From: Grizzle, Betty
To: Bush, Jodi; Shoemaker, Justin
Subject: Example PVA
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Attachments: Nilsson 2013 PVA Scandinavia Lynx Wolv Bear.pdf

Not sure where things left off with Conor McGowan relative to providing assistance in developing scenarios, but I am attaching a 2013 PVA report for Scandinavian population of lynx, wolverine, and bear that could be useful for a similar effort for North America.

--

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Population viability analyses of the Scandinavian populations of bear *(Ursus arctos)*, lynx *(Lynx lynx)* and wolverine *(Gulo gulo)*

TORBJÖRN NILSSON

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Population viability analyses of the Scandinavian populations of bear (*Ursus arctos*), lynx (*Lynx lynx*) and wolverine (*Gulo gulo*)

by Torbjörn Nilsson

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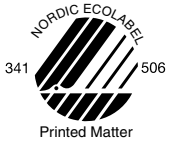

Förord

Regeringen gav den 31 maj 2012 Naturvårdsverket i uppdrag att redovisa sårbarhetsanalyser för varg, björn, järv och lodjur. I uppdraget anges följande: ”Naturvårdsverket ska presentera kvantitativa sårbarhetsanalyser som tydliggör minsta livskraftiga population (MVP, minimal viable population) för varg, björn, järv och lo baserade på IUCN:s kriterium E. Uppdraget ska redovisas till Regeringskansliet (Miljödepartementet) senast den 2 juli 2012 vad beträffar varg. För björn, järv och lo ska uppdraget redovisas senast den 15 januari 2013.”

De framtagna värdena för minsta livskraftiga population ska dels ingå i Naturvårdsverkets förvaltningsplaner för varg, björn, järv och lodjur, och dels användas som underlag för bedömning av bevarandestatus för arterna i 2013 års rapportering enligt artikel 17 i habitatdirektivet.

Med anledning av den senare delen av uppdraget gav Naturvårdsverket Torbjörn Nilsson (fil. dr. i zooekologi) i uppdrag att genomföra VORTEX-analyser för björn, järv och lodjur. Uppdraget omfattade även att ta fram andra beräkningar som kan underlätta Naturvårdsverkets fortsatta arbete med att besluta om referensvärden för gynnsam bevarandestatus för björn, järv och lo.

Författaren svarar själv för rapportens innehåll varför det inte kan åberopas som Naturvårdsverkets ståndpunkt. Koordinator och sakkunnig på Naturvårdsverket har varit Per Sjögren-Gulve. Framtagningen av rapporten har finansierats med stöd från Naturvårdsverkets miljöforskningsanslag.

Naturvårdsverket den 10 januari 2013

Marie Larsson
Projektledare

Contents – Innehåll

SAMMANFATTNING 6

SUMMARY 10

INTRODUCTION 11
Favourable Conservation Status and Favourable Reference Population 11
Population Viability Analysis and Minimum Viable Population 12
Dealing with uncertainty and variability 14
Partitioning MVPs between countries 16

MATERIAL AND METHODS 18
Population Viability Analysis software 18
Data collection 18
Input data 19
Modelling procedure 30

RESULTS 34
Long-term MVP and FRP 34
Short-term MVPs 38

DISCUSSION 48
Long-term MVPs 48
Short term MVPs and dealing with uncertainty 51
Conclusions 53

ACKNOWLEDGEMENTS 54

REFERENCES 55

ATTACHMENT 1: THE COMMISSION 60

ATTACHMENT 2: COMMENTS FROM SPECIALISTS AND EXTERNAL REVIEWERS 63
Prof. Henrik Andrén, Swedish University of Agricultural Sciences 63
Dr. Guillaume Chapron, Swedish University of Agricultural Sciences 64
Prof. Linda Laikre and Prof. Nils Ryman, Stockholm University 65
Dr. Philip S. Miller, IUCN/SSC Conservation Breeding Specialist Group 67
Prof. L. Scott Mills, University of Montana 68
Prof. Jon E. Swenson, Norwegian University of Life Sciences, and
Dr. Jonas Kindberg, Swedish Association for Hunting and Wildlife Management 69

Sammanfattning

I denna rapport redovisas sårbarhetsanalyser avseende björn, lodjur respektive järv. Analyserna baseras på data från de skandinaviska populationerna av dessa arter.

Sårbarhetsanalys är en sammanfattande benämning på olika analyser av populationers utdöenderisk och/eller av hur snabbt populationer förlorar genetisk variation. I den här studien har jag undersökt både utdöenderisk och förlust av genetisk variation.

Om man väljer ett kriterium, antingen beträffande utdöenderisk eller beträffande förlust av genetisk variation, för vad man anser vara en livskraftig population, så kan sårbarhetsanalyser användas för att uppskatta vilken populationsstorlek som är tillräcklig för att uppfylla det kriteriet. Den populationsstorleken brukar kallas MVP (minimum viable population – minsta livskraftiga population). Storleken på MVP beror i hög grad på vilket kriterium för livskraftig som valts.

Populationer förlorar hela tiden genetisk variation genom en process som kallas genetisk drift. Samtidigt skapas variation genom mutationer. I en isolerad population kommer på sikt mängden genetisk variation att bestämmas av balansen mellan dessa båda processer. Ju mindre populationen är, desto snabbare går driften, så en liten population kommer så småningom att förlora mycket av sin variation och därmed sin förmåga att anpassa sig till miljöförändringar.

Förlust av genetisk variation kan mätas antingen per tidsenhet (exempelvis per 100 år) eller per generationstid (hos det djur man studerar). När man anger förlusten per tidsenhet brukar man göra det med procent, men när man anger förlusten per generationstid brukar man använda ett mått som kallas genetiskt effektiv populationsstorlek och förkortas N_e. Ju mindre N_e är, desto snabbare går förlusten av variation i populationen. N_e påverkas av hur stor populationen är, men också av dess könskvot, hur förökningsframgången varierar mellan olika individer, hur mycket populationsstorleken varierar från år till år, med mera. Vanligen är en populations N_e betydligt mindre än dess faktiska storlek.

Huvudsyftet med de analyser som presenteras här är att de ska utgöra en del av underlaget för Sveriges rapportering 2013 till EU beträffande arternas bevarandestatus. För var och en av arterna ska Sverige bedöma om den har vad som i EU:s art- och habitatdirektiv kallas för gynnsam bevarandestatus (GBS). EU-kommissionen har rekommenderat att medlemsländerna för varje art ska ta fram något som kallas Favourable Reference Population (FRP), och att bedömningen av om arterna har GBS bland annat ska baseras på om deras populationer i landet är stora nog för att nå upp till FRP.

Av art- och habitatdirektivets definition av GBS, och av EU-kommissionens definition av FRP, framgår att båda dessa begrepp kräver att populationen ska vara långsiktigt livskraftig. I den vetenskapliga litteraturen inom ämnet naturvårdsbiologi (synonym bevarandebiologi, engelska conservation biology) finns en bred samsyn om att en population för att vara långsiktigt livskraftig behöver ha en genetiskt effektiv populationsstorlek, N_e, om minst 500. Jag har därför använt $N_e > 500$ som kriterium för långsiktig livskraft, och uppskattat hur stora populationer av de tre arterna som behövs för att uppfylla det kriteriet.

Om en art finns i flera närliggande länder, och om djurens in- och utvandring mellan populationerna i olika länder är tillräckligt omfattande, så behöver inte varje land ha en egen population som motsvarar en långsiktig MVP, utan långsiktig livskraft kan uppnås genom att en geografiskt och genetiskt sammanhängande population i flera länder sammantaget är tillräckligt stor. Därför har jag också analyserat hur FRP för Sverige skulle kunna sättas genom att fördela arternas långsiktiga MVP, antingen mellan Sverige och Finland, eller mellan Sverige, Finland och Norge.

Några exempel på kortsiktiga kriterier för populationers livskraft är < 10 % utdöenderisk på 100 år och < 5 % förlust av genetisk variation på 100 år. Sådana kortsiktiga MVP-kriterier kan till exempel vara till hjälp om man vill sätta etappmål för en populations utveckling. Jag har uppskattat MVP även utifrån dessa båda kriterier, samt ytterligare tre alternativa kortsiktiga MVP-kriterier.

Flera tidigare studier har visat att en måttlig osäkerhet i de ingångsvärden som används i sårbarhetsanalyser, och som beskriver olika aspekter av djurens ekologi och genetik, kan leda till stor osäkerhet i de utdöenderisker som uppskattas, och därmed även i de MVP-värden som bedöms motsvara en viss utdöenderisk. En viktig utmaning för naturvårdsbiologer är att göra denna osäkerhet tydlig för beslutsfattare och andra icke-experter som drar slutsatser av sårbarhetsanalysernas resultat. Jag har försökt tydliggöra denna osäkerhet genom att analysera flera olika scenarier med varierade värden på ingångsdata för varje art.

Jag har dels analyserat scenarier som använder de troligaste ingångsvärdena enligt nuvarande kunskap (som jag kallar Base scenarios), och dels scenarier med lite större säkerhetsmariginal i ingångsvärdena (som jag kallar Safe scenarios). Safe scenarios representerar inte värsta tänkbara fall, utan bygger på biologiskt och statistiskt rimliga ingångsvärden fast med en något lägre sannolikhet utifrån de fältdata som finns. Vidare så har både Base scenarios och Safe scenarios analyserats dels med och dels utan inslag av sällsynta katastrofhändelser (till exempel utbrott av nya, allvarliga sjukdomar) som plötsligt dödar mer än halva populationen. Dessutom har björn och lodjur analyserats i olika scenarier baserade på data från två respektive tre olika studieområden i Skandinavien.

För att komma fram till FRP är de långsiktiga MVP-värdena enligt Base scenarios mest relevanta. Dessa blev strax under 1 400 för järv, mellan 5 000 och 6 900 för björn utifrån data från de två studieområdena, och mellan 1 100 och 1 900 för lodjur utifrån data från de olika studieområdena:

Art	Data från studieområde	Långsiktig MVP
Järv		1 378
Björn	Södra	6 838
	Norra	5 003
Lodjur	Bergslagen	1 821
	Hedmark	1 311
	Sarek	1 179

Om man tar det högsta av dessa värden för respektive art, fördelar det antalet djur ungefärligen efter ytan av möjligt habitat för arten i Sverige, Finland respektive Norge, och sedan avrundar uppåt till närmaste hundratal, så ger det följande förslag på svenska FRP-värden:

Art	Föreslagen FRP
Järv	500
Björn	2 800
Lodjur	800

De kortsiktiga MVP-uppskattningarna varierade kraftigt, både mellan olika MVP-kriterier och mellan olika scenarier. Det kriterium som gav de lägsta MVP-uppskattningarna var kriteriet om < 10 % utdöenderisk på 100 år. MVP-värdena i de olika scenarierna enligt detta kriterium, samt det kortsiktiga genetiska MVP-kriteriet om < 5 % förlust av genetisk variation på 100 år, framgår av tabellen nedan.

Om man bland dessa MVP-uppskattningar väljer att för varje art fokusera på det högsta troliga (Base scenario) värdet med katastrofer inkluderade, så ger kriteriet om < 10 % utdöenderisk MVP-värden på 35 för björn, 210 för lodjur och 150 för järv. Om man på motsvarande sätt väljer MVP utifrån kriteriet om < 5 % förlust av genetisk variation så blir MVP-värdena 1 100 för björn, 700 för lodjur och 500 för järv.

Art	Scenario			< 10 % utdöenderisk på 100 år	< 5 % förlust av genetisk variation på 100 år
Lodjur	Bergslagen	Base scenario	Utan katastrofer	30	500
			Med katastrofer	40	500
		Safe scenario	Utan katastrofer	100	500
			Med katastrofer	150	600
	Hedmark	Base scenario	Utan katastrofer	50	280
			Med katastrofer	65	320
		Safe scenario	Utan katastrofer	700	1 000
			Med katastrofer	1 500	1 700
	Sarek	Base scenario	Utan katastrofer	140	500
			Med katastrofer	210	700
		Safe scenario	Utan katastrofer	(> 2 000)	(> 2 000)
			Med katastrofer	(> 2 000)	(> 2 000)

Art	Scenario			< 10 % utdöenderisk på 100 år	< 5 % förlust av genetisk variation på 100 år
Björn	Södra studie-området	Base scenario	Utan katastrofer	25	1 000
			Med katastrofer	35	1 100
		Safe scenario	Utan katastrofer	45	1 200
			Med katastrofer	65	1 300
	Norra studie-området	Base scenario	Utan katastrofer	25	900
			Med katastrofer	30	1 000
		Safe scenario	Utan katastrofer	40	1 000
			Med katastrofer	55	1 000
Järv		Base scenario	Utan katastrofer	90	370
			Med katastrofer	150	500
		Safe scenario	Utan katastrofer	350	700
			Med katastrofer	700	1 300

MVP-värden för lodjur, björn respektive järv, enligt de kortsiktiga MVP-kriterierna < 10 % utdöenderisk på 100 år respektive < 5 % förlust av genetisk variation på 100 år, uppskattade under olika scenarier för respektive art. (Ingångsvärdena för lodjur i Sarek Safe-scenarierna visade sig ha egenskaper som gör att dessa värden egentligen inte var meningsfulla för denna typ av beräkningar.)

Summary

Population viability analyses have been performed concerning populations of bear, lynx and wolverine. The main purpose of these analyses was to form part of the scientific basis for Sweden's reporting to the European Commission according to the Habitats Directive. Estimates of minimum viable population size (MVP) under the long-term viability criterion of a genetically effective population size (N_e) exceeding 500 were derived in two different ways: using empirical estimates of rates of loss of genetic variation, when such data were available, and otherwise using computer simulations with the program Vortex. The possibility of setting Favourable Reference Population (FRP) values by partitioning these long-term MVP estimates between neighbouring countries is discussed, and the following tentative FRP values for Sweden are suggested: 800 lynx, 2,800 bears, and 500 wolverines.

Population viability was also analyzed in relation to five different short-term viability criteria. Moderate uncertainty in the input parameters describing the ecology and genetics of a population may lead to very high uncertainty in the estimated extinction risk, and also in the resulting MVP values. A crucial challenge for conservation biologists is to make this uncertainty in MVP estimates clear and comprehensible to decision-makers and other non-experts. I developed a series of alternative scenarios for each population, with slightly different input parameters, and estimated separate MVP values for each scenario. Under the MVP criterion of < 10 % extinction risk in 100 years, the MVP estimates derived from different scenarios ranged between 25 and 65 for bear, between 90 and 700 for wolverine, and between 30 and 1,500 for lynx. If one chooses to focus on estimates from the most likely scenarios, but with catastrophes included, and then among scenarios representing different geographical areas chooses the highest estimate for each species, those MVP estimates were 35 for bear, 210 for lynx and 150 for wolverine, under the < 10 % extinction risk criterion. Compared to the other four short-term viability criteria, < 10 % extinction risk in 100 years was the criterion giving the lowest MVP estimates.

In most cases, short-term genetic MVP values were higher than the short-term extinction risk MVP values; hence, populations meeting the extinction risk criteria will often not fulfill the genetic MVP criteria. Under the short-term genetic MVP criterion of < 5 % loss of genetic variation in 100 years, the MVP estimates derived from different scenarios varied between 900 and 1,300 for bear, between 370 and 1,300 for wolverine, and between 280 and 1,700 for lynx. If one chooses to focus on estimates from the most likely scenarios, but with catastrophes included, and then among scenarios representing different geographical areas chooses the highest estimate for each species, those MVP estimates were 1,100 for bear, 700 for lynx and 500 for wolverine, under the criterion of < 5 % loss of genetic variation in 100 years.

The author alone is responsible for the contents of the report; hence, the views and conclusions presented should not be taken as or referred to as the views or position of the Swedish Environmental Protection Agency.

Introduction

In 2013, all member states of the European Union are obliged to report the conservation status of species listed in the annexes of the Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora (briefly: the Habitats Directive). The analyses presented in this report are primarily intended as part of the scientific basis for Sweden's reporting concerning the bear *(Ursus arctos)*, the lynx *(Lynx lynx)* and the wolverine *(Gulo gulo)*.

In May 2012, the Swedish Government commissioned the Swedish Environmental Protection Agency (Naturvårdsverket) to prepare Sweden's reporting under the Habitats Directive by presenting new population viability analyses for the four large carnivore species occurring in Sweden: wolf *(Canis lupus)*, bear, lynx and wolverine. An analysis for the wolf has been produced by Chapron et al. (2012), and I was given the task to produce analyses of the other three species.

The analyses presented here are also intended to form support for further development of the national management plans for the three species. National management plans for bear, lynx and wolverine have been established by Naturvårdsverket in 2012, but these may be complemented with management goals based on population viability analyses.

Favourable Conservation Status and Favourable Reference Population

In Article 1i of the Habitats Directive, the concept of Favourable Conservation Status (FCS) is defined as follows:

> *"conservation status of a species means the sum of the influences acting on the species concerned that may affect the long-term distribution and abundance of its populations within the territory referred to in Article 2;*
>
> *The conservation status will be taken as 'favourable' when:*
>
> *– population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats, and*
>
> *– the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and*
>
> *– there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis"*

As pointed out previously, e.g. by Laikre et al. (2009), this definition shows that

a) to have FCS, the species needs to be a "viable" component of its habitats; hence, the legal concept of favourable conservation status has a clear connection to the scientific concept of population viability: a population being viable is a necessary, but not sufficient, requisite for its conservation status to be favourable;
b) to have FCS, the species must maintain itself "on a long-term basis"; hence, short-term viability is not sufficient, but long-term viability is required;
c) FCS includes three components, each of which must be favourable for the conservation status of the species or population to be favourable: not only must the status of the population be favourable (i.e., long-term population viability), but also the distribution of the species and the distribution of its habitat must be favourable.

The analyses presented here primarily focus on long-term and short-term population viability. The components of FCS regarding the distributions of the species and their habitats will have to be addressed separately.

In a note from the European Commission (2005), member states are encouraged to base their assessments of species conservation status on reference values for populations and their distributions. The Commission defines Favourable Reference Population (FRP) as

> *"Population in a given biogeographical region considered the minimum necessary to ensure the long-term viability of the species"*

Hence, one requisite for a population to have FCS is that the population meets FRP, and the Commission's definition of FRP explicitly focuses on long-term population viability.

