Demographic Viability of the Scandinavian Wolf Population

A report by SKANDULV

SWEDISH ENVIRONMENTAL
PROTECTION AGENCY

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Svensk sammanfattning

Denna rapport är ett svar på ett uppdrag från Naturvårdsverket till Det Skandinaviska Vargforskninsprojektet SKANDULV, som i huvudsak innebar att genomföra en kvantitativ, rent demografisk, sårbarhetsanalys med avseende på varg i Sverige, som skall tydliggöra minsta livskraftiga population (Minimum Viable Population MVP) av varg baserat på IUCN:s kriterium E (utdöenderisk <10% på 100 år). Genetiska aspekter skulle inte beaktas. Hela uppdragets formulering finns i Appendix.

Delar av det vetenskapliga samhället idag avråder generellt från att ge kvantitativa svar på frågor om livskraftig population och utdöenderisk. Trots detta presenterar vi ändå kvantitativa svar i denna rapport på grund av det behov för sådana som vi förstår att de svenska myndigheterna har. Vi vill dock varna för att övertolka våra resultat, och betonar att utfallen av våra modeller är beroende av de antaganden som görs. Särskilt vill vi betona att vi enligt uppdraget endast beaktat demografisk och miljömässig stochasticitet (variation orsakad av slump). Våra resultat gäller endast under förutsättningen att de genetiska problem, som idag förekommer i vår vargpopulation, är lösta. För att säkerställa en genetisk livskraft är det inte i första hand antalet djur i den egna populationen som är avgörande, utan att det sker ett tillräckligt stort genetiskt utbyte med andra populationer som tillsammans utgör en tillräckligt stor metapopulation för att ha en egen genetisk livskraft. De nivåer vi presenterar skall inte heller likställas med kraven på Gynnsam Bevarandestatus, vilken enligt befintlig lagtext ska vara *avsevärt högre än minsta livskraftiga population MVP*.

Vi beräknade minsta livskraftiga population (MVP) med hjälp av tre olika populationsmodeller med ökande grad av komplexitet. Vi startade med en enkel modell som endast bygger på de tillväxttakter som vi uppmätt i den skandinaviska vargpopulationen de senaste 13 åren, under antagandet att tillväxten i framtidens vargpopulation kommer att hålla sig inom den variation vi redan uppmätt. I modell två beräknar vi tillväxttakten i populationen med hjälp av data från den skandinaviska populationen på reproduktion och dödlighet och den variation vi har i dessa parameter. Den tredje modellen är mer komplex och mer vargspecifik, men samtidigt den minst robusta, eftersom den bygger på flera antaganden. Detta är en individbaserad modell där de skilda individernas öden beror på de "regler" för deras övergång mellan olika faser i livet, som vi lägger in i modellen. Även dessa "regler" är baserade på data från vår population.

För att utröna effekten av möjliga framtida okända katastrofer, testade vi för varje modell vilken frekvens och magnitud av katastrofer som skulle krävas för att utdöenderisken vid olika givna nivåer på populationen (vi testade nivåer mellan 30 och 1000 individer) skulle ligga högre än 10 % under 100 år (enligt IUCN kriterium E).

Vi avstod från att använda färdiga analysprogram, t.ex. VORTEX, på grund av att detta inte kan hantera de detaljerade artspecifika aspekter som lagt in i modell tre. Eftersom vi hade tillgång till kompetent modellerings- och programmeringsexpertis utförde vi analyserna själva. Vi jämför dock våra resultat med tidigare analyser som gjorts i VORTEX (se nedan).

En utvärdering av de tre modellerna (anpassning till den verkliga populations-utvecklingen 1998 – 2012) visade att de var realistiska. De gav också likartade svar. För utdöenderisker på 10% respektive 5 % på 100 år gav den första (enklaste) modellen MVP-nivåer på 22 respektive 25 individer. Motsvarande värden för modell två var 33 och 42 individer och för modell tre (den mest komplicerade och vargspecifika) 38 och 41 individer. I dessa simuleringar ingick inte några oväntade katastrofer. När vi testade hur stora och frekventa katastrofer som skulle krävas för att utdöenderisken skulle överstiga 10% på 100 år, var samstämmigheten mellan modellerna ännu större. Med små skillnader mellan modellerna angav samtliga att utdöenderisken för en population på 100 djur var mindre än 10 % för ett scenario med katastrofer var 10´e år som slog ut 55-60 % av populationen, eller för katastro-fer som slog ut drygt 90 % av populationen om de inträffade högst en gång per 100 år,. Dessa katastrofscenarier ligger väl över de som hittills uppmätts för varg och för andra populationer av stora däggdjur.

