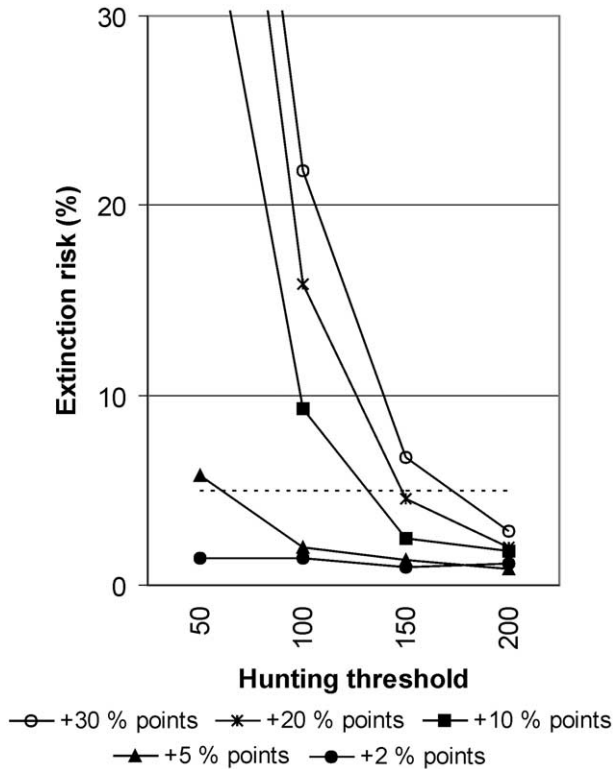

Fig. 3. Extinction risk between year 20 and 120 of the simulations, with a catastrophe striking the population within this period, estimated under scenario A for various combinations of hunting pressure (causing mortality to increase by 2, 5, 10, 20, or 30 percentage points) and threshold population size above which hunting is permitted. The broken line represents 5% extinction risk.
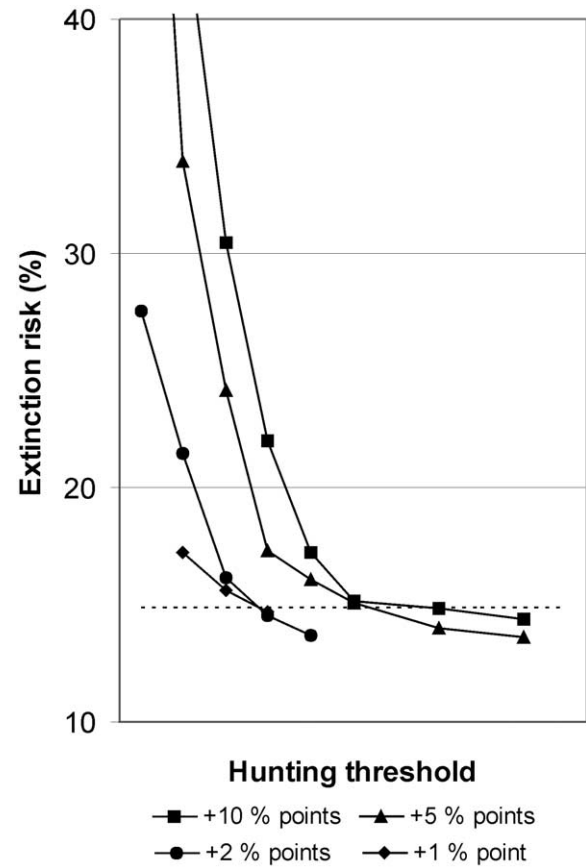