Population Viability Analysis and Minimum Viable Population

Population viability analysis (PVA) is a concept that summarizes various types of analyses of a population's extinction risk, its loss of genetic variation and/or its degree of inbreeding. If a criterion for population viability has been chosen, then a PVA can be used to estimate what population size is needed to meet that criterion, and this population size is then termed the minimum viable population (MVP). The value of MVP for any population is strongly dependent on which criterion is applied.

Small populations will in the long run lose much of their genetic variation, making them less able to adapt to a changing environment. Within the scientific community of conservation biologists, there is a broad unanimity that to be viable in the long term, a species or population must have what is called a genetically effective population size of 500 or more (e.g., Allendorf &

Ryman 2002, Laikre et al. 2009, Liberg et al. 2009, Frankham et al. 2010). Genetically effective population size, usually denoted N_e, is principally a measure of how quickly genetic changes take place in a population, e.g. how fast the population loses genetic variation. N_e is affected by the actual size of the population (often denoted N), but also by many other factors such as sex ratio, differences in lifetime reproductive success between individuals, and population fluctuations. In general, N is several times larger than N_e, so an effective population size of 500 may correspond to an actual population of a few thousand animals.

$N_e > 500$ is the most well-established criterion for long-term population viability. If the ratio N_e/N is estimated for a given population, then the actual population size required to meet the long-term viability criterion $N_e > 500$ can be calculated from that ratio, and that population size can be termed a long-term MVP for the population.

Some criteria that may be used for short-term population viability assessments are < 10 %, < 5 % or < 1 % extinction risk within 100 years, losing < 5 % of the genetic variation within 100 years, and upper confidence limit for loss of genetic variation in 100 years < 5 %. MVP estimates relating to any of these criteria may be termed short-term MVPs.

The extinction risk of a population is determined by the population's size, its demographic rates (reproduction and mortality), and by various kinds of stochasticity, i.e. random events, including environmental fluctuations between years and inbreeding effects. When MVP estimates are intended as a basis for setting management goals or assessing the conservation status of a population, they should as far as possible take into account all factors that may be important in affecting extinction risk (cf. Akcakaya & Sjögren-Gulve 2000, Ralls et al. 2002, O'Grady et al. 2006, Frankham 2010, IUCN 2011).

In the commission underlying the present study, the Swedish Government explicitly said that MVPs according to the criterion of < 10 % extinction risk within 100 years should be presented. An estimated extinction risk of 10 % or more within 100 years is one of five criteria qualifying a population for being classified to threat category Vulnerable (VU) in the system of threat classification (e.g., IUCN 2011) developed by the International Union for Conservation of Nature, IUCN. Linnell et al. (2008) suggested that < 10 % extinction risk in 100 years could be one of several criteria for FRP, and hence for FCS, but that suggestion was not motivated from the definition of FCS in the Habitats Directive, nor from the definition of FRP established by the European Commission (2005). However, as pointed out also by Jamieson & Allendorf (2012), short-term MVPs may be useful in setting short-term management goals.

In the present study, I estimate MVPs both according to the < 10 % extinction risk criterion as requested by the Government, according to four alternative short-term criteria for comparison, and according to the long-term viability criterion of genetically effective population size > 500.

Dealing with uncertainty and variability

Ludwig (1999) and Ellner et al. (2002) showed that moderate uncertainty about deterministic growth rate (or the factors that determine growth rate) leads to large uncertainty about extinction risk. This lead them to question the usefulness of making quantitative predictions from PVA, and also to question the relevance of such predictions for management decisions. On the other hand, if quantitative PVA were absent or ignored, important management decisions would instead have to be based on intuitive expert opinion. Although PVA modelling has its shortcomings, its methods are transparent, and both methods and input data may be subject to continuous improvement, which makes it strongly preferable over such expert assessment (cf. Burgman et al. 2011, Brook et al. 2011).

Realizing both the necessity of using PVA and the considerable uncertainty in its output, a crucial challenge for conservation biologists is to make this uncertainty and its implications clear and comprehensible to decision-makers and other non-experts. This cannot be done merely by providing standard errors or confidence limits for simulation outputs; such figures describe the variation in the output, provided that the mean values of the input parameters are correct, but they do not reflect the uncertainty caused by the fact that mean values of input parameters may differ from the true mean values of the population. Neither will the application of several different modelling approaches to the same input data achieve this task; parallel use of alternative modelling techniques is wise because it may reveal to what extent the output is dependent on the modelling procedure, but it does not illustrate the effects on PVA output of uncertainties in the estimates of the parameters describing the population. Similarly, sensitivity analysis is useful for describing for which input parameters a slight change of input values will give a relatively large change of output, but often do not combine effects of the known uncertainties of different input parameter values to illustrate how large the uncertainty of the estimated MVP actually is.

The approach used here is to model a series of alternative scenarios for the population of each species, where some scenarios represent what is most likely, given the available knowledge (here termed Base scenarios), while other scenarios make use of alternative – but biologically and statistically reasonable – input values to err on the safe side (here termed Safe scenarios). This is in line with the recommendation of e.g. Reed et al. (2002) to provide a range of predicted values rather than relying on a single point estimate of MVP.

Ideally, I think the result of analysing a Safe scenarios should have a statistically defined probability, e.g. 5 or 10 % probability that reality is that bad or worse. In modelling the Scandinavian wolf population, Nilsson (2004) came rather close to this ideal, by iteratively fitting the input values for extra safety scenarios so that they gave the population a 5 % probability of growing as fast as the population had actually done during a period of 20 years. However, that approach was possible because the population was very small,

had grown rapidly for an extended time period, and had been closely monitored during this population growth. This was an unusual combination of circumstances, and the situation is not comparable for the bear, lynx and wolverine populations modelled here.

Therefore, in the present study I developed the Safe scenarios in a way that should be more generally applicable than the approach described in the previous paragraph. For input parameters for which there were empirical estimates for the actual populations, I added or subtracted 0.48 times the standard error (SE) to the estimated mean. Adding 0.48 SE to an estimated mortality rate implies that there is 31.6 % probability that the true mortality rate in the population is that high or higher. Similarly, subtracting 0.48 SE from an estimated proportion of females producing young implies that there is 31.6 % probability that the true proportion in the population is that low or lower. If mortality rates and reproductive rates are measured independently of each other, it is not far-fetched to think that the probability of both these being that unfavourable or worse should be in the vicinity of $(31.6\ \%)^2$, which is 10 %. Such an MVP-value should not be neglected as being extremely unlikely, as may easily be done with a worst-possible-case MVP estimate.

For the effects of inbreeding depression on demographic rates, there are no empirical estimates available for the modelled wild populations, nor for any other free-living populations of the same species. To find out what would be reasonable input values, I gathered values from studies of other mammal populations under natural or semi-natural conditions, and in the Base scenarios I used the mean of the values calculated for those other populations. Since uncertainty is much larger when input values are based on data from other species in other environments, I used the mean plus 1 standard deviation (SD) of the values for those populations in the Safe scenarios.

An important factor affecting population viability, for which published studies provide little empirical basis for input data, is the effect of between-year environmental variation on the demographic rates, i.e., the environmental stochasticity. In the program Vortex (Lacy et al. 2005), which was used in the present study, environmental stochasticity is modelled by defining standard deviations (SD) for the annual probabilities of females reproducing and of animals dying. Most published estimates of demographic rates for the three modelled populations are based on pooling data from several years, and the standard errors (SE) presented contain both within-year and between-year-variation. Furthermore, since the number of individuals studied usually varies between years, SE-values for demographic rates based on the whole data set cannot readily be transformed into between-year SD-values, which otherwise might be taken as an upper limit for environmental stochasticity. Therefore, as suggested by Miller & Lacy (2005), I partially needed to base the values of environmental stochasticity on biologically reasonable guesses. Since the modelled populations all represent relatively large, long-lived, carnivorous mammals living in a boreal and alpine environment, I chose to use estimates of environmental stochasticity in one of the species as

the basis for guessing the amount of environmental stochasticity affecting the same demographic rate in the other two species[1].

A separate kind of uncertainty relates to the geographic representativity of the studied segments of the populations. Variation of demographic rates between different parts of a species' range is not in itself an uncertainty, but it leads to uncertainty about how to draw inferences from data collected in one or a few study areas. For the bear and lynx, which inhabit a larger part of Scandinavia and a wider climatic range, I developed separate Base- and Safe-scenarios for different study areas (two study areas for bear and three for lynx). The differences between these geographic scenarios will illustrate how MVP may vary depending on what the field data look like and in which part of the country the species will occur.

Finally, among the most uncertain aspects in PVA modelling is usually the risk of rare catastrophic events striking the modelled 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. To readers in Sweden, the most well-known example of such catastrophic die-offs in wildlife populations is probably the parvo-virus outbreak among seals in the late 1980s. A main obstacle to incorporating factors such as the emergence of new, severe diseases in PVA-modelling is that we can never know the absolute probability or frequency of such events. Nilsson (2004) suggested that this problem could be circumvented by defining MVP as a population with a certain chance of persistence, provided that a severe catastrophe occurs. In a similar vein, Chapron et al. (2012) estimated MVP values for wolves both without and with catastrophes of various magnitudes, and presented alternative MVP estimates based on either no catastrophe or inclusion of the most severe catastrophes simulated. Similarly, in this study I run each scenario (Base, Safe, and data from various geographic areas) both without any catastrophe and with a rather severe catastrophe occurring, and present the alternative resulting MVP values.

Partitioning MVPs between countries

If there were little gene flow between the Swedish populations and those of other countries, then the long-term MVPs estimated should be the FRP values for Sweden. However, the populations of all three species seem to be continuous across the Swedish-Norwegian border, and in northern Scandinavia these populations also have more or less contact with Finnish, and indirectly or potentially also with Karelian, populations. Provided that this gene flow is

[1] An alternative could have been to search the scientific literature for empirical estimates of environmental stochasticity for a wide range of different species, and then use estimates based on the mean and range among many other species, but after some initial literature search, I deemed that would be too time-consuming for this commissioned study.

sufficient, the FRP for Sweden can be set as a reasonable fraction of the long-term MVP, so to speak representing Sweden's part of the common responsibility of several countries for maintaining long-term viable populations.

This, however, requires several questions to be answered: When MVPs are used as a basis for FRP / FCS, between which countries can the MVPs then be divided? Should partitioning be proportional to the amount of potential habitat for the species within each country, or should it take into account present-day population sizes or current management goals in the countries? Must the countries agree on this partitioning before any of the states can set an FRP that presumes that other states will take their share of the responsibility? So far, neither the European Commission nor the Habitats Committee of the European Union has established any standards or recommendations regarding these issues.

In this report, I demonstrate how the long-term MVPs estimated might be partitioned in a reasonable way, either between the EU member states Sweden and Finland, or between Sweden, Finland and Norway, since Norway too has signed the Bern Convention on the Conservation of European Wildlife and Natural Habitats. Since FCS and FRP are goals aiming at ascertaining long-term viability of the species, my suggestion is that they may be set by partitioning long-term MVPs according to the amount of suitable habitat in the countries, without regarding momentary management goals or population sizes. Under the assumption that partitioning between all three countries is legitimate, I also propose tentative FRP values for bear, lynx and wolverine in Sweden.

Material and methods

Population Viability Analysis software

All simulations were performed with the program Vortex version 9.99c (Lacy et al. 2005), which is available at http://www.vortex9.org/vortex.html. The program is described in detail by Miller & Lacy (2005).

Data collection

Most input data for the simulations were gathered from scientific publications. Jens Persson, Jon Swenson and Henrik Andrén kindly provided advice on what estimate to use for some parameters regarding wolverine, bear and lynx, respectively. Jens Persson also helpfully provided updated figures for litter sizes and litter sex ratio in the wolverine.

Data were not modified to make the simulated populations mimic known population trajectories, due to the limited amount and quality of older monitoring data.

Study areas

In recent times, ecological field research on lynx has been performed in five study areas in Scandinavia. In the present analysis, I designed scenarios based on data from three of these areas: Bergslagen (around Grimsö, 59° N, 15° E; south-central Sweden, mainly in Örebro county), Hedmark (61° N, 11° E; south-eastern Norway, Hedmark county) and Sarek (around Kvikkjokk, 67° N, 17° E; northern Sweden, Norrbotten county). The study areas are described in more detail e.g. by Andrén et al. (2006) and Nilsen et al. (2012).

Long-term field research on bear is carried out primarily in two study areas in Scandinavia, with marked differences between the reproductive parameters of bears in these areas (Zedrosser et al. 2009), so I designed separate scenarios also for these. The southern study area was around 61° N, 18° E in south-central Sweden (Dalarna and Gävleborg counties) and south-eastern Norway, while the northern study area was around 67° N, 17° E in northern Sweden (Norrbotten county). The study areas are described in more detail e.g. by Swenson et al. (2001).

For the scenarios describing wolverine populations, I used pooled data from two study areas: Sarek (around Kvikkjokk, 67° N, 17° E; northern Sweden, Norrbotten county) and Troms (around Dividalen, 68° N, 19° E; northern Norway, Troms county). These study areas are described in more detail by Persson et al. (2006). Inference about the mating system in wolverines was drawn from genetic data from wolverines in the Sarek area and around the Snøhetta plateau (62° N, 10° E; southern Norway) (Hedmark et al. 2007).

Input data

Initial population

Since the present study primarily aims to support the setting of goals – either long-term or interim goals – for the modelled populations, the estimated MVPs should be based on the extinction risk and heterozygosity loss after a certain population size has been reached. Therefore, in all simulations (except part of the sensitivity analyses) I let the initial population size (N_0) be the same as the ceiling (K) above which the population was not allowed to grow[2]. If the simulations instead had been started with a smaller N_0, then the estimated extinction risks would have been elevated by the initial risk of dying out before reaching the population size K. I also let al. simulations start with the stable age distribution calculated by Vortex.

Mating system

The program Vortex allows a choice between five types of mating systems, called Monogamous; Long-term monogamy; Polygynous; Long-term polygyny; and Hermaphroditic. Among these, neither the monogamous nor the hermaphroditic systems are relevant to any of the three species under study, so the question is whether Polygynous or Long-term polygyny is most accurate. Long-term polygyny implies that a female will reproduce with the same male in successive years as long as the male is alive, while Polygynous means that reproducing pairs are randomly combined in every year of the simulations.

Although males and females live separately for most of the year in all three species, if territories are stable from year to year and males efficiently exclude other males from mating with females within their territory, the mating system may be best represented as Long-term polygyny. For wolverine, the genetically based data in Appendix 1 of Hedmark et al. (2007) reveal no certain case of multi-paternity among 36 litters, and among 10 females known to have produced young in more than one year, only 2 exchanged their partner between years. These results are compatible with a mating system where males efficiently monopolize the females within their territory and females take new males primarily when their former partner dies. Hence, I used the option of Long-term polygyny for wolverine.

For bear, on the other hand, Bellemain et al. (2006) found multiple paternity in 14.5 % and 28 % of litters with at least 2 and at least 3 cubs, respectively. This suggests that dominating males do not monopolize individual females very efficiently, but rather that there is a considerable degree of randomness in which male mates with which female in a given year, so I simulated the bear populations as being Polygynous without any long term pair bonding.

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[2] This is different from the situation when the aim of a PVA is to assess the actual extinction risk of a population at current circumstances. In such cases, the initial population should as much as possible resemble the current population, e.g. with regard to its size and age distribution.

For lynx, I found no conclusive empirical data to base this choice on. However, considering that females' home ranges show little overlap and that a male's home range often encompasses several females (Mattisson et al. 2011), and also that the high proportion of females breeding annually (Nilsen et al. 2012) implies that often several females within the same male territory will be in oestrous simultaneously, I judged it most likely that male monopolization of females is not very efficient in lynx. Hence, also the lynx populations were simulated as being Polygynous with partners randomly combined every year.

Demographic rates

Input values for reproduction and mortality are summarized in Table 1 for wolverine, Table 2 for bear, and Table 3 for lynx. Values for Base scenarios are the most likely estimates according to the empirical studies. Values for Safe scenarios were calculated from the empirical estimates and their standard errors, as described in the Introduction, section "Dealing with uncertainty".

For lynx and wolverine, values describing the annual proportion of females breeding were taken directly from the literature[3]. For bear, the proportion of females breeding was calculated from litter intervals, as suggested by Miller & Lacy (2005).

Litter size for wolverines was described as probabilities of having one, two or three cubs in a litter. For bear and lynx, litter size was described by its mean and standard deviation.

The mortality rates I used were those calculated excluding mortality from legal hunting[4]. While poaching is unpredictable and should be included in the stochastic process modelled, the amount of legal hunting is exactly known and determined by society, and will probably be ceased at some stage before a population goes extinct. Therefore I judged it preferable to use mortality rates excluding legal hunting mortality. This choice was also related to the aim of the study being to provide a basis for setting goals, rather than to assess the actual extinction risk faced by each population under current circumstances.

The mortality rates estimated for subadult wolverines by Persson et al. (2009) were lower than those estimated for adults, but the authors suggested that this may be an artefact caused by a high number of censored individuals in the subadult age class. Jens Persson (pers. comm.) judged it highly unlikely that subadults, most of which have recently left their mother and wandered off to search for a vacant area to settle in, would have lower mortality than the adults. Therefore, I applied the mortality rates estimated for adults also to the subadults.

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[3] The proportion of female wolverines breeding given in Table 1 of Persson et al. (2006) was based on counting during the denning season in early spring, while litter size frequencies and juvenile survival were measured among litters still present in May-June. To combine these values without exaggerating the recruitment rate, I reduced the proportion of breeding females to account for that 30 % of the litters found in early spring were lost before the young were counted. Furthermore, using information given in the text of Persson et al. (2006), I estimated different proportions breeding among 3-years-old and older females.

[4] An exception from this is that the mortality rates used for juvenile wolverines include a small fraction of mortality from lethal control, because no estimate of mortality excluding that fraction was found.