Med hjälp av modell 1, som enbart bygger på tillväxtdata, testade vi modellens känslighet för ändringar i tillväxttakten gentemot känslighet för variation i tillväxt-takten. Det visade sig att MVP var mycket känsligare för små ändringar i till-växttakten själv än för variationer i denna. Med hjälp av modell 2, där vi även lagt in reproduktion och dödlighet, testade vi livskraft i relation till olika nivåer på död-lighet (med fasthållande av samma fördelning på reproduktionen). I enlighet med empiriskt resultat, fann vi att inga vargpopulationer kan vara livskraftiga om deras dödlighet varaktigt är > 35%, ett värde vid vilket utdöendet är deterministisk. Idag ligger den totala dödligheten i den skandinaviska vargpopulationen på omkring 24%, vilket visar att vår population är sårbar för en varaktig ökning av dödligheten med c:a 10 procentenheter, t.ex. i form av en ökad illegal jakt, oavsett population-ens storlek.

Vid jämförelser med andra sårbarhetsanalyser, både för skandinaviska vargar, och andra vargpopulationer, överensstämmer våra resultat i stort sett med vad man fann i de flesta av dessa undersökningar. Ett par av dessa använde VORTEX, vilket gav likartade resultat till de som presenteras i denna rapport. Tillsammans med det faktum att vi får mycket likartade svar med våra tre olika modeller gör dessa över-ensstämmelser att vi betraktar våra resultat som robusta.

Baserat på resultaten av dessa modellkörningar drar vi slutsatsen att en population på minst 100 vargar uppfyller kraven för minsta livskraftiga population även med hänsyn tagna till rimliga framtida katastrofscenarier, och att därmed den nuvarande skandinaviska vargpopulationen utan tvekan är demografiskt (men ej genetiskt)

livskraftig under den utdöenderisk (10 % på 100 år) som anges i IUCN´s Rödliste-kriterium E. Vi vill dock påminna om de reservationer för ett numeriskt värde på MVP som vi anger i andra stycket i denna sammanfattning, och som utvecklats något mer i huvudtexten. Vi vill också betona att framtagande av ett MVP-värde, och därpå följande värde för Gynnsam Bevarande status (Favourable Reference Population) inte får ersätta en fortsatt noggrann bevakning av alla relevanta demografiska och genetiska parameterar i vargpopulationen. Den bästa garantin för populationens fortsatta livskraft in i framtiden är inte ett "magiskt tal" utan en adaptiv förvaltning som har tillgång till forlöpande uppdateringar av dess tillstånd.

Summary

This report attempts to evaluate the demographic viability of the Scandinavian wolf population under IUCN Red List Criteria E (extinction risk < 10% on 100 years). We estimated the Minimum Viable Population by using three different population models with increasing level of structural complexity, each relying on different assumptions, data and methods. We stress our results should be interpreted cautiously because they rely on the assumption that genetic issues have been solved and because legal texts indicate the Favourable Conservation Status should be much larger than the MVP. In addition, it is generally advised to avoid proposing firm numbers for viability levels. We ran similar simulations for all three models and find that they all return very consistent patterns. Our results show that small wolf populations (< 100 individuals) are large enough to escape stochastic extinctions and only extremely small wolf populations (< 40) are not viable. In agreement with empirical evidence, we also find that a wolf population is not viable if the mortality rate is > 35%, a value at which extinction is deterministic. There is no evidence that increased environmental fluctuations may seriously affect wolf viability, as the required frequency and intensity of catastrophes, which would make a MVP unviable remain unsupported by empirical data on catastrophes for any wolf population in the world. We conclude that a wolf population with the same size and growth as the ones of the current Scandinavian wolf population is undoubtedly demographically viable under IUCN Red List criteria E.

Introduction

Assignment and its context

On June 1st 2012, the Scandinavian Wolf Project (SKANDULV) received an assignment from the Swedish Environmental Protection Agency to conduct a population viability analysis (PVA) for wolves (*Canis lupus*) in Scandinavia. A preliminary report had to be delivered to the Swedish Environmental Protection Agency at latest by June 27th 2012, and a final report by July 1st 2012. The exact phrasing (translated from Swedish) of the core of the assignment reads as follows (for the full and original text of the assignment, see Appendix):

Conduct a quantitative (demographic only) viability analysis for wolves in Sweden. The viability analysis will clarify what is the minimum viable population of wolves based on the IUCN criterion E. The analysis shall be based on the most up-to-date scientific knowledge of the Scandinavian wolf population, and under the assumption that genetic issues have been resolved.

This report presents the answers to this assignment that we have produced within the limited time frame of only one month that we were given. The assignment asks for an analysis of "wolves in Sweden", but as the Swedish wolves are intimately interwoven with Norwegian wolves in the same population, our analysis will concern the Scandinavian population, of which Swedish wolves constitute more than 80 %. Views presented in this report are only the ones of the authors and not necessarily the ones of the Swedish Environmental Protection Agency. We have used several population models to delineate a range of possible values for a Minimum Viable Population (MVP) for wolves in Scandinavia. According to the definition of the assignment, our models have included only demographic aspects and have ignored genetic ones. All our conclusions should therefore be interpreted with the assumption that the inbreeding issues the Scandinavian wolf population is facing have been solved and that there is at least one unrelated migrant entering the breeding population per generation (Laikre et al. 2009). A FORMAS funded research project is under way to further develop quantitative analysis intended to provide insights in the demo-genetic viability of the Scandinavian wolf population and results should be available in 2015.