Fig. 4. Extinction risk between year 20 and 120 of the simulations, with a catastrophe striking the population within this period, estimated under scenario B for various combinations of hunting pressure (causing mortality to increase by 1, 2, 5, or 10 percentage points) and threshold population size above which hunting is permitted. The broken line represents 14.95% extinction risk.
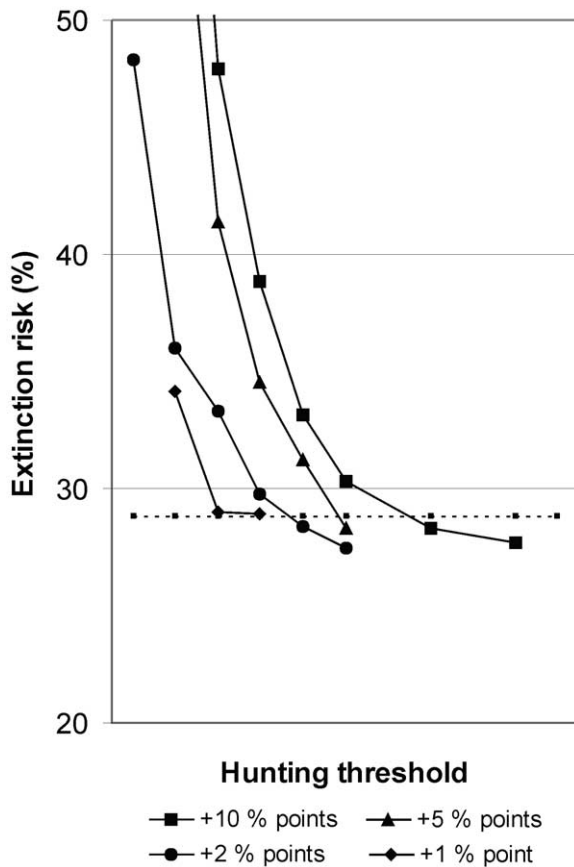
Fig. 5. Extinction risk between year 20 and 120 of the simulations, with a catastrophe striking the population within this period, estimated under scenario C for various combinations of hunting pressure (causing mortality to increase by 1, 2, 5, or 10 percentage points) and threshold population size above which hunting is permitted. The broken line represents 28.85% extinction risk.

by 5 percentage points or more) raised extinction risk considerably if permitted at such low population thresholds as suggested by the short-term analyses. Raising annual mortality by five percentage points at a population threshold of 100 individuals, which is fairly close to the current size of the population, caused an extinction risk of more than 40% (Fig. 6).

If for comparison we consider the extinction risk between year 800 and 900, which is a long-term extinction risk without catastrophic events being accounted for, an increase of mortality by five percentage points at population size 150, or 30 percentage points at size 300, did not raise extinction risk above the 5% limit (Fig. 7).

4. Discussion

4.1. Hunting in PVA

A conclusion that can be drawn from these analyses is that hunting a small population, even if hunting pressure is moderate and hunting is only permitted above a
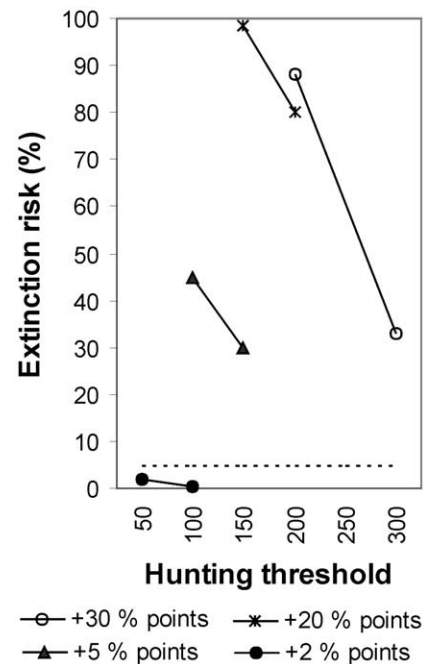

Fig. 6. Extinction risk between year 900 and 1000 of the simulations, with a catastrophe striking the population in year 910, estimated under scenario A for various combinations of hunting pressure (causing mortality to increase by 2, 5, 20, or 30 percentage points) and threshold population size above which hunting is permitted. The broken line represents 5% extinction risk.

threshold population size, can have a non-negligible effect on the population's risk of extinction. This does not imply that hunting below MVP can never be acceptable, but it means that the intuitive argument that hunting cannot pose a threat to a population, provided it is ceased when the population drops below the threshold, is false. Hence, biologists faced with the question of whether hunting will have a negative impact on the conservation status of a population should base their answer on a quantitative analysis of how extinction risk may be affected, rather than resorting to intuitive arguments.