Given the annual proportion of females breeding and the sex ratio among adults in the population, the annual proportion of males breeding can be estimated from the mean number of females mated per successful male, or vice versa. However, both the proportion of males breeding and the number of mates per successful male are rarely known for wild animals. Vortex uses the life table generated from other demographic parameters to estimate the adult sex ratio, and then calculates the number of mates the average successful male must have to achieve the estimated proportion breeding among females, if no males are excluded from the pool of potential breeders. As an alternative, for lynx and wolverine, I calculated the ratios of male to female home range sizes and multiplied this ratio by the proportion of females breeding; this might give a fair approximation for the number of mates per male. For Safe scenarios, I took the ratio of male home range size plus 0.48 times its standard error, divided by female home range size minus 0.48 times its standard error. In cases when this approximation gave a higher number of mates per male than the minimum value suggested by Vortex, then I used the value based on home range sizes and let Vortex calculate the corresponding proportion of males in the breeding pool.

For the bear populations, however, I adopted a different approach. The proportion of males breeding has an effect on the rate of loss of genetic variation, and Tallmon et al. (2004) have provided an empirical estimate of the rate of heterozygosity loss in the southern bear population. Therefore, I ran a series of simulations with demographic parameters for the southern bear population, initial population size and ceiling equaling 700 individuals, and 2,500 simulation runs for each tested value of proportion of males breeding. In this way, I iteratively found a proportion of males breeding which gave the rate of heterozygosity loss observed in the real population. Then I used the same proportion of males breeding also in the simulations of the northern bear population.

Alternatively, I could have used the annual proportions of male bears breeding estimated by Zedrosser et al. (2007). However, within the Scandinavian bear population, most female bears are concentrated in four core areas, while the distribution of male bears is several times larger (Swenson et al. 1998) because many male bears disperse out of the core areas to reside in areas where few mating opportunities are given. Therefore, since two of the female core areas also are the study areas for which proportions of males breeding were estimated by Zedrosser et al. (2007), I suspected those estimates were unrepresentative of the total bear population.

Life table analysis

Life tables for both sexes were set up for the Base and Safe scenarios of each species-area combination. The deterministically expected annual growth rate, λ, was calculated from the female life table for each scenario (Tables 1, 2 and 3). Generation time for each scenario (Table 6) was calculated as the mean between the values calculated for each sex.

For all that is known, the lynx and bear populations have grown well during the second half of the 20th century, and the wolverine population has developed positively in the last decade. Based on monitoring results, the annual growth rate of the bear population in Sweden 1987–2007 has been estimated at 4.5 %, in spite of hunting, and the number of documented wolverine litters has increased by 3.8 % per year in Sweden and by 5.3 % per year in Norway between 1996 and 2010 (Liljelund 2011). Outside the reindeer husbandry area, the estimated number of lynx family groups (females accompanied by young) in Sweden increased from 111 groups in 1994 to 208 groups in 2000 (Liberg & Andrén 2006), i.e. by 11 % per year. Hence these animals are capable of considerable population growth. Considering that there is uncertainty also in the growth rates estimated from monitoring results, the growth rates calculated from the Base scenario parameter values here are compatible with the population growth known to have occurred in the modelled populations. The parameter values used in the Safe scenarios make such population growth less likely, as intended, but not impossible (with one exception, the lynx Sarek Safe scenario).

The life table for lynx based on the demographic data of the Sarek Safe scenario revealed that these demographic rates would give the population a negative deterministic growth rate ($\lambda < 1$), which means that if such a demography were constant over an extended time period, the population would shrink to extinction even without any kind of stochasticity (random events and processes). If that were true, the population could not be considered viable irrespective of its size, and running stochastic simulations of a population with such a demography is usually considered meaningless. I performed a few analyses on this scenario anyway, for the sake of consistency and for illustrative purposes, but the reader should keep in mind that this scenario is in a sense extreme, although the demographic rates do not differ very strikingly from those of the Sarek Base scenario.

Table 1. Demographic input data used in simulations of wolverine populations, and deterministically expected growth rate calculated from life table. How SD_{EV} values were estimated is described in the text (section "Environmental stochasticity").

	Base scenarios	Safe scenarios	Values taken from or calculated from data in
Reproduction			
Age of 1st offspring for females	3	3	Persson et al. 2006
Age of 1st offspring for males	3	3	Persson et al. 2006
Maximum age of reproduction	13	13	Jens Persson, pers. comm.
Maximum # of broods per year	1	1	Persson et al. 2006
Maximum litter size	3	3	Persson et al. 2006
Sex ratio at birth, % males	45	45	Jens Persson, pers. comm.
% breeding among 3 years old females	21	14.5	Persson et al. 2006
SD_{EV} in % breeding among 3 years old females	8.8	8.7	
% breeding among older females	39.2	36.6	Persson et al. 2006

Table 1 continued.

	Base scenarios	Safe scenarios	Values taken from or calculated from data in
SD_{EV} in % breeding among older females	16.5	22	
Litter size distribution:			Jens Persson, pers. comm.
1 offspring	40%	40%	
2 offspring	54%	54%	
3 offspring	6%	6%	
Mean # of mates / breeding male	1.4	1.5	estimated from home range sizes in Mattisson et al. 2011
Mortality rates (%)			
Female mortality from age 0 to 1	21	23.6	Persson et al. 2009
SD_{EV} in 0 to 1 female mortality	15.3	17.3	
Female mortality from age 1 to 2	11	12.1	Jens Persson, pers. comm.
SD_{EV} in 1 to 2 female mortality	4.8	5.3	
Female mortality from age 2 to 3	11	12.1	Persson et al. 2009
SD_{EV} in 2 to 3 female mortality	4.8	5.3	
Female mortality after age 3	11	12.1	Persson et al. 2009
SD_{EV} in female mortality after age 3	1	1.1	
Male mortality from age 0 to 1	12	14.2	Persson et al. 2009
SD_{EV} in 0 to 1 male mortality	8.8	10.4	
Male mortality from age 1 to 2	16	18.1	Jens Persson, pers. comm.
SD_{EV} in 1 to 2 male mortality	7	8	
Male mortality from age 2 to 3	16	18.1	Persson et al. 2009
SD_{EV} in 2 to 3 male mortality	7	8	
Male mortality after age 3	16	18.1	Persson et al. 2009
SD_{EV} in Male mortality after 3	1.4	1.6	
Expected growth rate (λ)	1.046	1.016	

Table 2. Demographic input data used in simulations of bear populations, and deterministically expected growth rate calculated from life table. How SD_{EV} values were estimated is described in the text (section "Environmental stochasticity"); note that for rates > 0.5, the CV_{EV} values used were multiplied by (1 – the rate).

	Southern area, Base scenarios	Southern area, Safe scenarios	Northern area, Base scenarios	Northern area, Safe scenarios	Values taken from or calculated from data in
Reproduction					
Age of 1st offspring for females	4	4	5	5	Zedrosser et al. 2009, table 1 & 3
Age of 1st offspring for males	3	3	3	3	Zedrosser et al. 2007
Maximum age of reproduction	27	27	27	27	Zedrosser et al. 2007
Max litter size	4	4	4	4	Zedrosser et al. 2009
Mean litter size	2.289	2.289	2.425	2.425	Zedrosser et al. 2009, table 2
SD litter size	0.884	0.884	0.871	0.871	Zedrosser et al. 2009, table 2
Sex ratio at birth, % males	50	50	50	50	Jon Swenson, pers. comm.

Table 2 continued.

	Southern area, Base scenarios	Southern area, Safe scenarios	Northern area, Base scenarios	Northern area, Safe scenarios	Values taken from or calculated from data in
% adult females breeding	57.5	55.2	41	40	Zedrosser et al. 2009, table 2
SD_{EV} in # breeding females	17.8	33.1	17.2	24	
% of males breeding a certain year	3.3	3.3	3.3	3.3	iteratively sought to fit the Ne/N ratio measured for the southern population (Tallmon et al. 2004)
Mortality rates (%)					
Female mortality from age 0 to 1	35	37	4	5.1	Swenson et al. 2001
SD_{EV} in 0 to 1 female mortality	27.6	29.2	3.2	4	
Female mortality from age 1 to 2	17.7	19.3	17.7	19.3	Bischof et al. 2009, table 2
SD_{EV} in 1 to 2 female mortality	13.5	14.7	13.5	14.7	
Female mortality from age 2 to 3	6	6.8	6	6.8	Bischof et al. 2009, table 2
SD_{EV} in 2 to 3 female mortality	2.2	2.4	2.2	2.4	
Female mortality from age 3 to 4	6	6.8	6	6.8	Bischof et al. 2009, table 2
SD_{EV} in 3 to 4 female mortality	1.1	1.2	1.1	1.2	
Female mortality from age 4 to 5	6	6.8	6	6.8	Bischof et al. 2009, table 2
SD_{EV} in 4 to 5 female mortality	0.54	0.61	0.54	0.61	
Female annual mortality after age 5	6.6	7.2	6.6	7.2	Bischof et al. 2009, table 2
SD_{EV} in female mortality after age 5	0.59	0.65	0.59	0.65	
Male mortality from age 0 to 1	35	37	4	5.1	Swenson et al. 2001
SD_{EV} in 0 to 1 male mortality	27.6	29.2	3.2	4	
Male mortality from age 1 to 2	8.6	10.2	8.6	10.2	Bischof et al. 2009, table 2
SD_{EV} in 1 to 2 male mortality	6.5	7.8	6.5	7.8	
Male mortality from age 2 to 3	18.3	19.6	18.3	19.6	Bischof et al. 2009, table 2
SD_{EV} in 2 to 3 male mortality	6.6	7.1	6.6	7.1	
Male mortality from age 3 to 4	18.3	19.6	18.3	19.6	Bischof et al. 2009, table 2
SD_{EV} in 3 to 4 male mortality	3.3	3.5	3.3	3.5	
Male mortality from age 4 to 5	18.3	19.6	18.3	19.6	Bischof et al. 2009, table 2
SD_{EV} in 4 to 5 male mortality	1.6	1.8	1.6	1.8	
Male annual mortality after age 5	10.7	11.6	10.7	11.6	Bischof et al. 2009, table 2
SD_{EV} in male mortality after age 5	0.96	1	0.96	1	
Expected growth rate (λ)	1.142	1.123	1.131	1.118	

Table 3. Demographic input data used in simulations of lynx populations, and deterministically expected growth rate calculated from life table. How SD_{EV} values were estimated is described in the text (section "Environmental stochasticity"); note that for rates > 0.5, the CV_{EV} values used were multiplied by (1 – the rate). (The table continues on next page.)

	Bergslagen, Base scenarios	Bergslagen, Safe scenarios	Hedmark, Base scenarios	Values taken from or calculated from data in
Reproduction				
Age of 1st offspring for females	2	2	2	Nilsen et al. 2012
Age of 1st offspring for males	2	2	2	
Maximum age of reproduction	18	18	18	Henrik Andrén, pers. comm
Max litter size	4	4	4	
Sex ratio at birth, % males	50	50	50	
% breeding among 2 years old females	74	69.1	40	Nilsen et al. 2012, table 3
SD_{EV} in % breeding among 2 years old females	10.9	18.5	16.8	
% breeding among older females	90	87.6	69	Nilsen et al. 2012, table 3
SD_{EV} in % breeding among older females	4.2	7.4	13	
Mean litter size	2.36	2.36	2.1	Nilsen et al. 2012, table 3
SD litter size	0.94	0.94	0.95	Nilsen et al. 2012, table 3
# of females mated per reproducing male	2.1	2.1	1.3	min values calculated by Vortex
Mortality rates (%)				
Female mortality from age 0 to 1	48.9	53.7	40.7	Andrén et al. 2006, table 2
SD_{EV} in 0 to 1 female mortality	35.7	33.8	29.7	
Female mortality from age 1 to 2	23.4	29.7	57.1	Andrén et al. 2006, table 2
SD_{EV} in 1 to 2 female mortality	10.3	13.1	18.9	
Female mortality after age 2	11	14.8	5.6	Andrén et al. 2006, table 2
SD_{EV} in female mortality after age 2	1	1.3	0.5	
Male mortality from age 0 to 1	71.8	76.1	63.5	Andrén et al. 2006, table 2
SD_{EV} in 0 to 1 male mortality	20.6	17.4	26.6	
Male mortality from age 1 to 2	42.9	53.3	27.1	Andrén et al. 2006, table 2
SD_{EV} in 1 to 2 male mortality	18.9	20.5	11.9	
Male mortality after age 2	6	9.1	0	Andrén et al. 2006, table 2
SD_{EV} in male mortality after age 2	0.54	0.82	0	
Expected growth rate (λ)	1.214	1.131	1.089	

Table 3 continued.

	Hedmark, Safe scenarios	Sarek, Base scenarios	Sarek, Safe scenarios	Values taken from or calculated from data in
Reproduction				
Age of 1st offspring for females	2	2	2	Nilsen et al. 2012
Age of 1st offspring for males	2	2	2	
Maximum age of reproduction	18	18	18	Henrik Andrén pers. comm
Max litter size	4	4	4	
Sex ratio at birth, % males	50	50	50	
% breeding among 2 years old females	31.2	22	16.2	Nilsen et al. 2012, table 3
SD_{EV} in % breeding among 2 years old females	18.7	9.2	9.7	
% breeding among older females	65.6	76	72.9	Nilsen et al. 2012, table 3
SD_{EV} in % breeding among older females	20.6	10.1	16.3	
Mean litter size	2.1	2.08	2.08	Nilsen et al. 2012, table 3
SD litter size	0.95	1.06	1.06	Nilsen et al. 2012, table 3
# of females mated per reproducing male	1.2	1.4	1.5	In Hedmark Safe estimated from home range sizes in Linnell et al. 2001, in Sarek min values calculated by Vortex
Mortality rates (%)				
Female mortality from age 0 to 1	46.7	59.3	62.5	Andrén et al. 2006, table 2
SD_{EV} in 0 to 1 female mortality	34.1	29.7	27.4	
Female mortality from age 1 to 2	66.1	10	14.3	Andrén et al. 2006, table 2
SD_{EV} in 1 to 2 female mortality	14.9	4.4	6.3	
Female mortality after age 2	8.7	17	20.5	Andrén et al. 2006, table 2
SD_{EV} in female mortality after age 2	0.78	1.5	1.8	
Male mortality from age 0 to 1	68.2	53.7	57.3	Andrén et al. 2006, table 2
SD_{EV} in 0 to 1 male mortality	23.2	33.8	31.2	
Male mortality from age 1 to 2	35.3	18.3	25.2	Andrén et al. 2006, table 2
SD_{EV} in 1 to 2 male mortality	15.5	8.1	11.1	
Male mortality after age 2	0	20.9	25.2	Andrén et al. 2006, table 2
SD_{EV} in male mortality after age 2	0	1.9	2.3	
Expected growth rate (λ)	1.007	1.057	0.996	

Environmental stochasticity

When a series of annual estimates of a demographic rate are available, and also for each year the n-value telling how many animals that year's estimate was based on, an estimate of environmental stochasticity can be calculated as suggested by Miller & Lacy (2005). The annual n-values are used to estimate the binomial sampling variance for each year and the mean of these (BSV), so that the total between-year variation can be reduced to account for such sampling variation. The total between-year variation is measured as the standard deviation SD_{tot} among the annual rate estimates, and the component of variation caused by environmental fluctuations is estimated to be SD_{EV} = square root of ($SD_{tot}^2 - BSV^2$). In this way, using data on bear cub survival (Swenson et al. 2001, table 1) in the southern study area between 1991 and 1998, I estimated mean annual cub mortality rate to 40.9 %, SD_{tot} to 32 %, SD_{EV} to 30 % and the environmentally caused coefficient of variation (SD divided by the mean) CV_{EV} to 73 %. In the years 1987–1990, only 2–5 cubs per year were studied, and in the northern study area only three occurrences of mortality were recorded during the whole study period, giving very little basis for analyzing fluctuations in mortality rate. Hence, I applied CV_{EV} = 73 % to estimate the standard deviation of cub/pup mortality also in the northern bear population, and also in lynx and wolverine.

A data series of annual proportions of females reproducing among wolverines was presented by Persson et al. (2006, table 1). Following the authors of the paper, I based estimates on the years 1997–2002. However, in this case, the same females were studied over several years and contributed to the annual estimates of subsequent years, suggesting that BSV makes up a larger part of between-year variation than accounted for by the equation SD_{EV} = square root of ($SD_{tot}^2 - BSV^2$). Therefore, for the Base scenarios, I instead estimated environmental stochasticity as $SD_{EV} = (SD_{tot} - BSV)$. For wolverine, this gave SD_{EV} = 24 % and CV_{EV} = 42 %, so I applied this CV_{EV} to proportion of females reproducing also in the bear and lynx simulations; for lynx, however, since the proportion reproducing was larger than 50%, I instead multiplied this CV_{EV} by the proportion not reproducing. For the Safe scenarios, I estimated CV_{EV} from the wolverine data by the same equation as for bear cub mortality (previous paragraph), which gave SD_{EV} = 35 % and CV_{EV} = 60 %, and then applied this CV_{EV} also to the Safe scenarios for bear and lynx, analogously to how it was done in the Base scenarios.

Sæther et al. (1998) estimated age-specific bear survival rates and their environmental stochasticity under a model where φ and ψ described the expectation and standard deviation, respectively, of annual survival. $\beta = e^{\varphi} / (1 + e^{\varphi})$ is the survival rate when ψ equals zero. Defining $\beta' = e^{\varphi-\psi} / (1 + e^{\varphi-\psi})$ and using the β- and ψ-values for the southern study area given by Sæther et al. (1998, table 1), I estimated CV_{EV} for mortality at different ages as $CV_{EV} = (\beta'-\beta) / (1-\beta)$. This gave CV_{EV} = 76 % for mortality between age 1 and 2, CV_{EV} = 36 % for mortality between age 2 and 3, CV_{EV} = 18 % for mortality between age 3 and 4, and CV_{EV} = 9 % for mortality of bears from age 4

and older. The ψ-values for the northern study area presented by Sæther et al. (1998) suggest lower environmental variation, but are based on fewer occurrencies of mortality, so I used the CV estimates just mentioned for both populations. For subadult lynx and wolverine, I used CV_{EV} = 44 %, i.e. the mean of the values calculated for bear between ages 1–4, and for adult lynx and wolverine mortality I used 9 % as estimated for bear. When a mortality rate was > 50 %, I multiplied the CV_{EV} by the survival rate instead.