Wolf recovery and management in Sweden

The Scandinavian wolf population started declining during the 19th century, and when protected, 1966 in Sweden and 1972 in Norway, the wolf was functionally extinct in Scandinavia (Wabakken et al. 2001). The nearest source population occurred in Russian Karelia along the eastern border of Finland. During the 1970's wolves expanded into eastern Finland, and by 1977 several wolves were recorded in northern Sweden. In 1982 a pair was formed in south-central Scandinavia and successful breeding was recorded in 1983 (Wabakken et al. 2001). This breeding pair and a third male immigrant arriving in 1990, also with origin in Finland/Russia, were the sole founders of this recovered Scandinavian wolf population

until 2008 (Liberg et al. 2005). In 2008 another two immigrants from the Finnish/Russian population entered the breeding Scandinavian population, making total number of founders by March 2011 to five. In spite of an increasing degree of inbreeding with negative effects on reproduction (Liberg et al. 2005), the wolf population has expanded and in early winter 2010/11 the total population size in Scandinavia was preliminary estimated to 289-325 wolves, of which 89 % occurred in Sweden or in border territories (Wabakken et al. 2011).

In 2009 the Swedish government decided on a new management policy for large carnivores in Sweden (2009/10:MJU8). For the Swedish wolf population this decision resulted in that 1) the population should for a 3-year period be restricted to a maximum level of 210 wolves, implemented through a regulating harvest, and 2) that active management actions should be jointly carried out to improve the genetic situation of the population. The latter included a strategy to introduce up to 20 wolves from other populations.

The Swedish government has at two occasions in 2010 (M2010/3062/R) and 2011 (M2011/647/R) been requested by the EU Commission to answer and provide further information about the new management policy for wolves in Sweden. The Commission states that the new wolf management policy adopted by Sweden in 2009 may directly interfere with the goal of attaining a Favourable Conservation Status (FCS) according to the Habitat Directive (92/43/EEC). In particular, the Commission questioned the decision to let the population be exposed to a regulating quota harvest aimed to control population size at a level of 210 wolves. As a result the Swedish government decided in August 2011 to remove the temporary cap of 210 for the Swedish wolf population.

In June 2010 the Swedish government decided to appoint a commission of enquiry aiming at evaluating the long-term goal for the population size of large carnivores, to consider further needs for improving the genetic status of the wolf population, and to suggest additional actions that will improve the coexistence between wolves and humans. The commission presented in April 2011 an interim document on the conservation status of large carnivores (SOU 2011:37) and in April 2012 the final document concerning the goals for the size of all four large carnivore populations (SOU 2012:22). The final report suggests that a long-term goal for the Scandinavian wolf population should be 500 wolves of which 450 should be seen as a preliminary reference value for Sweden and that a new evaluation should be done in 2019.

MVP and EU Habitat Directive

The concept of MVP has gained importance in management and conservation following the adoption by countries and supra-national bodies of regulations aiming a preventing species to go extinct. In the EU, this regulation is the Habitat Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora), which was adopted in 1992 and aims to protect habitats and species listed in the directive Annexes, including the wolf. The directive is a legally binding agreement for EU member states. In article 1, the directive defines the

Favourable Conservation Status (FCS) of a species 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: (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, and (2) the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and (3) there is, and will probably continue to be, a sufficiently large habitat to maintain its population on a long-term basis."* Revisions of the directive and guidance documents have further indicated that FCS should be based on both a Favourable Reference Range (FRR) and Favourable Reference Population (FRP). The FRP is itself defined as the *"population in a given bio-geographical region considered the minimum necessary to ensure the long-term viability of the species; favourable reference value must be at least the size of the population when the Directive came into force; information on historic distribution / population may be found useful when defining the favourable reference population; best expert judgement may be used to define it in absence of other data"*. The Commission provided further clarification by stating that *"however, as concepts to estimate MVP are rather used to evaluate the risk of extinction they can only provide a proxy for the lowest tolerable population size. MVP is by definition different – and in practice lower – from the population level considered at FCS"*. Therefore, as the Population Level Management Guidelines (Linnell et al. 2008) clarified: *"for a population to be at its FRP it must be at least greater than a MVP, but there is a clear intention within the Directive to maintain populations at levels significantly larger than those needed to prevent extinction"* and noted that the directive guidance document suggested that it may also be useful to estimate the size of the population *"when the potential range is fully occupied at an optimum population density"*.

As stated in the assignment, our report is intended to estimate what is the minimum demographically viable population of wolves in Scandinavia under IUCN Red List criteria E. This criteria proposes that for a population to qualify as not being Vulnerable or any other more serious category, a quantitative analysis should show that the probability of extinction is less than 10% within 100 years (IUCN 2003, 2006) – a time frame which may be shorter than long-term viability indicated in the FRP above. We therefore stress that in no way our conclusions can be interpreted as defining a FRP, which must, according to the official documents referred above, be significantly larger than a MVP and defined on a longer time frame than 100 years. We anticipate critics regarding the scope of the question defined in the assignment, in particular regarding the fact that the analysis should include demographic issues only and not genetic ones. We would like however to point out that genetic issues are more dependent on diversity and connectivity between populations than on population size alone. A population can be genetically connected to others while still being demographically isolated, i.e. the exchange of individuals is sufficient to mitigate genetic issues but does not contribute to a demographic increase in population size.