In most real life situations, hunting should be stopped if a population drops below a critical level. Therefore, earlier attempts to simulate effects of hunting on population persistence (e.g. for wolf, Johnsson and Eberhard, 1996; Angerbjörn et al., 1999; for lynx *Lynx lynx*, Kontio, 1999; for black bear *Ursus thibetanus*, Horino and Miura, 2000; for harbour seal *Phoca vitulina*, Bjorge et al., 1994) have been criticized for being over-pessimistic (Persson and Liberg, 1999; Persson et al., 1999) by letting hunting continue even though the population approaches extinction. In this perspective, the use of the recent VORTEX versions to vary mortality rates as a function of population size, to simulate 'proportional threshold harvesting' policies (Lande et al., 1997; Tufto et al., 1999), is an important step forward. This new capability may prove useful to many
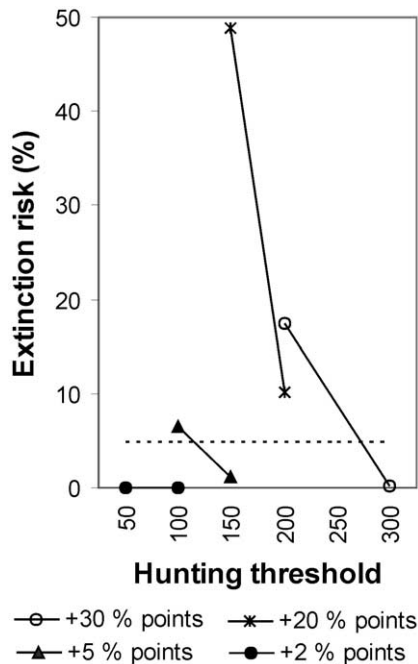
Fig. 7. Extinction risk between year 800 and 900 of the simulations, when no catastrophe was simulated, estimated under scenario A for various combinations of hunting pressure (causing mortality to increase by 2, 5, 20, or 30 percentage points) and threshold population size above which hunting is permitted. The broken line represents 5% extinction risk.

analyses of species where permitting some hunting is discussed already at low population sizes.

4.2. Catastrophes in PVA

In spite of a growing awareness of the potential importance of rare catastrophic events (e.g. Mangel and Tier, 1994; Young, 1994; Ludwig, 1999; Coulson et al., 2001), catastrophes are still commonly overlooked in PVAs (for exceptions, see Hamilton and Moller, 1995; Novellie et al., 1996; Armbruster et al., 1999; Haydon et al., 2002). Presumably, the main reason for this common omission is the difficulty in estimating the probable frequency of such rare events. As stressed by Coulson et al. (2001), when the distribution of catastrophes is unknown, it is sensible to model the potential impact of catastrophes to help devise management strategies that can cope with such eventualities. The approach taken here to achieve this was to modify the classical MVP criterion of a maximal extinction risk within a specified time period (Shaffer, 1981; Belovsky, 1987; Saltz, 1996; Howells and Edwards-Jones, 1997; Pfab and Witkowski, 2000) by including the persistence of a catastrophe in the criterion for viability; i.e. the population was considered viable if its extinction risk in a time period was below a certain limit given that a severe catastrophe would strike the population during that period. This approach should be widely applicable.

4.3. Time perspective and genetics in PVA

Another important conclusion from this study is that short-term analyses are not sufficient to find out which strategy will give a high chance of long-term persistence. As was seen in Fig. 1, a population of a certain size may seem safely viable if simulated for only 100 years, while its risk of going extinct rises sharply if it is held at such low size for some centuries (cf. similar results in Kontio, 1999). This is probably an effect of inbreeding accumulating over long time and extinction risk showing a threshold relationship to inbreeding (Frankham, 1995). Hence, when inbreeding depression is integrated in demographic PVA simulations it is wise to use a relatively long time perspective, or to check whether conclusions from short-term modelling hold when the simulation time span is extended.

Likewise, regarding the effects of hunting, although the short-term results are interesting in their own right and may have important implications for management, they are not sufficient to tell what hunting pressure is acceptable in a longer time perspective. Interestingly, if we would prefer to base our decision on the results between year 800 and year 900 of the simulations (Fig. 7), when no catastrophe occurred, we would still not accept hunting pressures that would increase mortality by 5–30 percentage points at such low population sizes as suggested by short-term analyses with catastrophes included. Hence, long-term extinction risk excluding catastrophic events here turned out to be a more restrictive criterion than short-term extinction risk accounting for a severe catastrophe. This further emphasizes the importance of including a long-term perspective in modelling threatened populations.