Assuming that environmental variation in reproduction is strongly affected by food abundance, while environmental variation in survival (except for cubs/pups) is mainly determined by other environmental factors, in all simulations I let reproduction and mortality vary independently of each other.

Inbreeding depression

The strength of inbreeding effects on the demography of a population, i.e, the inbreeding depression, depends on the genetic load, i.e., the amount of deleterious recessive alleles present in the population. This is quantified in terms of lethal equivalents (LE). There were no empirical estimates of LE in the populations I modelled. In the absence of population-specific data on genetic load, Miller & Lacy (2005) suggest using the value of 3.14 LE, which was the mean value found in a seminal review paper by Ralls et al. (1988) on inbreeding depression in captive mammal populations. However, later research has shown that inbreeding depression is strongly dependent on the environment the animals experience, and specifically that inbreeding depression often (though not always) is stronger in free-living populations than in captivity (Jiménez et al. 1994, Crnokrak & Roff 1999, Meagher et al. 2000, Keller & Waller 2002, Armbruster & Reed 2005, O'Grady et al. 2006, Halverson et al. 2006, Mills 2012).

Therefore, I searched for research papers providing empirical estimates of LE in wild mammal populations, or data enabling me to calculate the LE. Most studies reporting inbreeding depression in wild populations infer this from correlations between fitness characters and heterozygosity (not inbreeding coefficient)[5]. Such data may be indicative of inbreeding depression, but the correlation between heterozygosity and inbreeding coefficient is sometimes low (cf. Pemberton 2004, and references therein), making it questionable to estimate the genetic load in a population without knowledge of inbreeding coefficients. However, I found six studies of different mammal populations where fitness aspects were correlated with inbreeding coefficients so that LE could be calculated (Table 4). When separate estimates of LE were given for males and females, I used those of the females, since in polygynous species it is primarily the females that limit the population growth. The mean value of the six studies then became 6.5, with a standard deviation of 4.01, so

[5] Also many of the studies quoted in the review papers by Crnokrak & Roff (1999) and Keller & Waller (2002) lack information about inbreeding coefficients.

Table 4. Empirical studies providing estimates of lethal equivalents (LE) in wild mammal populations.

Animal			Parameter affected	LE per diploid genome (=2B)	Source
Common name	Scientific name	Order			
Muskox	Ovibos moschatus	Artiodactyla	Longevity + annual female reproductive success	9.77	calculated from data in Laikre et al. 1997
Mexican wolf	Canis lupus baileyi	Carnivora	Litter size	5.19	Fredrickson et al. 2007
Scandinavian wolf	Canis lupus lupus	Carnivora	Litter size measured in 1st winter after birth	6.04	Liberg et al. 2005
Golden lion tamarin	Leontopithecus rosalia	Primates	Survival to age 7 days	3.40	Dietz et al. 2000
House mouse	Mus domesticus	Rodentia	Number of weaned offspringg per female	1.99	calculated from data in Meagher et al. 2000
White-footed mouse	Peromyscus leucopus	Rodentia	Survival	12.64	Jiménez et al. 1994
Mean ± SD				6.50	± 4.01

I used LE = 6.5 in the Base scenarios and LE = 10.51 (mean + 1 SD) in the Safe scenarios.[6]

Catastrophic events

Among 96 reported instances of catastrophic die-offs among large and middle-sized mammals compiled by Young (1994), he found a relative overabundance of die-offs reducing the population by 70–90 %, and an underabundance of die-offs greater than 90 %. In the six reports that concerned large carnivores (African wild dog *Lycaon pictus*, coyote *Canis latrans*, and lion *Panthera leo*), reductions ranged from 50 to 87 %. To simulate catastrophes within this range of severity, I let survival be reduced by half in one year, and all reproduction failed in that year. The annual probability of such a catastrophe was set at 1 %, so on average there was one catastrophe per simulation run of 100 years.

Density dependence

By default, Vortex applies a ceiling model of density dependence, letting all animals exceeding the 'carrying capacity' die. To some extent, this is similar to a situation where the human society decides to keep a population below

[6] An alternative could have been to follow the suggestion of O'Grady et al. (2006) to use a default value of 12 LE, which they estimated by comparing twelve studies on different species. However, only three of those studies concerned mammals, while nine were studies on bird populations.

a certain size[7]. Vortex also allows modelling density dependence in demographic rates below the ceiling in various ways, if there are data suggesting how this should be done. However, considering that there are large areas of unoccupied potential habitat for the three species in Sweden, I do not think the size of the total Swedish (or Scandinavian or Fennoscandian) population is a good measure of the intraspecific competition experienced by the animals. Furthermore, food availability for each of the three species may be more affected by the density of other species (carnivores and humans) than by the population density of the own species, implying that a multi-species model might be required to account for food competition in a meaningful way. And regarding lynx and bear, their population size is regulated (lynx) or population growth reduced (bear) by annual legal hunting. Hence, I did not attempt modelling any kind of density dependence except for the ceiling on population size.

Modelling procedure

All in all, MVP values were estimated under 24 different scenarios. For lynx, scenarios based on data from three study areas were modelled separately, for bear scenarios based on data from two study areas, while for wolverine data from two different areas were pooled and modelled in the same scenarios. For each of these six species-area combinations, I modelled two Base (most likely) scenarios: with and without catastrophes, and two Safe (extra safety margin) scenarios: with and without catastrophes. All models were run without immigration of unrelated animals from external populations.

Long-term MVPs

For the bear population in the southern study area, Tallmon et al. (2004) published empirically based estimates of effective population size, N_e, and its ratio to actual population size, N_e/N. They measured the amount of change in allele frequencies over a period of 14–15 years, and assuming that this period corresponded to one, two or three generation times, they estimated N_e at 44.8, 64.4 or 88.3, respectively. I set up a life table, using the demographic values for the Base scenario of this population, and from this I calculated 15 years to be 1.367 generation times. Then I logarithmized the N_e values calculated for one and two generation times, respectively, and interpolated between these to find what would correspond to 1.367 generation times. Following Tallmon et al. (2004), I divided this number by an estimated population size of 700 to produce an estimate of N_e/N. Then I calculated a Base (most likely) value for the long-term MVP by dividing 500 by that N_e/N ratio.

The lower 95 % confidence intervals presented by Tallmon et al. (2004) were N_e = 30.9 or 41.4 for one or two generation times, respectively.

[7] A difference, though, is that Vortex holds the population below the ceiling ('carrying capacity') by randomly culling animals across age-sex classes in accordance with their relative abundance, while human hunting usually spares the juveniles and females accompanied by young.

These values are the most likely estimate minus 1.96 standard errors (SE), and they correspond to a probability of 2.5 % that the true N_e is that low or lower. To produce a Safe value for long-term MVP which is not so extreme, I calculated N_e values representing the most likely estimate minus 1.28 SE (corresponding to a 10 % probability that the true N_e is that low or lower): N_e = 35.7 and N_e = 49.4 for one or two generation times, respectively. Then I derived estimates of N_e/N and of long-term MVP in the same way as for the Base value.

For all other populations, for which there were no empirical estimates of N_e/N, I used Vortex to estimate this ratio. For each species-area combination I first ran the Base and Safe scenarios without catastrophes for 2,500 iterations and 100 years, with $N_0 = K$ = 1,000 animals, to estimate the loss of expected heterozygosity. This measure of genetic diversity is reduced by the fraction $1/(2\ N_e)$ for each generation. Since Vortex produces erroneous estimates of generation times when functions[8] are used to describe some demographic input parameters (Miller & Lacy 2005), I set up life tables using the input values of each scenario and calculated generation time from these. As an approximation for mean population size during the simulations, I used the mean size of extant populations at year 100. Hence, combining the loss of expected heterozygosity and the mean population size according to the simulation results with the generation times calculated from the life tables, I calculated the ratio N_e/N for each species-area combination, and hence the long-term MVP according to the criterion $N_e > 500$.

Partitioning long-term MVPs between countries

From the highest Base scenario estimate of long-term MVP for each species, I calculated tentative FRP values for the three species, under the assumption that either Sweden, Finland and Norway, or only Sweden and Finland, could share the responsibility for maintaining long-term viable populations of them.

For lynx and bear, which can inhabit any climatic zone within these countries, I partitioned the long-term MVP proportionally to the whole land area of the countries, excluding some large islands (Gotland, Åland and Svalbard) which presumably are too isolated to be colonized naturally by large carnivores from the mainland.

For wolverine, which is primarily alpine but also may inhabit the northern boreal forest zone, a large part of southern Sweden and minor parts of Finland and Norway are unsuitable habitat. Therefore, I first excluded those Swedish counties which are predominantly situated within the nemoral or the boreo-nemoral (hemi-boreal) zone, and counted only the area of the seven counties which have most of their area in the northern boreal zone. Then I partitioned the long-term MVP for wolverine proportionally to the area of alpine mountainous habitat (according to Påhlsson 1984) combined with three alternative percentages (10 %, 50 %, 90 %) of the remaining areas of the countries.

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[8] I used functions to model age dependent probability of reproduction in female lynx and wolverines, and to model age dependent mortality rates in 3- and 4-year old bears.

Short-term MVPs

First, for all scenarios except those already simulated for calculating long-term MVPs, I ran simulations for 1,000 iterations with $N_0 = K$ = 1,000, 300, 100 and 30 animals, respectively. Thereafter, for each scenario, I ran additional simulations with various $N_0 = K$ values to find population sizes meeting the MVP criterion of < 10 % extinction risk in 100 years, and also some alternative short-term MVP criteria: < 5 % extinction risk within 100 years; < 1 % extinction risk within 100 years; losing < 5 % of genetic variation within 100 years; and upper confidence interval of genetic variation-loss in 100 years < 5 % (i.e., mean amount of retained heterozygosity among the simulation replicates minus 1.96 standard deviations > 95 %).

When seeking MVP values below 100, I used multiples of 5 as $N_0 = K$, and among these values, the lowest number that met the criterion was considered the MVP. For MVP values between 100 and 400, I used multiples of 10 in the same way, and for MVP values between 400 and 1,000, multiples of 100.

MVP values between 1,000 and 2,000 were estimated by running a simulation with $N_0 = K$ = 2,000, logarithmizing output values from this and from the corresponding previously done simulations with $N_0 = K$ = 1,000, then interpolating between these to find a population size closely matching the criterion[9], and then round that value upwards to the nearest multiple of 100. Due to time limits for this work, short-term MVP values larger than 2,000 were not estimated.

Sensitivity analyses

To assess the relative importance of various uncertainties in the input data, I ran a series of separate analyses where different input parameters or sets of parameters were modified from Base scenarios with catastrophes. The extinction probability, heterozygosity loss and observed growth rate[10] resulting from each such modification was compared to that resulting from the Base scenario with catastrophes, and the difference between the modified scenario and the Base scenario was calculated as a measure of the importance of uncertainty in the modified parameter. This was done for each combination of species and study area, i.e. with three scenarios for lynx, two for bear, and one for wolverine.

For each species-area combination analyzed, I separately modified reproduction, juvenile and subadult mortality rates, adult mortality rates or lethal equivalents to the values they had in the corresponding Safe scenario, i.e. proportion of females breeding was lowered by 0.48 SE, mortality rates were raised by 0.48 SE, and lethal equivalents were raised by 62 % (from 6.50 LE to 10.51 LE). To modify other parameters with large uncertainty in a way

[9] The relationship between extinction risk or heterozygosity loss and population size is often curved, not linear; therefore, I think interpolating between logarithmized values gives a better approximation than interpolating between the original values.

[10] Vortex reports the mean exponential growth rate, prior to truncation at the population ceiling, observed during the simulations.

comparable to how the lethal equivalents were modified, I also tried increasing all environmental stochasticity parameters by 62 %, and reducing the proportion of males breeding by 38 % (which corresponds to increasing number of mates per successful male by 62 %). I also separately tested making environmental variation in reproduction and mortality correlated to each other, and I separately tried switching mating system between "polygyny" and "long-term polygyny". Then I tried reducing the proportion of the genetic load which is due to recessive lethal alleles from 50 % to 19 % (thereby increasing the part of genetic load that cannot be purged from 50 % to 81 %, i.e. an increase by 62% relative to the proportion used in the other simulations). I tried increasing the severity of catastrophes by 62 %, by increasing the survival reduction at catastrophes from 50 % to 81 %. All these modifications were tested first with initial population size and population ceiling equaling 100, and then with the same initial population size but with the ceiling set at 500 individuals. Every test included 1,000 simulation runs.

Results

Long-term MVP and FRP

Estimates of long-term MVP for the three species

Long-term MVP estimates for lynx varied between 1,100 and 1,900 individuals (except for the Sarek Safe scenario, which differs from all other scenarios by describing a population with negative deterministic growth rate), the long-term MVP estimates for bear ranged from 4,700 to 8,700 individuals, and the two long-term MVP estimates for wolverine were between 1,300 and 1,400 individuals (Table 5). Somewhat surprisingly, in several cases the long-term MVP estimated under a Safe scenario was lower than the estimate derived from the corresponding Base scenario. The underlying estimates of generation time, expected heterozygosity after 100 years, mean population size after 100 years, and N_e/N ratio, for all scenarios except those of the southern bear population, are given in Table 6, while the calculation of long-term MVP estimates for bear in the southern study area is summarized in Table 7.

Table 5. Estimated population sizes required to meet the long-term MVP criterion of $N_e > 500$. (The value for lynx under the Sarek Safe scenario is in brackets because the modelled populations had a negative deterministic growth rate.)

Lynx	Bergslagen	Base scenario	1,821
		Safe scenario	1,633
	Hedmark	Base scenario	1,311
		Safe scenario	1,408
	Sarek	Base scenario	1,179
		Safe scenario	(807)
Bear	Southern area	Base estimate	6,838
		Safe estimate	8,700
	Northern area	Base scenario	5,003
		Safe scenario	4,708
Wolverine		Base scenario	1,378
		Safe scenario	1,302

Table 6. Estimates of generation time, expected heterozygosity after 100 years, mean population size after 100 years, and N_e/N ratio for the modelled populations.

	Lynx						Bear		Wolverine	
	Bergslagen		Hedmark		Sarek		Northern area			
	Base	Safe	Base	Safe	Base	Safe	Base	Safe	Base	Safe
Generation time	8.186	7.53	9.6075	9.3835	6.199	5.646	11.3455	11.035	7.6	7.6
Final expected heterozygosity	0.9766	0.9751	0.9856	0.9522	0.9771	0.8770	0.9564	0.9577	0.9810	0.9688
Mean final population size	940.27	860.98	941.76	307.09	821.25	109.29	991.72	989.44	945.74	541.26
Ne/N	0.2746	0.3061	0.3813	0.3551	0.4243	0.6197	0.09994	0.1062	0.3629	0.3839

Table 7. Calculation of N_e/N for bear in the southern study area, and of population size meeting the long term MVP criterion of $N_e > 500$, based on values provided by Tallmon et al. (2004) combined with a new estimate of generation time.

Values provided by Tallmon et al. (2004)				Values estimated in the present study						
N	Assumed number of generation times between sampling periods	N_e		N_e	Generation time	Generation times between sampling periods		Interpolated N_e corresponding to the estimated number of generation times	N_e/N	MVP
		Estimate	Lower CI	Est – 1,28 SE						
700	1	44.8	30.9	35.7	10.97	1.367	Base estimate	51.2	0.07312	6,838
	2	64.4	41.4	49.4			Safe estimate	40.2	0.05747	8,700

Suggesting FRP values by partitioning the long-term MVPs

If FRP can be set by partitioning long-term MVP values between Sweden, Norway and Finland and rounding off upwards to the nearest hundreds, then Sweden's FRP values may be 800 for lynx and 2,800 for bear. If the long-term MVP only should be partitioned between the EU member states, i.e. Sweden and Finland, then Sweden's FRP values may be 1,100 for lynx and 4,000 for bear. Exact numbers for the proportionally partitioned MVPs are shown in Table 8.

For wolverine, as shown in Table 9, the tentative FRP values range from 320 to 908, depending on how the partitioning is done. Anyhow, if FRP can be set by partitioning the long-term MVP value between all three countries and rounding off upwards to the nearest hundreds, then a Swedish FRP value of 500 seems to be sufficient, irrespective of which way the amount of available habitat for wolverine in the three countries is estimated.

Table 8. Tentative partitioning between neighbouring countries of the responsibility for maintaining long-term MVPs of lynx and bear.

		Sweden (excluding Gotland)	Finland (excluding Åland)	Norway (excluding Svalbard)	Sum
	Total land area (1,000 km²)	408	303	306	1,017
Proportional part of long-term MVP, if partitioned only between the EU countries Sweden and Finland	Lynx	1,045	776	–	1,821
	Bear	3,924	2,914	–	6,838
Proportional part of long-term MVP, if partitioned between Sweden, Finland and Norway	Lynx	731	543	548	1,821
	Bear	2,743	2,037	2,057	6,838

Table 9. Tentative partitioning between neighbouring countries of the responsibility for maintaining a long-term MVP of wolverine.

		Sweden (excluding counties mainly outside the northern boreal zone)	Finland (excluding Åland)	Norway (excluding Svalbard)	Sum
	Total land area (1,000 km²)	289	303	306	898
	Alpine mountainous zone (1,000 km²)	33		148	181
	Alpine mountainous zone plus 90 % of other area	263	273	290	826
	Alpine mountainous zone plus 50 % of other area	161	152	227	490
	Alpine mountainous zone plus 10 % of other area	59	30	164	263
Proportional part of long-term MVP, if partitioned only between the EU countries Sweden and Finland	Part of long-term MVP proportional to alpine mountainous zone plus 90 % of other area	677	701	–	1,378
	Part of long-term MVP proportional to alpine mountainous zone plus 50 % of other area	710	668		
	Part of long-term MVP proportional to alpine mountainous zone plus 10 % of other area	908	470		
Proportional part of long-term MVP, if partitioned between Sweden, Finland and Norway	Part of long-term MVP proportional to alpine mountainous zone plus 90 % of other area	439	455	484	1,378
	Part of long-term MVP proportional to alpine mountainous zone plus 50 % of other area	411	387	580	
	Part of long-term MVP proportional to alpine mountainous zone plus 10 % of other area	320	165	893	

Short-term MVPs

Lynx

For lynx, the MVP estimates according to various short-term criteria varied enormously between different scenarios, as can be seen in Table 10. Even if the Sarek Safe Scenarios are disregarded, since they had a negative deterministic growth rate, the population size required for meeting the MVP criterion of < 10 % extinction risk in 100 years varied from 30 in the most favourable scenario (Bergslagen Base without catastrophes) to 1,500 in the most pessimistic scenario (Hedmark Safe with catastrophes). If we decide to focus on Base scenarios with catastrophes included, the < 10 % extinction risk MVPs still varied from 40 when the demography from Bergslagen was simulated, to 210 when the demography found in Sarek was modelled.