Estimating a MVP in practice

From extinction risk to MVP

The concept of MVP was originally introduced by Shaffer (1981) who proposed the following definition: "*A minimum viable population for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes.*" Shaffer (1981) further stressed that the criteria level for chances of persistence or the time frame were tentatively and arbitrarily set and other values may be proposed. In practice, a MVP is in fact the smallest population size of a wild animal or plant population under which society considers the risk of extinction is unacceptably too high. Most conservation biologists consider that an acceptable risk of extinction should be less than 5% over 100 years (Flather et al. 2011) but the IUCN has adopted a twice as high acceptable risk under the Red List criteria E where a population is considered not threatened if its risk of extinction is smaller than 10% over 100 years (IUCN 2003, 2006). In this report, we adopt the criteria recommended by IUCN – as stated in the assignment, but also provide some results for the more widespread 5% standard.

The concept of MVP has been widely used in conservation biology both in theoretical and applied perspectives. Population models have been successfully used in delineating management decisions for several species (e.g. spotted owls *Strix occidentalis*, grizzly bears *Ursus arctos* see Boyce 1993) even its generality and usefulness in conservation and management have recently come under questioning (Flather et al. 2011). Before going further, it is important to clarify that a MVP can be estimated and interpreted in two broad different ways. The most widespread one assumes that there is no limit on population growth and is understood as the smallest population size a population should not go under in order to avoid extinction. This interpretation concerns mostly endangered species, in particular when implementing reintroduction projects and choosing what is the minimum propagule size, i.e. how many individuals have to be released to make sure this new population does not go extinct. The second interpretation is somewhat analogue to computing the minimum reserve size for species living in a human dominated landscape and having particular habitat requirements. The question then is typically "how much is enough?" and it turns out this is the same question asked when managing conflict-prone species experiencing a successful recovery such as the wolf in Sweden. Therefore, it is the latter interpretation we follow in this report, where we compute what should be the minimum population size of wolves in Sweden, above which no more individuals would be needed and at which extinction risk would remain acceptable.

Quantifying extinction risk

Because the concept of MVP emerges from quantifying extinction risk, the use of MVP in real world conservation and management is dependent on the availability of robust, proven and accurate tools to quantify such risk (Flather et al. 2011). Modern ecological sciences now make an extensive use of models, which are mathematical or algorithm-based formalizations of processes and patterns that scientists wish to investigate. It is now widely accepted that understanding demographic mechanisms and their implications for population management requires developing and using population models (Mann & Plummer 1999, Coulson et al. 2001) and reviews have revealed that population models are able to rigorously quantify extinction risks. Because using models in management makes straightforward the test of several biological assumptions and management strategies, they are rightly viewed as a critical part of sustainable policy making (Chapron & Arlettaz 2006) and despite their caveats should be preferred to the less reliable and transparent expert assessment (Burgman et al. 2011).

When quantifying extinction risk, models – or their use – are often termed a Population Viability Analysis (PVA) (Beissinger & McCullough 2002) and one variable of interest returned by these models is the extinction risk. There are different methods of estimating this risk, but the most widespread one is to run Monte Carlo simulations. These simulations are repeated stochastic (i.e. random) trajectories where at each trajectory the model starts from the same initial conditions and parameters. After many trajectories (typically 1,000 or more) have been run, one simply counts how many of these trajectories have seen their population going extinct. The extinction risk or probability of extinction is calculated by dividing the number of extinct trajectories by the number of total trajectories run. By varying the initial conditions, in our case by iterating the population ceiling at which the population is prevented to exceed, one can select the MVP that satisfies the criterion chosen.

To better understand our results, it is also important to explain that there are two broad kinds of extinction. The first one is called a deterministic extinction and will happen when the population growth rate (λ) consistently remains < 1. Such extinctions typically occur as a result of habitat destruction or– legally or illegally – over-exploitation. They can push even some of the most abundant species to extinction as illustrated by the example of the passenger pigeon (*Ectopistes migratorius,* see Halliday 1980). The second kind of extinction is called a stochastic (i.e. random) extinction and affects populations of particularly small sizes, which are consequently vulnerable to random events. These extinctions can be triggered by demographic stochasticiy (i.e. random occurrences in deaths, litter sizes and sex ratio), environmental stochasticity (harsh winters, droughts or prey fluctuations) or catastrophes, which we address in the next section. In these cases the population growth rate is on average > 1, but due to stochastic events it might be < 1 and suddenly triggers an extinction.