An old 'rule of thumb' in conservation biology says that a genetically effective population size (N_e) of 50 animals is required to avoid short-term inbreeding problems (Franklin, 1980). Andrén et al. (1999) estimated the ratio of effective population size to actual population size (N_e/N) for wolves to 0.10, implying a required actual population of about 500 wolves. However, the results of the present study suggest that the 'rule of thumb' may be inadequate. In the short-term perspective of a few decades or a century, much smaller wolf populations seem to persist. In a long-term perspective, the most likely scenario led to a recommendation similar to the 'rule of thumb', while two less probable but still plausible alternative scenarios led to several times higher estimates of the number of wolves required for long-term viability. Obviously, integrating inbreeding depression with demography in simulation modelling is more informative than the general 'rule of thumb', and I suggest the latter could be abandoned, not only in the case of wolves, but for any species for which we have some basis for sensible guesses about its genetic load.

Still, there are other genetic aspects which are not covered by this study, namely the risk that decreasing heterozygosity might make the population unable to adapt to environmental change (Franklin, 1980; Lande and Barrowclough, 1987; Lande and Shannon, 1996; Franklin and Frankham, 1998) and the risk of 'mutational meltdown' (Lynch et al., 1993; Lynch and Lande, 1998). Regarding potential for genetic adaptation, an interesting but apparently still overlooked question is whether this is more important for species with less phenotypic plasticity, and a less crucial aspect for phenotypically flexible species like the wolf.

4.4. Management implications: population size goal

If the criterion for viability used in this study is accepted, a definite goal or ceiling for the population size should not be set lower than the MVP estimated under scenario A, i.e. 400 individuals.

By simulating the development of a population 100 or 1000 years ahead, we can estimate the risk of extinction under various conditions, provided that other important factors do not change in a way that is not covered by the simulations. Of course, this exercise does not imply that we believe such changes will not come. In reality there may be changes in climate, food abundance, human attitudes, and other important factors which we cannot anticipate. Such unforeseen changes may force us to redo the analyses, perhaps with considerable alterations of both model structure and model input. Nevertheless, long-term simulation can help us avoid unwise management strategies. If a strategy leads to an unacceptably high extinction risk within 100 or 1000 years, then that strategy must be considered unwise. The inevitable uncertainty about what will change in the future may be an argument for having more safety margins in management than suggested by the analyses, but it can hardly be a valid argument for having less safety margins.

Scenarios B and C here serve to illustrate the uncertainty of the results of scenario A. Although scenarios B and C may seem pessimistic, they are compatible with the rapid growth shown by the Scandinavian wolf population in the past 20 years. The relevance of a somewhat pessimistic scenario concerning inbreeding can be motivated by several studies suggesting that in a given population, inbreeding depression may be many times stronger under natural conditions than in captivity (Chen, 1993; Jiménez et al., 1994; Miller, 1994; Crnokrak and Roff, 1999).

A wise management strategy should not rely solely on the scenario considered most likely, but should have some extra safety margins to cope with uncertainty. In this case, valid arguments for having wide safety margins could be that the past decade may have been an unusually favourable period for wolf population growth; that a larger population may have to spread into less favourable habitat (cf. Thiel, 1985; Mladenoff et al., 1995); and that the social structure of the wolf has not been accounted for in the analysis (cf. Vucetich et al., 1997; Ebenhard, 2000). Valid arguments for relying primarily on scenario A could be that the rapid growth shown by the Scandinavian wolf population is not extraordinary compared to wolves in other areas (cf. Rausch, 1967; Fuller, 1989; Pletscher et al., 1997); and that the analysis is conservative by modelling inbreeding depression only as heterozygote advantage, hence not allowing purging of deleterious alleles (cf. Hedrick, 1994; Keller and Waller, 2002).

It may seem discouraging that the span between the results of the three scenarios is so wide. In this respect, the results are consistent with the finding of Ludwig (1999) and Ellner et al. (2002) that moderate uncertainty about deterministic growth rate leads to large uncertainty about extinction risk. The results of Ellner et al. (2002) suggest that very long series of good field data are needed to estimate extinction risk with good precision, and until we have such data decision-makers have to cope with a considerable amount of uncertainty.

4.5. Management implications: hunting

This study suggests that a very limited amount of hunting may be permitted at the present low population size without seriously increasing the risk of extinction in a long-term perspective. Under the most likely scenario (A), raising annual mortality by two percentage points when the population exceeds 50 animals did not cause extinction risk in the last 100 years of the simulations to exceed 5%, even though a severe catastrophe struck the population during that century. However, all tested combinations of a higher hunting pressure with various hunting thresholds, for example, raising annual mortality rates by five percentage points at a threshold of 100 or 150 animals, caused an alarming increase of long-term extinction risk (Fig. 6).