Comparing the MVPs relating to different criteria, we see that the short-term genetic criteria generally gave higher MVP values than the short-term extinction risk criteria, and that this difference was most pronounced in the more favourable scenarios. An exception from this pattern was the Hedmark Safe scenarios (with or without catastrophes), where the MVP for the < 5 % extinction risk criterion was slightly higher than the MVP for < 5 % loss of genetic variation.

The relationship between estimated extinction risk and population ceiling is illustrated for the Bergslagen scenarios in Fig. 1, and the relationship between estimated heterozygosity loss and population ceiling is illustrated for the Hedmark scenarios in Fig. 2.

Table 10. MVP values for lynx, according to five different criteria for short-term population viability, estimated under twelve different scenarios. (The values for the Sarek Safe scenario are in brackets because the modelled populations had a negative deterministic growth rate.)

				MVP criterion				
				Extinction risk in 100 years			Heterozygosity loss in 100 years	
				< 10 %	< 5 %	< 1 %	< 5 %	Upper CI < 5 %
Scenario	Bergslagen	Base scenario	Without catastrophes	30	35	45	500	700
			With catastrophes	40	45	60	500	700
		Safe scenario	Without catastrophes	100	120	170	500	700
			With catastrophes	150	180	310	600	900
	Hedmark	Base scenario	Without catastrophes	50	55	75	280	370
			With catastrophes	65	85	140	320	500
		Safe scenario	Without catastrophes	700	1,100	> 2,000	1,000	> 2,000
			With catastrophes	1,500	2,000	> 2,000	1,700	> 2,000
	Sarek	Base scenario	Without catastrophes	140	160	250	500	700
			With catastrophes	210	300	600	700	1,900
		Safe scenario	Without catastrophes	(> 2,000)	(> 2,000)	(> 2,000)	(> 2,000)	(> 2,000)
			With catastrophes	(> 2,000)	(> 2,000)	(> 2,000)	(> 2,000)	(> 2,000)

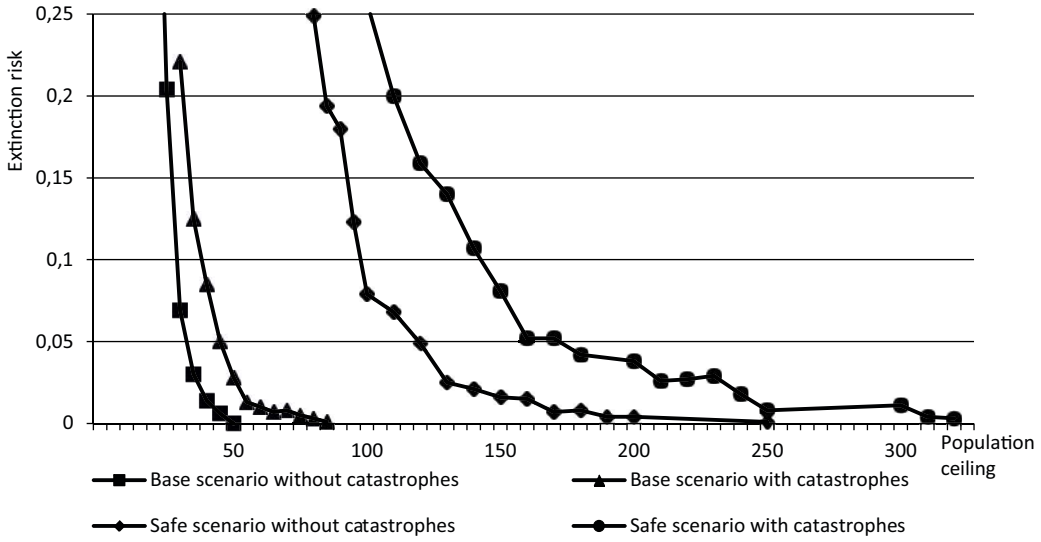

Fig. 1. Estimated extinction risk in 100 years for lynx populations, simulated under four different scenarios based on demographic data from the Bergslagen study area, with various population size ceiling. For the sake of visibility, when a curve has gone down to 0.002 or lower, points farther to the right on the same curve are not shown.

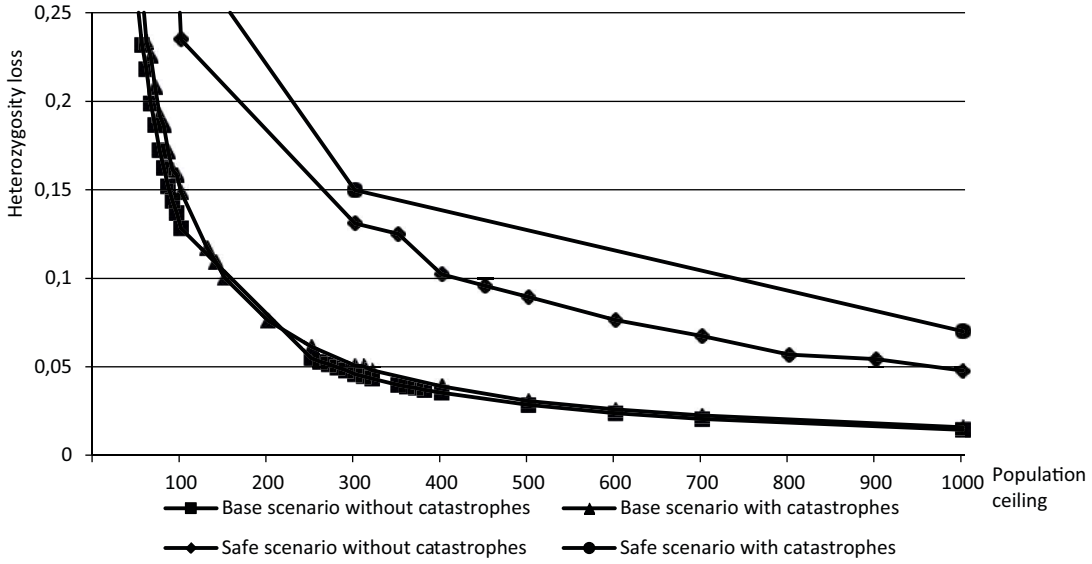

Fig. 2. Estimated proportion lost in 100 years of initial heterozygosity for lynx populations, simulated under four different scenarios based on demographic data from the Hedmark study area, with various population size ceiling.

Bear

Contrary to the result for lynx, the MVP estimates for extinction risk criteria in bear are relatively similar between different scenarios, and for all scenarios they are strikingly low (Table 11). The population size required for meeting the MVP criterion of < 10 % extinction risk in 100 years varies from 25 to 65, and even for the < 1 % extinction risk criterion I estimated as low MVPs as between 30 and 110, depending on scenario.

The MVP criteria regarding heterozygosity loss, on the other hand, gave MVP estimates ranging from 900 to 1,800 individuals. Compared to the MVPs for extinction risk criteria under the same scenario, the corresponding MVPs according to genetic criteria were between 11 and 60 times higher.

The relationship between estimated extinction risk and population ceiling is illustrated for the northern study area scenarios in Fig. 3, and the relationship between estimated heterozygosity loss and population ceiling is illustrated for the southern study area scenarios in Fig. 4.

Table 11. MVP val ues for bear, according to five different criteria for short-term population viability, estimated under eight different scenarios.

				MVP criterion				
				Extinction risk in 100 years			Heterozygosity loss in 100 years	
				< 10 %	< 5 %	< 1 %	< 5 %	Upper CI < 5 %
Scenario	Southern area	Base scenario	Without catastrophes	25	25	35	1,000	1,500
			With catastrophes	35	40	60	1,100	1,600
		Safe scenario	Without catastrophes	45	50	65	1,200	1,700
			With catastrophes	65	75	110	1,300	1,800
	Northern area	Base scenario	Without catastrophes	25	25	30	900	1,300
			With catastrophes	30	35	50	1,000	1,300
		Safe scenario	Without catastrophes	40	45	55	1,000	1,400
			With catastrophes	55	65	90	1,000	1,500

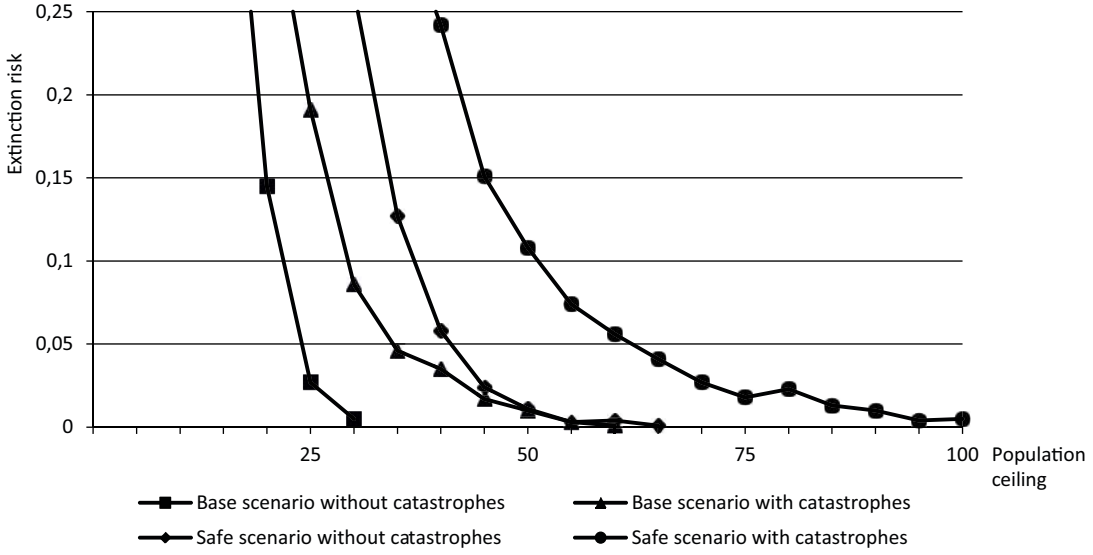

Fig. 3. Estimated extinction risk in 100 years for bear populations, simulated under four different scenarios based on demographic data from the northern study area, with various population size ceiling. For the sake of visibility, when a curve has gone down to 0.002 or lower, points farther to the right on the same curve are not shown.

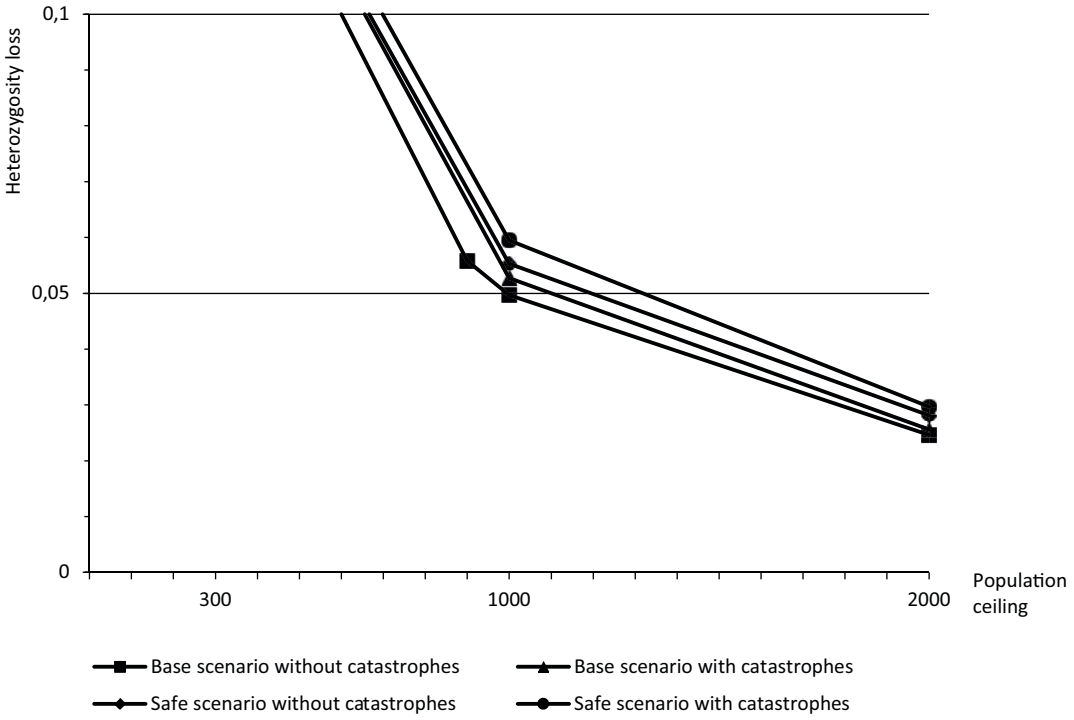

Fig. 4. Estimated proportion lost in 100 years of initial heterozygosity for bear populations, simulated under four different scenarios based on demographic data from the southern study area, with various population size ceiling.

Wolverine

The short-term MVP estimates for wolverine (Table 12) showed a pattern intermediate between those of the other two species: not extremely varying as for the lynx, but neither as closely gathered as for the bear. The population size required for meeting the MVP criterion of < 10 % extinction risk in 100 years varied from 90 in the most favourable scenario to 700 in the least favourable. If we decide to focus on the Base scenario with catastrophes included, the < 10 % extinction risk MVP was estimated to be 150.

The MVP criteria regarding heterozygosity loss gave higher MVP estimates than the corresponding extinction risk criteria, as in the other two species, but not as much higher as in the bear.

The relationship between estimated extinction risk and population ceiling is illustrated in Fig. 5, and the relationship between estimated heterozygosity loss and population ceiling is illustrated in Fig. 6.

Table 12. MVP values for wolverine, according to five different criteria for short-term population viability, estimated under four different scenarios.

			MVP criterion				
			Extinction risk in 100 years			Heterozygosity loss in 100 years	
			< 10 %	< 5 %	< 1 %	< 5 %	Upper CI < 5 %
Scenario	Base scenario	Without catastrophes	90	110	140	370	500
		With catastrophes	150	190	320	500	1,400
	Safe scenario	Without catastrophes	350	500	600	700	1,500
		With catastrophes	700	1,000	2,000	1,300	> 2,000

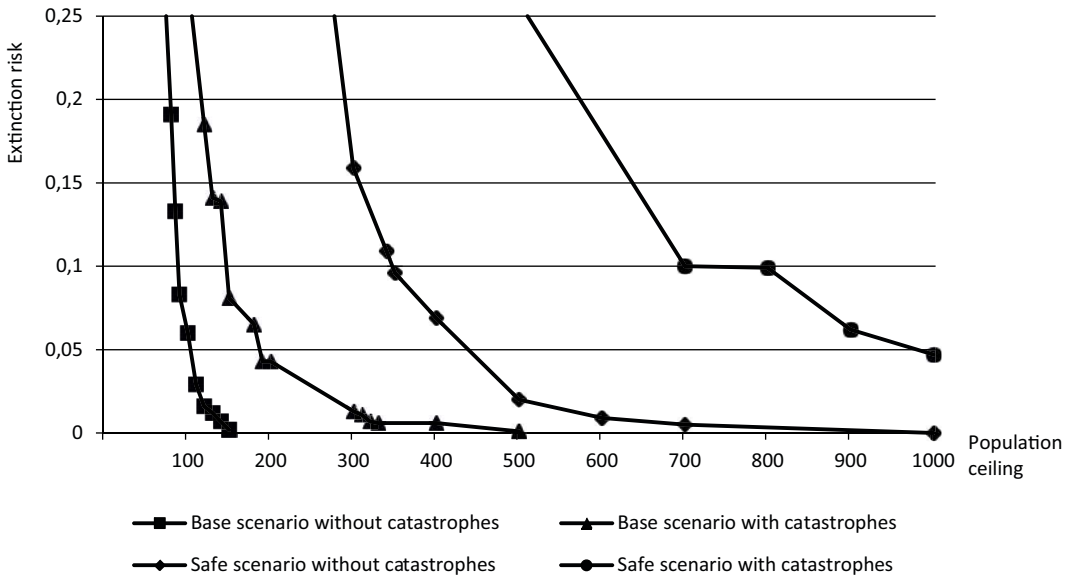

Fig. 5. Estimated extinction risk in 100 years for wolverine populations, simulated under four different scenarios, with various population size ceiling. For the sake of visibility, when a curve has gone down to 0.002 or lower, points farther to the right on the same curve are not shown.

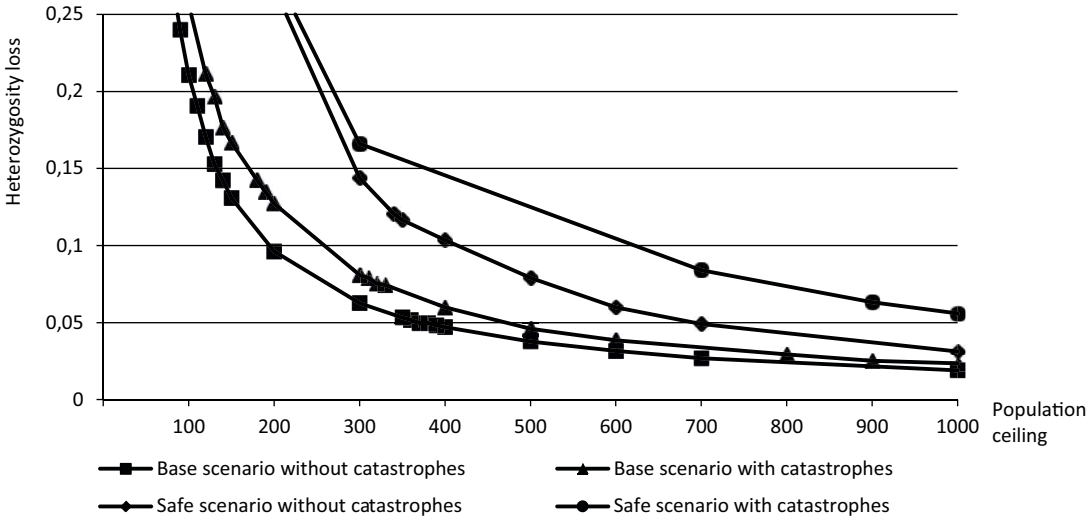

Fig. 6. Estimated proportion lost in 100 years of initial heterozygosity for wolverine populations, simulated under four different scenarios, with various population size ceiling.