Importance of catastrophes

"Catastrophes" in the terminology of conservation biology have been defined as "local extinctions of a metapopulation" (Ewens et al. 1987), or " rare, severe environmental events" (Hanson & Tuckwell 1978). The former definition appears to be less useable though, as it seems to exclude all die-offs less than 100 %. A better general definition was offered by Reed et al (2003) as "*particularly extreme bouts of environmental variation that severely decrease the size of wildlife populations over a relatively short time*". However, Reed et al (2003) also found that the use of the term catastrophe might be arbitrary. Time series analyses of 12 populations, from ten species, indicated that the growth rate (*r*) was normally distributed and "catastrophes" only represented the lower tail of the distribution (Reed et al 2003). Thus more operational quantitative definitions are needed. Actually, one such definition had been given already ten years earlier by Young et al. (1994): "*a monotonic drop in population numbers that occurs between two or among more than two population surveys with at least a 25% reduction in population size*". Reed et al. (2003) themselves proposed a somewhat stricter definition, namely, "*any 1-year decrease in population size of 50% or greater*". However, Juarez et al (2011) pointed out that "*choosing a fixed mortality threshold to identify die-offs overlooks the fact that the same population loss can be more severe for some species than for others owing to differences in their life histories*". They thus suggested the following definition: "*a 1-year decline in the number of individuals within a population derived from one or more extreme natural events, where individual losses increase by at least 25% in comparison to that expected from the annual average mortality rate reported for the species*".

Examples of catastrophes in this sense are severe winters or droughts, storms, floods, wildfires, outbreaks of epidemic disease, insect infestations or sudden habitat changes for other reasons. The importance of including catastrophes in PVA´s has long been recognized, and it has even been suggested that such catastrophic events may be more likely to limit the viability of populations than genetic factors (Lande 1988). However, one serious drawback that often has made the inclusion of catastrophes in PVA´s more or less arbitrary has been lack of data on their frequency and severity. Young et al (1994) quantified mortality in 96 cases of catastrophes in large mammals, varying from 30 to 100 %. They found that starvation caused by extreme weather (winters or droughts) was the most common cause of large die-offs in ungulates; while for carnivores it was epidemic diseases. The frequency of cases increased with severity (i.e. die-offs with 70 % mortality was more common than those with 30 %), up to 90 % mortality, after which it dropped of drastically, but the authors believed the reason was that less severe catastrophes were less frequently reported (confirmed by the results of Reed et al, see below). The authors also pointed out that their material could not be used to measure how often catastrophes occur, since they had subjectively selected all cases of die-offs fitting their definition of a catastrophes they could find in the literature.

The first attempt to quantify also frequency of catastrophes was instead made by Reed et al (2003). They collected long-term population census data for vertebrates

from the Global Population Dynamics Database (NERC, 1999). The census data they used included 308 cases of 1-year peak-to-trough declines in estimated numbers of 50% or greater, among 88 species. The frequency of catastrophes measured per year was negatively correlated with generation length of the organism, i.e. animals with longer generations experienced catastrophes less often. The weighted mean probability of a die-off of 50 % or more was 14.7% per generation with a standard error of 1.0%, irrespective of taxa. The frequency of occurrence also was negatively correlated with severity, i.e. serious catastrophes occurred more seldom than milder. The per generation probability of a 33%, 75%, and 90% die-off was 52.5%, 3.2% and 1.0%, respectively.

In table I, we have presented the five large carnivore species that appeared in the material of Reed et al. (2003). For wolf, three catastrophes had been reported for a combined time series of 105 years, i.e. one per 35 years or 0.20 per generation. Unfortunately, the authors did not give details for the different species, so we do not know the severity or the cause of the three catastrophes reported. Among the 96 catastrophes reported by Young et al. (1994), none concerned wolf, and only six concerned other species of large carnivores. There were three cases for African wild dog (*Lycaon pictus*) varying between 63 and 84 % mortality, two for coyote (*Canis latrans*) with a severity of 50 and 87 % respectively, and one for Lion (*Panthera leo*) with 75% mortality. All cases but one were caused by disease.

Table I. Frequency of die-offs with 50% or higher mortality within 1 year in five taxa of large carnivores (from Reed et al. 2003).

Species	Years	N catastr.	Years/Cat	Gen length	N gen.	Cat/gen
Canis lupus	105	3	35	7	15	0.20
Gulo gulo	58	1	58	7	8.3	0.12
Lynx lynx	135	6	22,5	4	33.8	0.18
Panthera leo	37	1	37	5	7	0.12
Ursus arctos	38	1	38	11	3.5	0.29

Murray et al. (1999) reports 7 cases of die-offs in wolves caused by disease, four by rabies, one by distemper and one by parvovirus. In one case it was unclear whether the causing agent was parvovirus or distemper. Mortality varied between 9 and 30 %, except for one case of rabies, where it was 60 %. This latter mortality regarded only one pack of ten wolves though. Apart from these cases we also know of one large die off on Isle Royale, where the population went down from 50 to 14 in 1980-82, i.e. a reduction with 72 % in two years (Peterson 1995). The causing agent was canine parvovirus (CPV). The disease persisted in the population for another six years causing high chronic mortality, until it suddenly disappeared. The population on Isle Royale has existed for more than 60 years, and this is the only catastrophic die-off reported for this population. We do not know whether the Isle Royale time series was included in the material of Reed et al. 2003, but find that unlikely. At present, the population is in very bad shape, consisting of only 9 animals, of which maximum two are mature females. The present situation is probably

mainly caused by a combination of strong inbreeding and demographic stochasticity. The Scandinavian wolf population has now existed for 30 years without any catastrophic die-off.