In the simulations, mortality rates changed immediately when population size passed the hunting threshold, and extra mortality due to hunting never occurred in the year of a catastrophe. This corresponds to a situation where the population is accurately censused every year, and the amount of hunting permitted is adjusted according to the census results. If resources for monitoring are not sufficient for accurate annual censuses, then hunting will be more risky and extra safety margins needed (cf. Lande et al., 1997; Milner-Gulland et al., 2000). One way to meet this requirement is to base management decisions not on estimated population size but on thoroughly verified minimum counts (cf. Government of Sweden, 2000, p. 29).

An important question for the manager is whether culling a certain number of animals means increasing

total mortality by the same amount. Mortality could increase more than the number of animals shot if, as suggested by Feingold (1996), the remaining wolves in a family group are less efficient in acquiring food after their hunting unit has been disrupted some members being killed. Although no field data directly demonstrate this, it seems plausible for cases when alpha individuals are shot leaving less experienced animals behind. On the other hand, mortality could increase less if deaths due to hunting are partly compensated by density-dependent changes in other sources of mortality, like food shortage. However, in Sweden the moose *Alces alces* population numbers more than 200 000 animals (Hörnberg, 2001), and Persson (1996) estimated that if hunters and other predators would take half of the potential harvest of the Swedish ungulate populations, roughly 4000–6000 wolves could live on the other half (cf. also Glowacinski and Profus, 1997). Hence, food shortage is not likely to be important to the wolves in Scandinavia at the population sizes modelled under scenarios A and B in this study. As long as this is the case, the relationship between the percentage of animals shot and the hunting-induced increase of mortality rates should be close to a 1:1 ratio.

If the population ceiling ('K') here is interpreted as a level above which all animals are killed by hunters, then the control policies modelled include a drastic increase in hunting pressure at this population size. From social and practical points of views, it would be preferable to increase hunting pressure more smoothly as the population grows. Such a smoothened control policy, which still fulfils the criterion for long-term viability, is certainly possible to design, though the potential number of combinations of various hunting pressures at various population sizes is immense, so the computing effort will be considerable. To be worth the effort, such an analysis should preferably be planned in partnership with researchers, authorities, and interest groups.

The focus in this study on extinction risk does not imply this is the only relevant aspect of the issue of wolf hunting. Other aspects deserving further discussion and research include the sociological question of how wolf hunting is perceived by the public (Karlsson et al., 1999), the ethical questions concerning hunting a highly social animal (Haber, 1995), the ethological question of how hunting could affect the avoidance behaviour of the animals towards humans (cf. Caro, 1999; Bshary, 2001; Mazzolli et al., 2002), and the question of the potential ecological role of a larger wolf population (cf. Ripple et al., 2001). However, extinction is a central concern to most conservationists, it is a crucial issue in the Bern Convention and in the UN Convention on Biological Diversity, and it is an aspect that ecologists are asked to provide answers about. Therefore, it is both urgent and relevant to focus some attention on how we can assess the effects of hunting on extinction risk.

5. Conclusions

The general messages from the present study for future work in the field of population viability analysis may be summarised as follows:

- Hunting a small population can have a non-negligible effect on the population's extinction risk, even if hunting pressure is moderate and hunting is only permitted above a defined threshold population size.
- The effect of such hunting policies on extinction risk can be analysed with models allowing mortality rate to be varied as a function of population size.
- Catastrophic events should be taken into account in PVA, and one way to do it is to include the persistence of a catastrophe in the criterion for viability.
- Inbreeding depression should also be integrated in demographic risk assessment, and important effects of inbreeding depression may be concealed if only a time frame of 100 years or less is applied.

For the management of the Scandinavian wolf population, provided the criteria used in this study are accepted, the following recommendations can be given:

- A definite goal or ceiling for the population size should not be set lower than 400 individuals.
- At a population size of 50–150 animals, allowing hunting to increase annual mortality by two percentage points may be acceptable, but raising annual mortality by five percentage points is too much.
- To these numbers, which are based on a most likely scenario given current knowledge, is it wise to add some extra safety margin with respect to the uncertainty inherent in any modelling procedure and especially in models estimating probabilities in the future.

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