Sensitivity analyses

The pattern of which parameter changes had the largest impact on extinction risk, heterozygosity loss and growth rate varied both between species and between study areas.

For lynx, increasing adult mortality had a strong impact on both extinction risk, heterozygosity loss and growth rate in the Sarek scenario; increasing juvenile and subadult mortality had stronger impact on all three response variables in the Hedmark scenario; while in the Bergslagen scenario, making catastrophes more severe had the strongest impact on extinction risk and heterozygosity loss (Table 13).

For bear, increasing the severity of catastrophic events was the only change that had a measurable effect on extinction risk, so the low extinction risks estimated in this study seem very robust; heterozygosity loss and growth rate were affected both by increasing catastrophe severity and by increasing normal year-to-year environmental fluctuations; and the rate of heterozygosity loss was also affected by changing the proportion reproducing among male bears (Table 14).

For wolverine, when the population was held below a ceiling of 100, increasing the genetic load caused the largest increase in both extinction risk, heterozygosity loss and growth rate; irrespective of population size, changes in the proportion breeding among females had considerable effects on all three response variables; and increasing catastrophe severity or environmental stochasticity also gave marked effects on extinction risk and on rate of heterozygosity loss (Table 15). Since there was a specific uncertainty regarding the mortality rates of subadult wolverines (cf. page 20), it is also worth noting that modifying juvenile and subadult mortality rates had a non-negligible effect on estimated extinction risk.

Changes in two of the tested input parameters did not have a strong effect on any species in any study area; these were the mating system (polygynous or long-term polygyny) and the proportion of LE subject to purging.

Table 13. Results of sensitivity analyses for simulated lynx populations. The first column shows values estimated in the unmodified Base scenarios. The following columns show differences, positive or negative, generated by various changes as explained in the head of the table. In each row, the figure showing the highest absolute value, i.e. indicating the largest change relative to the Base scenario, is bold. Values are only given with three decimals when this is relevant for showing which parameter change had the strongest impact.

			Value in base scenario with catastrophes	Change in value when:									
				proportion of females breeding decreased	proportion of males breeding decreased	mating system switched	adult mortality increased	juvenile & subadult mortality increased	SD_{EV} concordant between mortality and reproduction	SD_{EV} increased	catastrophe severity increased	lethal equivalents increased	proportion of LE subject to purging decreased
Extinction risk	Bergslagen	$N_0 = K = 100$	0	0	0	0	0.01	0.01	0	0.03	**0.08**	0.01	0
		$N_0 = 100, K = 500$	0	0	0	0	0	0	0	0	**0.01**	0	0
	Hedmark	$N_0 = K = 100$	0.03	0.02	–0.01	–0.01	0.13	**0.32**	–0.01	0.2	0.21	0.03	0.01
		$N_0 = 100, K = 500$	0	0	0	0	0.04	**0.15**	0	0.09	0.08	0.01	0
	Sarek	$N_0 = K = 100$	0.46	0.1	0.01	0.02	**0.45**	0.29	–0.15	0.37	0.18	0.3	0.13
		$N_0 = 100, K = 500$	0.14	0.06	0	–0.02	**0.42**	0.25	–0.08	0.34	0.16	0.11	0.03
Heterozygosity loss	Bergslagen	$N_0 = K = 100$	0.2	0	0.01	0.01	0.02	0.02	0.01	0.02	**0.04**	–0.01	0
		$N_0 = 100, K = 500$	0.05	0	0	0	0	0.006	0	0.006	**0.015**	0	0
	Hedmark	$N_0 = K = 100$	0.15	0.01	0	0.01	0.04	**0.05**	0	**0.05**	0.04	0	0
		$N_0 = 100, K = 500$	0.04	0	0	0.01	0.02	**0.06**	0	0.02	0.02	0	0
	Sarek	$N_0 = K = 100$	0.3	–0.01	0.01	0.01	0.07	0.03	–0.03	**0.09**	0	0	0.01
		$N_0 = 100, K = 500$	0.1	0.03	0	0.01	**0.09**	0.06	–0.01	0.08	0.02	0	0
Growth rate	Bergslagen	$N_0 = K = 100$	0.13	–0.01	0	0	–0.03	**–0.04**	0	–0.02	–0.01	–0.02	–0.01
		$N_0 = 100, K = 500$	0.15	0.02	0.03	0.03	0	–0.01	**0.04**	0.01	0.02	0.02	0.03
	Hedmark	$N_0 = K = 100$	0.04	–0.01	0	0	–0.03	**–0.05**	0.01	–0.02	–0.01	–0.01	0
		$N_0 = 100, K = 500$	0.06	–0.01	0	0	–0.03	**–0.05**	0.01	–0.02	–0.01	–0.01	0
	Sarek	$N_0 = K = 100$	–0.01	–0.01	0	0	**–0.03**	–0.02	0.02	–0.02	0	–0.02	–0.01
		$N_0 = 100, K = 500$	0.01	–0.01	0	0	**–0.04**	–0.03	0.02	–0.03	–0.01	–0.01	0

Table 14. Results of sensitivity analyses for simulated bear populations. The first row shows values estimated in the unmodified Base scenarios. The rows below show differences, positive or negative, generated by various changes as explained in the column to the left. In each column, the figure showing the highest absolute value, i.e. indicating the largest change relative to the Base scenario, is bold. Values are only given with three decimals when this is relevant for showing which parameter change had the strongest impact.

		Extinction risk				Heterozygosity loss				Growth rate			
		Northern area		Southern area		Northern area		So_{uthern} area		Northern area		Southern area	
		N_0 = K = 100	N0 = 100, K = 500	N0 = K = 100	N0 = 100, K = 500	N0 = K = 100	N0 = 100, K = 500	N0 = K = 100	N0 = 100, K = 500	N0 = K = 100	N0 = 100, K = 500	N0 = K = 100	N0 = 100, K = 500
Value in Base scenario with catastrophes		0	0	0	0	0.25	0.10	0.27	0.12	0.08	0.10	0.08	0.10
Change in value when:	proportion of females breeding decreased	0	0	0	0	–0.01	0	0	0	0	0	0	0
	proportion of males breeding decreased	0	0	0	0	0.025	**0.03**	0.03	0.03	0	0	0	0
	mating system switched	0	0	0	0	0.02	0.01	0.02	0	0	0	0	0
	adult mortality increased	0	0	0	0	0.01	0.01	0.01	0.01	0	0	0	0
	juvenile & subadult mortality increased	0	0	0	0	0	0	0	0	–0.01	–0.005	–0.01	–0.008
	SDEV concordant between mortality and reproduction	0	0	0	0	0	0	0.02	0.01	0	0	0.01	0.011
	SDEV increased	0	0	0	0	0.01	0.02	**0.04**	**0.04**	0	0	–0.01	**–0.013**
	catastrophe severity increased	**0.08**	**0.01**	**0.08**	**0.01**	**0.033**	0.02	**0.04**	0.02	–0.01	**–0.011**	–0.01	**–0.013**
	lethal equivalents increased	0	0	0	0	–0.02	0	–0.02	–0.01	**–0.02**	–0.008	**–0.02**	–0.011
	proportion of LE subject to purging decreased	0	0	0	0	–0.01	0	–0.01	0	–0.01	0	–0.01	0

Table 15. Results of sensitivity analysis for the simulated wolverine population. The first row shows values estimated in the unmodified Base scenario. The rows below show differences, positive or negative, generated by various changes as explained in the column to the left. In each column, the figure showing the highest absolute value, i.e. indicating the largest change relative to the Base scenario, is bold. Values are only given with three decimals when this is relevant for showing which parameter change had the strongest impact.

		Extinction risk		Heterozygosity loss		Growth rate	
		N0 = K = 100	N0 = 100, K = 500	N0 = K = 100	N0 = 100, K = 500	N0 = K = 100	N0 = 100, K = 500
Value in base scenario with catastrophes		0.27	0.07	0.26	0.10	0	0.01
Change in value when:	proportion of females breeding decreased	0.23	0.15	**0.032**	**0.05**	–0.015	**–0.02**
	proportion of males breeding decreased	0.03	0.02	0.01	0.01	0	0
	mating system switched	–0.04	–0.01	–0.02	–0.01	0	0
	adult mortality increased	0.16	0.08	0.01	0.02	–0.01	–0.01
	juvenile & subadult mortality increased	0.14	0.07	0.02	0.02	–0.01	–0.01
	SDEV concordant between mortality and reproduction	–0.01	–0.02	–0.01	–0.01	0.01	0.01
	SDEV increased	0.23	0.11	0.031	0.03	–0.01	–0.01
	catastrophe severity increased	0.27	**0.22**	–0.01	0.02	–0.01	–0.01
	lethal equivalents increased	**0.36**	0.10	**0.032**	0.01	**–0.017**	–0.01
	proportion of LE subject to purging decreased	0.07	0.02	0	0	0	0

Discussion

Long-term MVPs

To be in accordance with the Habitats Directive and the note of the European Commission (2005), national Favourable Reference Population (FRP) values should be based on analyses of what is required for long-term viability of the populations. This report, focusing on bear, lynx and wolverine, shows how such analyses can be done in two different ways: using empirical estimates of rates of loss of genetic variation, when such data are available, and otherwise using computer simulations of stochastic processes in the populations. Either of these approaches should be applicable to many other species as well.

A somewhat counter-intuitive aspect of the results was that long-term MVP estimates from Safe scenarios in some cases were lower than those from the corresponding Base scenario. The sensitivity analyses did not clearly indicate which parameter was likely to cause this effect, so this may deserve some further investigation. Anyhow, the span between long-term MVP estimates of Base scenarios and their corresponding Safe scenarios were not very large, so these long-term MVPs seem to be rather robust with respect the uncertainties represented by the Safe scenarios.

The large difference between the long-term MVPs estimated for bear and for the other two species may lead to concern about whether this difference has some biological explanation, or if there is some methodological problem, either in estimating N_e/N ratios with Vortex or in the empirical method applied by Tallmon et al. (2004). I think the biological reason for this difference is a very uneven distribution of reproductive success among male bears. Zedrosser et al. (2007) estimated the annual proportion reproducing among male bears (age 3 or older) to be 21 % in the southern study area and 57 % in the northern study area. To some extent, these figures are biased low because they were based on assigning paternity to yearlings, so some additional males may have produced only cubs that died in their first year, and also because they were based only on the young of radio-marked females, thus missing that some other males may have sired young with unmarked females. At the same time, a considerable fraction of male bears in Scandinavia reside outside the core areas where females are found, so when these displaced males are taken into account the annual proportion of males reproducing within the total bear population should be lower than the figures presented by Zedrosser et al. (2007). Still, the true proportion may very well be higher than the 3.3 % suggested by my iterative simulations. In addition to many males being excluded from breeding, Zedrosser et al. (2007) found that reproductive success is strongly correlated to age and body size, suggesting that the distribution of reproductive success is more than randomly uneven among the breeding males. This will increase the rate of heterozygosity loss, in a way that was not explicitly accounted for in the simulations, and when iteratively searching a proportion of males breeding to match the observed rate of heterozygosity

loss, that discrepancy will be compensated by choosing a lower proportion of males that reproduce at all. Hence, the fact that the simulations suggested a very low proportion of males breeding, to achieve the rate of heterozygosity loss measured empirically, does not render the empirical estimate less reliable.

It should be admitted, though, that the long-term MVP for bear based on the empirically measured rate of loss of genetic variation is directly dependent on the estimate of actual population size during the time between the sampling periods. If the actual population size during that time was lower than estimated, then the N_e/N ratio would be higher and the resulting long-term MVP lower; and vice versa. With this reservation, I think the long-term MVP estimated from empirically measured heterozygosity loss is at least as credible as MVP values estimated from computer simulations.

So, does this imply that the presented long-term MVP values for the other two species are too low? If the distribution of reproductive success among individuals is more than randomly uneven in lynx and/or in wolverine, then Vortex will underestimate the rate of loss of heterozygosity, which will lead to long-term MVP estimates being biased low. However, I do not know of any data indicating the presence or magnitude of such skewness in the distribution of reproductive success within the lynx or wolverine populations. Therefore, I think the long-term MVP estimates based on Vortex simulations are accurate enough for these species. Obviously, estimates derived from Vortex simulations may become more accurate if we get more empirical knowledge about proportions of males breeding and number of mates per breeding male. Hopefully, the increasing use of non-invasive DNA sampling methods as part of the continuous monitoring of large carnivores will provide an increasingly useful basis for genetical studies of both mating systems and population level processes such as heterozygosity loss through genetic drift.

An aspect of uncertainty that has not been accounted for in this modelling is the future development of the human population and its willingness to maintain viable populations of large carnivores. In the last half-century, the human population has grown both in Sweden and in the European Union as a whole, but so have also the populations of large carnivores, due to a successively more positive attitude to such animals, and perhaps partly due to the establishment of the Habitats Directive. Of course, if the member states of the European Union should decide to abolish the goal of reaching and maintaining long-term viable populations of these species, then such populations will not be maintained either. But as long as the Habitats Directive is in place and the member states do their best to comply with it, the prospects for reaching and maintaining long-term viable populations of bear, lynx and wolverine should be fairly good.

FRPs based on long-term MVPs

According to the Guidelines for reporting under Article 17 of the Habitats Directive (Evans & Arvela 2011), FRP values should be set according to best available knowledge. Hence these can be based on what is considered most

likely, and need not include extra safety margins due to uncertainty. Therefore I propose basing FRP values on MVP estimates from what I here have called Base (or most likely) scenarios, and not on the alternative Safe (extra safety margin) scenarios. As new knowledge accumulates, the national FRP values may be updated every six years, so any misjudgement done in the reporting in 2013 may be repaired in 2019 or later.

The Guidelines for reporting under Article 17 also say that FRP values should be considerably larger than an MVP. My interpretation is that this statement refers to short-term MVP criteria, but that it would be legitimate to set FRP at or near an MVP according to the long-term criterion of $N_e > 500$. This interpretation of mine is based on the clear emphasis given to long-term population viability in the European Commission's definition of FRP.

While the estimation of long-term MVP is based on well-established population genetics theory, the appropriate partitioning between neighbouring countries of the responsibility for reaching and maintaining this MVP is a matter that has hardly been discussed so far, neither by conservation biologists nor by legislators or politicians. A pioneering example, however, is the report on wolf population viability by Møller Hansen et al. (2011), in which the authors suggested that a long-term MVP for wolves could be shared between Sweden, Norway, Finland and the Karelian part of Russia. This suggestion was based solely on biological considerations, without any regard to whether the countries have a clearly declared ambition to cooperate with the aim of maintaining a genetically and geographically continuous, long-term viable population.

To be a little bit more precautionary, I suggest that FRP can be set by partitioning a long-term MVP not only between EU member states, but also between other countries that have signed the Bern Convention on the Conservation of European Wildlife and Natural Habitats. This includes Norway, but not Russia, so far. It might be objected that Norway has set extremely low national goals for their populations of large carnivores, and that the Bern Convention has not been efficient in affecting this Norwegian policy. But on the other hand, this may be partly because other countries have not yet attempted to use the Convention as a forum for discussing this issue, or have not had enough knowledge basis for initiating a discussion on how large the shared populations should be. I think the issue of how to partition population goals between countries deserves being considered by the Habitats Committee of the European Union, which could provide guidance to the member states on this point before the next reporting occasion in 2019.

To summarize, my tentative recommendation is that FRP values should be based on the highest Base scenario estimates of a long-term MVP, and on partitioning the responsibility for maintaining this MVP between Sweden, Finland and Norway in proportion to the amount of potential habitat for the species in the different countries. The analyses presented in this report suggest that this might mean Swedish FRP values of 800 for lynx, 2,800 for bear, and 500 for wolverine.

The importance of immigration

Maintaining populations of the size suggested as FRP values, or a bit larger, should not be not very problematic for Sweden. However, it should be remembered that to maintain long-term viability, populations of that size must be connected to reasonably large populations in our neighbouring countries. Therefore, it is important to know more about the gene flow between the countries in different species. Based on general population genetics theory, Linnell et al. (2008) recommended immigration of at least one genetically effective migrant per generation as a criterion in this context. This general guideline may be modified in cases where there is detailed genetic information motivating such a change (cf. Mills & Allendorf 1996, Wang 2006), but in the absence of such information the rule of thumb of one migrant per generation is a useful guideline (Laikre et al. 2009).

Since all three species occur in the most northern parts of Sweden, Finland and Norway, where the three countries meet, it might be assumed that sufficient connectivity between the populations in these countries should already be ensured. However, recent genetic research on lynx and bear, respectively, indicate that this should not be taken for granted. Hellborg et al. (2002) estimated lynx migration rates between Finland and various parts of Scandinavia ranging from 0.6 to 1.2 effective migrants per generation time; although this is in the vicinity of one migrant per generation time, the authors suggested that gene flow through northern Scandinavia may be severely restricted. Schregel et al. (2012) reported so called F_{ST} values (a measure of genetic differentiation) of 0.091 and 0.109, respectively, between bears in Västerbotten and bears in two different areas near the Finnish-Russian border, and suggested that the data indicated the existence of a barrier to migration between eastern and western bear populations in northern Fennoscandia. More research on all three species regarding these matters is certainly motivated, and if migration rates are too low to prevent long-term erosion of the genetic variation within the Scandinavian populations, it must be considered whether gene flow can be facilitated by allowing higher densities of the species in the northern parts of Fennoscandia.