Methodology overview

The question we have been asked in the assignment goes against the recommended use of population models. It is generally advised to interpret results in a qualitative (why, how, and what if questions) rather than in a strict quantitative (when, where and how much questions) way (Beissinger 2002). Furthermore, a consensus in the modelling literature recommends avoiding proposing firm numbers for viability levels (Reed et al. 2002). While we understand the need of quantitative requirements by real-world policy makers, we urge readers to not over-interpret our conclusions and to recognize that model outcomes are strongly dependent on their assumptions. By interpreting model findings as absolute numbers, one may find that a population size considered as viable with one model might not be viable with another model. It is important to understand that the dynamics of biological systems (such as a population) is the stochastic result of complex, interacting and often non-linear feedbacks, which renders their absolute quantitative interpretation inappropriate (Pilkey & Pilkey-Jarvis 2007). This stands in contrast to many physical systems, which show a deterministic dynamics and for which scientists are able to make extremely accurate quantitative predictions, e.g. the future positions of planets or the resistance of a bridge have very little, if any, quantitative uncertainty. Interpreting biological models as it is possible to interpret physical models, especially to make real-world management decisions, is therefore hazardous both in the short-term as there is no guarantee these outputs are accurate and in the long-term as this spuriously may lead to a broader defiance against model-based inferences among society.

In an attempt to address the request we have been given, without breaking the accepted practices of using models, we have developed three different population models with increasing level of structural complexity, each relying on different assumptions, data and methods (Figure 1). By using different models, we aim at delineating a pool of results which taken together should generate a more robust confidence. Note that using different models is not the same as accounting for uncertainty, which is done independently in each model. This approach is analogue to the one adopted by the International Panel of Climate Change where several climate models and scenarios are considered (Randall et al. 2007). We start with a simple model; having as few assumptions as possible and using only population count data. We follow with a model of intermediate complexity that uses more detailed data on survival and reproduction. Finally, we present a more realistic model – but also based on a lot more assumptions taking the form of biological rules. Each model is presented in its own separate section and a final section provides a synthesis of our findings.
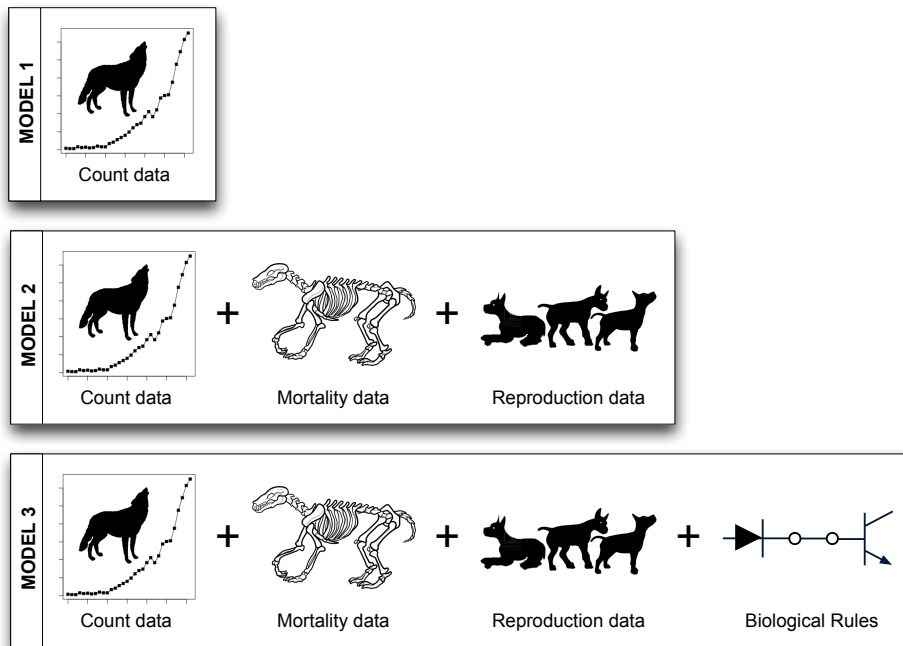
Figure 1: Schematic representation of the three models developed in this report. All models are used to compute extinction risk and to estimate a MVP for the Scandinavian wolf population.