Short term MVPs and dealing with uncertainty

The extinction risk MVPs estimated for lynx and wolverine conform to the pattern demonstrated for hypothetical populations by Ludwig (1999) and Ellner et al. (2002), and for wolf MVPs by Nilsson (2004), that moderate uncertainty of input parameters may lead to very large uncertainty in estimated extinction risk and hence in the size of MVPs. The approach developed here to illustrate this uncertainty, by making slight and statistically defined modifications to input parameters and trace the effect this will have on extinction risk, is widely applicable and should have the potential to make this uncertainty more obvious to non-experts.

If short-term viability criteria are used in setting interim management goals, I suggest that these goals should be based primarily on the most likely scenario but with inclusion of catastrophic events, since we know that catastrophic die-offs e.g. due to outbreaks of new diseases occur in nature, and we cannot know which species will be struck by such disasters. Alternative scenarios with lower probability should also be taken into account, by setting management goals somewhat higher than the most likely MVP estimate, and the more uncertainty is indicated by the alternative MVP values, the more safety margin should be added between the goal and most likely MVP value.

The MVP estimates derived here for lynx showed that varying demography between different parts of a species' range may have even larger impact on MVP estimates than the moderate uncertainty reflected by standard errors and confidence limits on the estimates for a particular population. This may seem discouraging with regard to the usefulness of PVA, but the differences shown between different areas are also informative. The high MVP values estimated for lynx with demographic parameters from Sarek or Hedmark should not lead one to think that lynx populations in these areas are acutely threatened with extinction. There is no reason to believe that the lynx populations inhabiting those areas are isolated. As long as they are continuously connected to large populations in more favourable areas, their extinction risk is efficiently reduced. In that sense, the analysis results may be seen as an illustration of the importance of geographic connectivity of wildlife populations. Another aspect of the results are that the low population growth rate and high MVP estimates for Hedmark probably reflect the fact that density of large prey such as roe deer *(Capreolus capreolus)* is low there. This supports the view that to maintain a healthy population of lynx in Scandinavia, we may have to consider the managing of roe deer populations as well. So from various angles, the estimation of short-term MVPs may have interesting implications for management, even if these short-term MVP criteria should not be mixed up with the concepts of FRP and FCS.

In the red list classification system of IUCN, estimated extinction risk is one of five main criteria for assigning species to threat categories. An extinction risk of 10 % or more in 100 years qualifies a species for belonging to threat category Vulnerable (VU); if extinction risk is 20 % or more in 20 years or in five generations, this motivates classifying the species as Endangered (EN); and if extinction risk is estimated to be 50 % or more in 10 years or in three generations, the species is classified as Critically Endangered (CR). This somehow lead Sæther et al. (1998) to the interpretation that the IUCN had recommended < 10 % extinction risk in 100 years as the criterion for which populations are considered viable. However, to my knowledge, there is no statement at all in any policy document of IUCN as to what should be considered a viable population – that is not a concept within the IUCN classification system. This misapprehension of Sæther et al. (1998) has been taken up by others as well (e.g., Pettersson 2007), and seems to be the main reason why Linnell et al. (2008) suggested < 10 % extinction risk within 100 years as a criterion for FRP and FCS. That suggestion was not motivated from the

definition of FCS in the Habitats Directive, nor from the definition of FRP established by the European Commission (2005), and considering the focus on long-term viability in the Commission's definition, it is hard to see the relevance of extinction risk in 100 years as a criterion in that context. Several studies have indicated that even if a small population has a high chance of persisting for 100 years, it may have little chance of surviving the next century (Kontio 1999, Nilsson 2004, Allendorf et al. 2005).

The very low estimates of extinction-risk based MVP for bear may be surprising. My suggestion is that this is partly an effect of bears being more long-lived than the other two species. With a generation time of ca 11 years, and with some individuals living for more than 25 years, a century is a short time period for extinction to take place. Sæther et al. (1998) also got very low MVP estimates for bear under the criterion of < 10 % extinction risk in 100 years, and suggested that lower percentage criteria might be preferable. The results found in the present study showed, however, that even the criterion of < 1 % extinction risk in 100 years leads to very low MVP estimates for this species. My interpretation is that 100 years may be a too short time periods for making meaningful assessments of the viability of such long-lived animals.

For all three species, the MVP estimates based on the < 10 % extinction risk criterion are low relative to the present populations of these species in Sweden. However, these MVP values may be useful in setting interim management goals for subpopulations that establish outside the continuous range of its species, such as the wolverine in eastern middle Sweden, the lynx in Götaland, and in the future perhaps also the bear in Götaland. The long-term goal for such subpopulations then should be that they become sufficiently connected to the larger population which they stem from.

Conclusions

Population sizes required for long-term viability are so large that for area-demanding species such as bear, lynx and wolverine, populations must be allowed to range continuously over hundreds of thousands of square kilometers. Sweden should cooperate with neighbouring countries to ensure that the Swedish population of each species is a sufficiently connected part of a total population large enough to be viable in the long term.

Short-term MVP estimates are also useful in some contexts. It should be remembered that for the species studied here, MVPs according to the criterion of < 10 % extinction risk in 100 years were not in the vicinity of genetic MVPs according to the criterion of < 5 % loss of genetic variation in 100 years. When such short-term MVPs are used,

– both an extinction risk MVP and a genetic MVP should be estimated, since both contribute information that may have implications for management;

– alternative scenarios should be modeled and used to include safety margins in the goals set; and

– catastrophes should be included in the analyses, since we know that catastrophic die-offs occur in nature and we cannot know which species will be struck by them.

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Attachment 1: The commission

REGERINGEN

Regeringsbeslut **I:9**

2012-05-31 M2012/1490/Nm

Miljödepartementet

Naturvårdsverket
106 48 STOCKHOLM

Uppdrag att presentera sårbarhetsanalyser för varg, björn, järv och lo

Regeringens beslut

Naturvårdsverket ska presentera kvantitativa sårbarhetsanalyser som tydliggör minsta livskraftiga population (s.k. MVP, minimal viable population) för varg, björn, järv och lo baserade på IUCN:s kriterium E. Uppdraget ska redovisas till Regeringskansliet (Miljödepartementet) senast den 2 juli 2012 vad beträffar varg. För björn, järv och lo ska uppdraget redovisas senast den 15 januari 2013.

Skäl för regeringens beslut

Rådets direktiv 92/43/EEG av den 21 maj 1992 om bevarande av livsmiljöer samt vilda djur och växter (habitatdirektivet) ställer bl.a. krav på att medlemsstaterna ska säkerställa gynnsam bevarandestatus för de arter som omfattas av direktivet.

I habitatdirektivet anges att en arts bevarandestatus är summan av de faktorer som påverkar den berörda arten och som på lång sikt kan påverka den naturliga utbredningen och mängden hos dess populationer inom medlemsstaten.

Bevarandestatusen ska anses gynnsam när
– uppgifter om den berörda artens populationsutveckling visar att arten på lång sikt kommer att förbli en livskraftig del av sin livsmiljö,
– artens naturliga utbredningsområde varken minskar eller sannolikt kommer att minska inom en överskådlig framtid, och
– det finns, och sannolikt kommer att finnas, en tillräckligt stor livsmiljö för att artens populationer skall behållas på lång sikt.

Enligt artikel 17 i habitatdirektivet ska medlemsstaterna vart sjätte år rapportera till EU-kommissionen om genomförandet av de åtgärder som vidtagits till följd av direktivet. Denna rapporteringsskyldighet innefattar

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bl.a. varg, björn, järv och lo. Den senaste rapporteringen gjordes 2007 för perioden 2001 – 2006. Nästa rapporteringstillfälle är 2013 för perioden 2007 – 2012. Vid rapporteringen ska bl.a. bevarandestatus bedömas och ett referensvärde anges för när gynnsam bevarandestatus uppnås. Med referensvärde avses den populationsstorlek som bedöms vara ett minimum för att på lång sikt garantera artens livskraftighet.

Av de riktlinjer som EU-kommissionen antog 2008 (Riktlinjer för förvaltning av stora rovdjur på populationsnivå) framgår att referensvärdet för populationsstorlek ska utgöra summan av följande kriterier:

1) Populationen ska vara minst så stor som den var vid tidpunkten av direktivets ikraftträdande, och
2) Populationen ska vara som minst lika stor (men gärna mycket större) än minsta livskraftiga population (MVP), definierat genom IUCN:s (International Union for Conservation of Nature) kriterium E (en utdöenderisk baserad på en kvantitativ sårbarhetsanalys med mindre än 10 % utdöenderisk över 100 år) eller kriterium D (antalet könsmogna individer).
3) Populationens tillstånd övervakas kontinuerligt genom en robust övervakningsmetod.

Av riktlinjerna följer att gynnsam bevarandestatus för en art ska ligga över den nivå som utgör minsta livskraftiga population för arten. Det är därför viktigt att definiera minsta livskraftiga population. Om det finns detaljerad kunskap om arten i fråga är det enligt Riktlinjer för förvaltning av stora rovdjur på populationsnivå lämpligt att genomföra sårbarhetsanalyser för att ta fram minsta livskraftiga population. För de svenska rovdjursstammarna finns detaljerade kunskaper och framtagande av minsta livskraftiga population bör därför ske med kvantitativa sårbarhetsanalyser enligt IUCN:s kriterium E.

Regeringen beslutade den 10 juni 2010 att tillsätta en särskild utredare med uppdrag att utvärdera de långsiktiga målen för rovdjursstammarna (Rovdjursutredningen). Rovdjursutredningen överlämnade i april 2011 delbetänkandet Rovdjurens bevarandestatus (SOU 2011:37). Utredningen redovisar bedömningar om populationerna av varg, björn, järv och lo har uppnått gynnsam bevarandestatus. Som underlag för bedömning av referensvärde och gynnsam bevarandestatus användes inte sårbarhetsanalyser.

Rovdjursutredningens delbetänkande Rovdjurens bevarandestatus (SOU 2011:37) har remitterats under tiden den 4 maj 2011 till 15 augusti 2011. En remissammanställning har upprättats (dnr 2011/1767/Nm). Av samman-ställningen framgår att flera remissinstanser är kritiska mot att utredningen inte baserade sin bedömning på sårbarhetsanalyser. Det framgår också att det finns stora skillnader mellan remissinstanserna om vad som ska bedömas utgöra gynnsam bevarandestatus för varg, björn, järv och lo.

Mot denna bakgrund bedömer regeringen att kvantitativa sårbarhetsanalyser bör genomföras avseende varg, björn, järv och lo i Sverige. Sårbarhetsanalyserna ska tydliggöra minsta livskraftiga population av dessa arter baserade på IUCN:s kriterium E. Analyserna ska bygga på senast dokumenterade kunskaper om arternas populationer i Fennoskandia.

De framtagna värdena för minsta livskraftiga population ska dels ingå i de förvaltningsplaner som Naturvårdsverket ska fastställa för varg, björn, järv och lo, och dels användas som underlag för bedömning av referensvärde för arterna i nästa års rapportering enligt artikel 17 i habitatdirektivet för varg, björn, järv och lo i Sverige.

Uppdraget att presentera sårbarhetsanalyser ska redovisas till Regeringskansliet (Miljödepartementet) senast den 2 juli 2012 vad beträffar varg. För björn, järv och lo ska uppdraget redovisas senast den 15 januari 2013.

På regeringens vägnar

Lena Ek

Magnus Bergström

Kopia till

Statsrådsberedningen
Finansdepartementet/BA
Landsbygdsdepartementet/JFS

Attachment 2: Comments from specialists and external reviewers

Prof. Henrik Andrén, Swedish University of Agricultural Sciences

Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences (SLU), SE-730 91 Riddarhyttan, Sweden

I think the report is well done, especially given the very short time frame. Available data on survival and reproduction in brown bear, lynx and wolverine have been used in an appropriate way. The report is based on several different scenarios; both from different study areas and based on different assumptions about worse scenarios and effects of catastrophes. Uncertainty and variability in the data are well described in the method section. But I disagree that the safe scenario has some special biologically and statistically support. Adding or subtracting 0.48 SE (with a resulting probability of 0.316) to survival and reproduction and conclude that this should represent a probability of an unfavorable scenario of about 0.10 (0.316^2). In non-linear interactive models, like MVP-analyses, the outcome of two probabilities is not a simple multiplication. Thus, the way to get a worse safe scenario can not be calculated as it is done in the report, it should have been done within more thoroughly statistical framework.

In the report, there is a negative relationship between long-term MVP and extinction risk based MVP. This is very counter-intuitive relationship, i.e. if the population is more vital (higher growth rate as a result of higher survival and reproduction) then the long-term MVP has to be larger. This is mentioned very shortly on page 47 in the discussion, but the effect should have been further elaborated. However, given the very short time for this report I understand that this was not possible.

In the report, there is a good relationship between growth rate (lambda) and extinction risk based MVP, as well as loosing genetic variation. For growth rates (lambda) >1.045 the extinction risk based MVP without catastrophes (p_{ext} <0.10 in 100 years) is <200 individuals for all three species and the population size for loosing <5 % heterozygosity in 100 years in is <500 for both lynx and wolverine. Therefore, I disagree that brown bear had surprisingly low extinction risk based MVP and that lynx had enormous variation in extinction risk based MVP. Both these statements are based on how much the growth rate has varied in the different scenarios, which depends on the variation in ecological context where the data have been collected. For the lynx the growth rate varied between 0.996 and 1.214, for wolverine between 1.016 and 1.046 and for bear between 1.118 and 1.142. If the lynx data only had been available from the Bergslagen study area then the variation in MVP had been very low for lynx, or if there had been bear data from an additional study area with a saturated bear population (with a lambda close to 1) then

variation in MVP had been much larger for bear. The ecological context (e.g. an expanding and colonizing population, a population close to saturation or a population close to its distribution range) for the species in the different study areas can explain some of the variation in growth rates and I think this should have been discussed in the report, but I understand that this was not possible given the very short time frame.

Dr. Guillaume Chapron, Swedish University of Agricultural Sciences

Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences (SLU), SE-730 91 Riddarhyttan, Sweden

I have read the final draft of your report "Population viability analyses of the Scandinavian populations of bear *(Ursus arctos)*, lynx *(Lynx lynx)* and wolverine *(Gulo gulo)*" with great interest. I have general and technical comments, the latter being the consequences of the former.

My general comment is that you have obviously done an impressive amount of work in a short amount of time. I particularly appreciated that the methods and assumptions you made were clearly and honestly stated. While you ought to be congratulated for this, I find it very problematic and worrying that Miljödepartementet is developing a habit of imposing on scientists such insanely short timeframes to produce reports on large carnivores. What this ultimately only achieves is to prevent the scientific community from thoroughly discussing and elaborating at length on complex issues of high stakeholder interests and to have management relying on the best science.

Because of the short timeframe within which you needed to deliver the report, you have chosen approaches and assumptions which I believe may require adjustments and alternatives. For example, I question the use of VORTEX as a suitable tool to conduct species specific PVA. It has been used a lot, but this is not an indication of appropriateness, but rather an indication of the fact that the software is well designed and easy to use. As you describe it yourself in the report, VORTEX is not very flexible and I believe a custom-made model would have been better (e.g. regarding the bear mating system). The modeling approach that you have chosen therefore comes with limitations that hinder a correct consideration of uncertainty in ecological processes. For example, iteratively finding which numerical value of a parameter leads to a model fitting well the data should not be done by hand but by using specific algorithms such as Monte Carlo Markov Chain or Approximate Bayesian Computation.

Also, I do not believe the safe scenario approach is statistically robust. Assume that you have a function z = f(x,y), by taking the first 30% quantiles of x and y values, you will not necessarily get the first 30%*30% = 10% quantile of z values (e.g. see what happens if z = 1/(x*y)), unless the function is linear and with no interaction between x and y. I am not sure this is the case for a function returning MVP from demographic parameters.

Finally, your results are presented as mean values, which is known as being a biased estimator towards large values and it would have been more informative to present median values.

Having expressed the shortcomings of your report, I am however (and readers should be too) perfectly aware that you could not in any way follow the alternative approaches I mention given the short deadline you were imposed.

Prof. Linda Laikre and Prof. Nils Ryman, Stockholm University

Linda Laikre and Nils Ryman, Division of Population Genetics, Stockholm University, SE-106 91 Stockholm, Sweden

This report presents data that is of importance for accomplishing Favourable Conservation Status (FCS) for the brown bear, lynx, and wolverine in Sweden and Scandinavia. Unfortunately, the report has been produced under great time pressure (~1.5 months). As a result the time allocated for external review has also been very short; the draft version was only available for three working-days and the final one for five. We are impressed with the author's accomplishments during this short time, but the brevity and some of the technical shortcomings of the presentation could probably have been avoided had the author been given more time to finalize the work.

As referees we feel frustrated with the short review process, because it prohibits the in depth examination of the report that is warranted for scientific quality. Now there is an obvious risk that we have missed shortcomings or misunderstood parts of the text or the underlying ideas. In general, we are concerned about the tight time schedule that typically involves scientific advice concerning the management of large carnivore species in Sweden. The extreme limitation of time for conducting analyses and producing and reviewing reports is not in line with the aim of obtaining the best possible scientific advice with respect to the management of these species.

Approach for assessing long term MVP and FRP

The approach to identify necessary population sizes for Favourable Reference Populations (FRPs), providing the basis for reaching Favourable Conservation Status (FCS), appears innovative and sound. In brief, the logic of the approach included:

1. Demographic information for the separate species was obtained from the literature and from ongoing research projects. Thus, best available demographic information appears to have been used.
2. Using that information the author applied the widely appreciated VORTEX software for assessing generation length, remaining expected heterozygosity, and population size at 100 years after starting at N=1000.

3. Remaining heterozygosity and generation length is then used to estimate effective population size (N_e).
4. The N_e and the number of remaining animals are used to estimate the N_e/N-ratio.
5. This ratio is then used to assess the number of animals necessary to meet the general long term goal of keeping $N_e > 500$ to assure long term viability and potential for adaptation.

Although time has prohibited in depth review of the approach, we find it generally attractive because we support the idea of using $N_e > 500$ as a basic criterion for assessing FRP, and to link the size and geographic distribution of such a population to the concept of FCS (cf. Laikre et al. 2009, 2013).

The author ends up with suggesting population sizes needed for FRP to comprise about 1,400 wolverines, 6,000 brown bears, and 1,500 lynx. Although we have not been able to go over the analyses in detail we think these estimates seem reasonable.

We support the idea that the long term viable populations should be shared over Sweden, Norway, and Finland, provided that sufficient gene flow is maintained over the area.

Short term MVP

The author also assesses short term MVP using several of the available criteria for providing short term MVP. We see no real reason for estimating short term MVPs in relation to the goal of the Habitats Directive for maintaining long term viable populations; it appears that these analyses were performed at a direct request from the Swedish Environmental Protection Agency (Naturvårdsverket).

General structure and presentation

We find the report a bit overly technical and therefore sometimes confusing and difficult to follow, particularly for readers who do not work with viability analyses on a regular basis.

To mention a few examples, there is no definition of “extinction” and there is no information on the maximum lifespan assumed for any of the species dealt with. Similarly, on p. 15 we find it difficult to understand the definition of the criterion described as “upper confidence limit for loss of genetic variation in 100 years < 5 %”, and the expansion on p. 34 is not very helpful. Here, one or a few formulas describing the logic, the different quantities, and their relationship could have clarified; this also applies to, e.g., the description of the procedure for calculating the N_e/N ratio for bear (p. 32, first paragraph under “Long-term MVPs”). Further, we would have liked to see an extended discussion of, e.g., the selected approach for obtaining averages when assessing N_e/N ratios.

References

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Overall, Nilsson develops a thoughtful and very useful demographic analysis to assist in the identification of minimum viable population sizes for three high-profile species in Scandinavia. The analyses described here can serve a valuable role in stimulating discussion about the essential characteristics of viable carnivore populations in the region. The author is to be congratulated for creating an important resource for conservation biologists and wildlife management authorities.

At the same time, I do see some weaknesses in the analyses that may weaken the utility of the results and their implications for species management. These issues are discussed below, listed in rough order of importance:

- The short-term minimum viable population size for any species is very tightly correlated to that population's stochastic growth rate over the same period of consideration. This is demonstrated in the current study, where populations with more robust growth rates (for example, the Bergslagen lynx population) also have lower MVP estimates derived from the extinction risk models (see Tables 10 and 13 for this example). Therefore, a simulation modeling approach for deriving MVP estimates must carefully evaluate the stochastic growth rates that emerge from the species-specific models. I believe that Nilsson's full analysis would benefit greatly from the addition of even a simple retrospective analysis of the baseline models against observed species-specific population trajectories in the field. Do the Base models appear to describe historic population trends of these species in Sweden with some degree of acceptable realism? Is the resultant growth rate from a given species' Base model acceptable as a starting point for future risk analysis? Why are the growth rates from the Base models given such little emphasis in the presentation of results?

- The choice of setting initial population size equal to carrying capacity (N_0 = K) in all simulations is not sufficiently justified. This approach implies that habitat will be the primary limiting factor across all population sizes considered in the analysis, which is unlikely given the observation here and elsewhere that the species are increasing in abundance in many portions of their range. As with the discussion of growth rate above, the relationship between carrying capacity and extinction risk can be very important. Therefore, careful consideration and thoughtful explanation of this aspect of the model input dataset is required for a more credible analysis.
- The linked concepts of Minimum Viable Population (MVP) size and the Favourable Reference Population (FRP) size are sometimes poorly differentiated, as for example in the subsection on partitioning long-term MVPs into FRP values (page 19). Only near the end of the document does Nilsson state his opinion about the basic equality of long-term MVP and FRP. A more direct and consistent distinction between these two estimates throughout the document would be most helpful for increasing overall clarity.
- Inbreeding depression is modeled most directly in Vortex as a reduction in first-year survival as a function of the inbreeding coefficient and the genetic load. Therefore, I'm skeptical of the validity of averaging LE values across studies that evaluate inbreeding effects across multiple fitness traits (Table 4). Inbreeding effects on, say, litter size may be quite different from those that affect juvenile survival.
- The logic of conducting the sensitivity analysis as described on page 17 is acceptable, but some more detail is needed here to fully understand how the method is being implemented. For example, it is critical to understand how the standard errors (SE) of the empirically-derived mortality or reproductive rate estimates are being calculated. If this variance is calculated across years, then the total variance is confounded by both measurement error and environmental variability and the stated methodology is not valid. So how is the variance of the rate estimated?

Prof. L. Scott Mills, University of Montana

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The task here – to conduct population viability analyses (PVA) and estimate minimum viable population sizes (MVP) according to applicable policy directives for 3 charismatic but understudied species – is daunting. I applaud the author for a sincere, earnest, and thoughtful effort that probably is about as good as can be done under what appear to be crippling time and financial limitations. Policy makers and the public should know, however, that the level of our science could support much better analyses of such questions, if the political will and funding were in place to implement the appropriate studies.

An analogy is that in the same way that landing an astronaut on the moon requires time and money to fully harvest the fruits of the aeronautical sciences, so too can population ecology science provide rigorous answers to complex biological questions (such as viability of wide ranging carnivores), but only if sufficient investments are made.

I say all this to make it clear that I think the author did a fine job with the apparently absurdly short time and small investment in this project. However, in an absolute sense, this analysis could be done much better if more resources were made available to fully harvest the power of applied population ecology science. For example, a team of several investigators, with the ability to do targeted field sampling, genetic and demographic analyses, and modern population modeling (eg specific custom models built to capture the idiosyncrasies of each species) would provide a truly rigorous answer to the policy directives. Such an effort would be what would be needed for an "Excellent" evaluation of viability for these 3 species.

However, given the constraints of time and effort that forced this exercise to rely on coarse genetic rules of thumb for 'long term viability' and coarse genetic criteria and simulations using defaults in VORTEX for the 'short term viability', the approach is satisfactory.

In short, the weaknesses of the approach are that they were done using a crude subset of the remarkable tools available for such analyses, and under too much time limitation, but I do not consider this a fault of the author but rather an inevitable outcome from the resources made available.

The strength of the report is that the author earnestly attempts to capture some of the primary uncertainties faced in conducting this analysis. Also, he quite honestly and correctly notes that the value of MVP depends strongly on the criteria applied. Further, he thoughtfully considers the interesting topic of setting reference population values in a multi-nation context.

Prof. Jon E. Swenson, Norwegian University of Life Sciences, and Dr. Jonas Kindberg, Swedish Association for Hunting and Wildlife Management

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Given the short deadline required for this report, we consider this report to be generally well done and an important document for making policy and management decisions regarding the conservation of large carnivores in Sweden. Nevertheless, we feel that there are some important weaknesses in the document regarding the population viability of the brown bear population. We hope that our reservations will be considered when policy makers and managers decide how to implement the results of this document.

The demographically based estimates of short-term minimum viable population size (MVP) of the brown bear population, i.e. extinction risk in 100 years, were based primarily on published data from the Bear Project and the results are similar to results we have obtained and published earlier. We feel comfortable with these results.

We are more concerned about the results regarding the long-term MVP, i.e. estimated population size required to meet the long-term criterion of $N_e > 500$. In the report, Dr. Nilsson estimated the ratio of N_e/N using the computer program Vortex for lynx and wolverines, but based his calculations for bears on a published estimate of N_e/N, which was based on a recorded change in allele frequencies from the southern bear subpopulation (Tallmon et al. 2004). These estimates of long-term MVP are the most important results presented in the report, because these estimates are used to propose the Favorable Reference Population (FRP) values, which must be reported to the European Commission.

Dr. Nilsson reported that: "Long-term MVP estimates for lynx varied between 1,100 and 1,900 individuals (except for the Sarek Safe scenario, which differs from all other scenarios by describing a population with negative deterministic growth rate), the long-term MVP estimates for bear ranged from 4,700 to 8,700 individuals, and the two long-term MVP estimates for wolverine were between 1,300 and 1,400 individuals (Table 5)" (page 36). Dr. Nilsson appears to be concerned about the large difference in the long-term MVP size for bears and the other species. On page 50, he wrote " The large difference between the long-term MVPs estimated for bear and for the other two species may lead to concern about whether this difference has some biological explanation, or if there is some methodological problem, either in estimating N_e/N ratios with Vortex or in the empirical method applied by Tallmon et al. (2004). I think the biological reason for this difference is a very uneven distribution of reproductive success among male bears." Using the N_e/N given in Tallmon et al. (2004), he iteratively calculated that 3.3% of the males bred in a given year (Table 2). Dr. Nilsson recognized that this value did not correspond with genetically based empirical estimates of breeding success in male Scandinavian brown bears and wrote that: "Zedrosser et al. (2007) estimated the annual proportion reproducing among male bears (age 3 or older) to be 21 % in the southern study area and 57 % in the northern study area. To some extent, these figures are biased low because they were based on assigning paternity to yearlings, so some additional males may have produced only cubs that died in their first year, and also because they were based only on the young of radio-marked females, thus missing that some other males may have sired young with unmarked females. At the same time, a considerable fraction of male bears in Scandinavia reside outside the core areas where females are found, so when these displaced males are taken into account the annual proportion of males reproducing within the total bear population should be lower than the figures presented by Zedrosser et al. (2007)" (page 50). Dr. Nilsson decided not to use these empirical data: "Alternatively, I could have used the annual proportions of male bears breeding estimated by

Zedrosser et al. (2007). However, within the Scandinavian bear population, most female bears are concentrated in four core areas, while the distribution of male bears is several times larger (Swenson et al. 1998) because many male bears disperse out of the core areas to reside in areas where few mating opportunities are given. Therefore, since two of the female core areas also are the study areas for which proportions of males breeding were estimated by Zedrosser et al. (2007), I suspected those estimates were unrepresentative of the total bear population." (pages 23–24).

We do not agree with Dr. Nilsson's conclusion that the estimates of male breeding success reported by Zedrosser et al. (2007) are unrepresentative underestimates. The distribution of males and females in Scandinavia, reported by Swenson et al. (1998, Fig. 2), showed that a relatively small proportion of the males were located outside of the core areas with females and that the densities there are low (see also Table 1 in this paper).

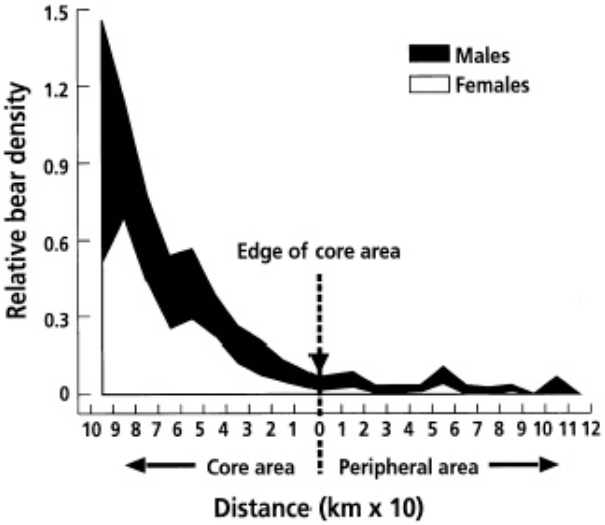

Fig. 2. Cross-section of the generalized expansion front of the increasing brown bear population in Sweden, showing relative densities of males (black) and females (white) along a gradient from the centre of the core areas to far out into the periphery. Relative densities are based on hunter-killed bears (Table 1), and zones are illustrated in Fig. 1.

In addition, Swenson et al. (1998) documented that the males outside the female core areas were significantly younger than those occurring inside the female core areas. Besides this, the female core areas have increased in size considerably and have grown together to a large extent with the recent increase in population size (Kindberg, J., 2010, Monitoring and management of the Swedish brown bear *(Ursus arctos)* population, PhD thesis, Swedish University of Agricultural Sciences, Umeå), which means that the relative size of the peripheral area in Sweden has declined. Also, we expect that the present high rates of hunter harvest rates have reduced the proportion of old-age males, thus increasing overall breeding success among younger males, based on the results of Zedrosser et al. (2007), and refer to the relatively high proportion of litters with mixed paternity that we have documented (Bellemain et al. 2006). All of these results argue against Dr. Nilsson's decision to prefer the very low proportion of males breeding that he found based on simulations (3.3%). Nilsson himself seemed unsure about this conclusion, as he wrote: "Still, the true proportion may very well be higher than the 3.3 % suggested by my iterative simulations" (page 50). We share this concern and believe that he should have based his calculations on the available empirical data.

We raised these and other concerns when commenting on an earlier draft of this report, particularly the heavy reliance on data and extrapolations from only one source (Tallmon et al. 2004). Our reservations have been added to the discussion, but have not resulted in new calculations. This was unfortunate.

We also have some philosophical concerns with the report:

1) It raises some fundamental concerns when Dr. Nilsson accepts the Vortex-based N_e/N ratios in the long-term MVP estimates for lynx and wolverines, but not for bears. This means that future large-carnivore policy will not be consistent across species. If one cannot trust the Vortex-based estimates for bears, can one really trust them for the other species? We feel that this question could have been handled better if Dr. Nilsson had calculated and compared two independent MVP estimates for the bear; one using the same method as for the other species, using breeding values from Zedrosser et al. (2007), and one based on the breeding success values he calculated from Tallmon et al. (2004).
2) We feel that it is not appropriate to quantify a division of the FRP (Favorable Reference Population) sizes among Sweden's neighboring countries and then propose the result as tentative FRP levels for Sweden. A partitioning of long-term population levels among countries must be based on political negotiations, which could be jeopardized by the unilateral recommendations given in this report.
3) Dr. Nilsson has defined FRP based primarily on genetic considerations. However, there are other operational definitions that should have been considered, such as the Guidelines for population-level management plans for large carnivores in Europe (Linnell et al. 2008), which were prepared for the European Commission. These guidelines state that: "The central challenge associated with operationalising FCS is to make a link between the philosophical / political / legal concept of FCS, the biological concepts of population viability, other existing forms of categorising species status (e.g. IUCN red lists), and the specific distribution patterns and biology of the large carnivores." Although the report with these guidelines was cited in Dr. Nilsson's report, we believe that it would have been improved if the recommendations in these guidelines had also been given more consideration.

These guidelines suggest that favorable reference population be defined as the sum of the following criteria:

(1) "The population must be at least as large as when the Habitats Directive came into effect, and,
(2) The population must be at least as large (and preferably much larger) as a MVP, as defined by the IUCN criterion E (extinction risk based on a quantitative PVA with <10% extinction risk in 100 years), or criterion D (number of mature individuals).
(3) The population's status is constantly monitored using robust methodology."

A final factor of crucial importance for species such as large carnivores that cause a wide range of conflicts with human interests is the issue of societal carrying capacity (Decker et al. 2001).

The guidelines therefore suggest that a population can be regarded as having reached FCS (Favourable Conservation Status), if it satisfies all of the following criteria;

(1) "Population dynamics data on the species concerned indicate that it is maintaining itself on a long term basis as a viable component of its natural habitat" (Article 1 (i)). We interpret this as implying that monitoring data indicate the population has a stable or increasing trend. We believe that a slight reduction in population size may be permitted if it is a result of response to changes in prey density or habitat quality that are not the cause of direct human action, unless conditions for derogations apply (see 6.4). All segments of a population should have stable or positive trends, and not just the population as a whole. And,

(2) "The natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future" (Article 1 (i)). We interpret this as implying that the overall distribution of the population is stable or increasing. And,

(3) "There is, and will probably continue to be, a sufficiently large habitat to maintain its population on a long-term basis" (Article 1 (i)). We interpret this to imply that the quality and continuity of habitat should be sufficient, and have a stable or increasing trend. And,

(4) The population size and range are equal to or greater than when the Directive came into force. And,

(5) The favourable reference population size has been reached. According to our proposal this will be set at levels greater than those regarded as being viable using the IUCN red list criteria E or D. And,

(6) The favourable reference range has been occupied. And,

(7) Connectivity within and between populations (at least one genetically effective migrant per generation) is being maintained or enhanced. And,

(8) "Member States shall undertake surveillance of the conservation status of the natural habitats and species referred to in Article 2 with particular regard to priority natural habitat types and priority species" (Article 11) and "Member States shall establish a system to monitor the incidental capture and killing of the animal species listed in Annex IV (a)" (Article 12.4).

Population viability analyses of the Scandinavian populations of bear *(Ursus arctos)*, lynx *(Lynx lynx)* and wolverine *(Gulo gulo)*

TORBJÖRN NILSSON

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The authors assume sole responsibility for the contents of this report, which therefore cannot be cited as representing the views of the Swedish EPA.

Denna rapport är ett av de vetenskapliga underlagen inom Naturvårdsverkets regeringsuppdrag att presentera sårbarhetsanalyser för varg, björn, järv och lo.

Rapporten är skriven på engelska och redovisar sårbarhetsanalyser av de skandinaviska populationerna av björn, lodjur och järv för att bedöma minsta livskraftiga populationsstorlek i relation till olika demografiska och genetiska kriterier. Analyserna gjordes med datorsimuleringar baserade på data från de skandinaviska populationerna, och undersökte populationernas utdöenderisk samt hur snabbt de förlorar genetisk variation.

Resultaten visade bland annat tydligt att i de flesta fall behövs betydligt större populationer för att uppfylla genetiska kriterier för långsiktigt eller kortsiktigt livskraftig populationsstorlek än för att uppfylla enbart demografiska kriterier.

This is one of the scientific reports commissioned by the Swedish Environmental Protection Agency in its government commission to present population viability analyses of wolf, brown bear, wolverine and lynx.

It presents analyses of the Scandinavian populations of bear, wolverine and lynx to quantify minimum viable population size (MVP) estimates in relation to various criteria for demographic and genetic viability, respectively. The analyses were based mainly on simulations using demographic data from empirical studies of the Scandinavian populations, and assessed risks of population extinction within 100 years and loss of genetic variation over time.

The results showed that much larger populations are required to fulfill genetic MVP criteria than to fulfill criteria based solely on population extinction risk.

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