Exponential growth model

Model description

Our first model is the simplest one as the population at year *t+1* is the population at year *t* minus harvest at year *t* multiplied by growth rate λ:

$$N_{t+1} = \lambda \cdot \left(N_t - H_t \right)$$

There is actually no wolf-specific assumption in this model. In fact any population has a growth rate and the only assumption that we make here is very general and needed in viability analysis: we assume that it is possible to infer about the future by observing the past – an assumption also known as the "principle of uniformitarianism". With this model, we run simulations to find out what is the most likely value of population growth rate λ to have the model fitting the observed data the best and then run forward simulations to investigate how likely are populations to become extinct according to its growth rate and its variation. Due to density-dependence, an increase in population size is expected to reduce growth rate and in turn to influence the viability of the population. However, density dependence is unlikely to be relevant for small populations that are well below their biological carrying capacity. The carrying capacity of wolves in Scandinavia is likely quite high because there is plenty of space and wild ungulate prey for larger wolf populations on the Scandinavian Peninsula (Karlsson et al. 2007), and both Sweden and Norway have some of the highest moose / wolf ratios in the world (Sand et al. 2012). We therefore do not include density-dependence in this model and the following ones. Similarly, we have assumed in all the three models that the population was isolated and there was neither immigration nor emigration.

We formalize this model in a hierarchical way, which is a particular statistical approach that provides the advantage of formalizing in a coherent probabilistic framework both the ecological process and the observation process from which the data emerge. In our case, the ecological process is the dynamics of the wolf population in Scandinavia, e.g. the survival and reproduction of packs and wolves that lead to a population growth (or decline). The observation process is the winter census carried out nation-wide by field teams and we used population counts from 1999 to 2011 because their quality was consistent and better than data for previous years. The simulations explicitly consider that the model is not perfect, i.e. we cannot predict with absolute certainty what is going to be the wolf population size next year. The simulations will also explicitly consider that the census data are not the truth but have some error that may vary in size between years. For example the data tells us that population size in December 2010 was 277 wolves, but we consider this is an *estimate* and the true population (which remains unknown) may actually have been 270 or 290 wolves. Accounting for this observation error (either underestimates or overestimates of wolf population sizes) may lead to a more uncertain prediction but is important because it is the true population size (and not its estimate), which should be viable. While this may sound as artificially introducing

noise in the data, this is actually the correct way to proceed and ignoring observation error is a mistake that can lead to spurious conclusions (Freckleton et al. 2006). We consider however that harvest data are perfectly observable. The results that we get are not a single value of λ, but rather a probability distribution of λ, indicating which values are more likely than others, but also which other values are still possible.

When written in a hierarchical way, we need to separate the process model and the observation model. The process equation is:

$$\begin{cases} \mu_t = \log\left(\lambda \cdot N_{t-1} - H_{t-1}\right) \\ N_t \sim \text{lognormal}\left(\mu_t, \sigma_{proc}\right) \end{cases}$$

where μ_t is the deterministic prediction of the median wolf population size at time t, N_t is the true population size at time t, σ_{proc} is the standard deviation of the true population size on the log scale, λ is the yearly population growth rate. The process equation is linked to data using the observation equation:

$$\begin{cases} \alpha_t = \dfrac{N_t^2}{\sigma_{Nobs}^2} \\ \beta_t = \dfrac{N_t}{\sigma_{Nobs}^2} \\ \psi_t \sim \text{gamma}\left(\alpha_t, \beta_t\right) \\ Nobs_t \sim \text{Poisson}\left(\psi_t\right) \end{cases}$$

where $Nobs_t$ is the observed population size at time t, σ_{Nobs} is the estimate of the error of observation of the population size. This formulation views the count data hierarchically – the mean observed count of wolves at time t is Poisson distributed with mean ψ_t and this mean is drawn from a gamma distribution with mean equal to the prediction of the process model and a standard deviation for observation error. We estimate the posterior distribution of each parameter by running Monte-Carlo Markov chains (MCMC), implemented in JAGS (Plummer et al. 2003) with R (R Development Core Team 2009). Three chains were initialized with different sets of parameter values chosen within biologically plausible bounds. After an initial burn-in period of 100,000 iterations, we obtained 1,000,000 iterations of each of the chains, thinning each by 10. We successfully checked for convergence using the Heidelberger & Welch stationarity and half-width tests with the CODA package (Plummer et al. 2006).

In order to compute MVP, we need to run simulations that will project the population dynamics into the future. We do this by considering that during the next 100 years, population growth rates are going to be drawn from the same probability distribution as the one they have been drawn from during the past 10 years – i.e. the posterior density we just obtained by MCMC sampling. This way we keep all uncertainty from parameters to MVP estimates. We model process error or demo-

graphic stochasticity by a Poisson function instead of the parameter σ_{proc} because we need to have integers for counting individuals. Environmental stochasticity is accounted for in the posterior distribution of λ.

Since we want to infer about a MVP, we cap the population at a ceiling K (considered as a maximum population size implemented by harvest) and we run Monte Carlo simulations (100,000 trajectories) with various values of K (K being constant during each simulations) and compute each time the resulting probability of extinction. The smallest value of K that leads to an extinction probability lower than 10% (or 5% when indicated) is the MVP.

Model assessment

Our simulations indicate that the Scandinavian wolf population has been growing at a median annual rate of $\lambda = 1.18\pm0.02$ during the period 1999-2011 (Figure 2). Worth clarifying is that this growth rate is not the realized growth rate but the potential one because harvest data is included in the model. In other words, we estimate the most likely growth rate the population would have shown if no harvest had taken place. Note also that our results take the form of a distribution of values and not of a point estimate: while our data supports the most a λ of 1.18, uncertainty in the process and the shortness of the time series indicate that there is also some support, but weaker, for other values of λ such as 1.16 or 1.20. The shape of the distribution indicates that the probability of having $\lambda < 1$ is almost equal to 0.
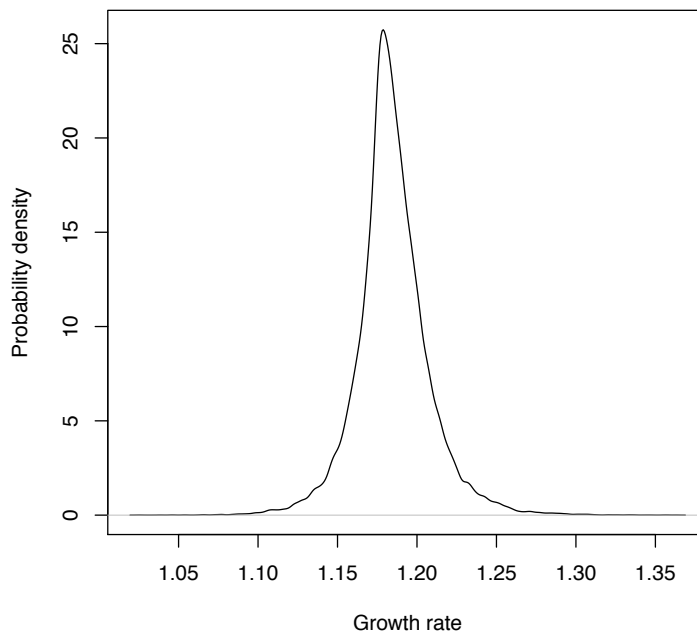

Figure 2: Posterior distribution of growth rate λ estimated by fitting an exponential growth model to the 1999-2011 time series of the Scandinavian wolf population. The most likely value for λ is 1.18 and the standard deviation is 0.02.

We can evaluate how well our model is able to explain our data by running simulations starting with the population size in 1999 and ran until 2011 (and considering the harvest that took place). We find that the model correctly matches the data (Figure 3) and this reveals that the distribution of the growth rate we have computed is able to well capture the population dynamics of wolves in Scandinavia during the past 12 years. However, Figure 3 also reveals that there is a wide standard deviation (shown by the dashed lines) and that the further the simulation moves forward in time, the less precise its forecast becomes. We are able to estimate well the median population size 12 years ahead (it is in fact almost the same as the observed data) but the standard deviation of the predicted population in 2011 is ±96 wolves. This is something important to be aware of because MVP computations consist in forward simulations lasting 100 years and have a very high uncertainty.
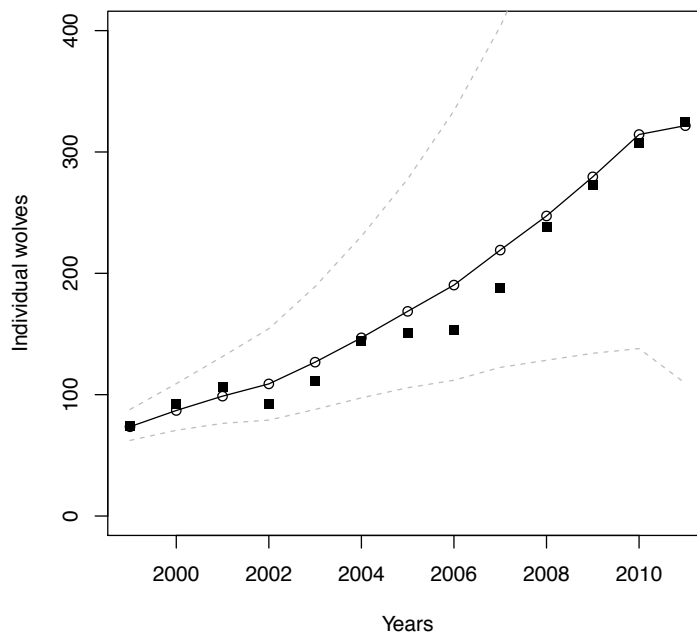

Figure 3: Forecasting simulation starting from 1999 with the exponential growth model (λ = 1.18±0.02). The black squares are annual census data of the Scandinavian wolf population, the open circles are the median population size predicted from the model and the dashed lines indicates ± standard deviation of our model predictions. Notice how this standard deviation becomes extremely large after just a few years of simulation.

Computations of MVP

When capping population size, stochastic simulations show that a wolf population with the same growth rate as the one of the Scandinavian population has an extinction risk less than 10% (resp. 5%) if it is capped at 22 individuals (resp. 25 individuals) (Figure 4). In other words, culling all surplus individuals above a threshold of 22 or 25 individuals does not lead to an extinction risk higher than 10% or 5% according to this model and its assumptions.
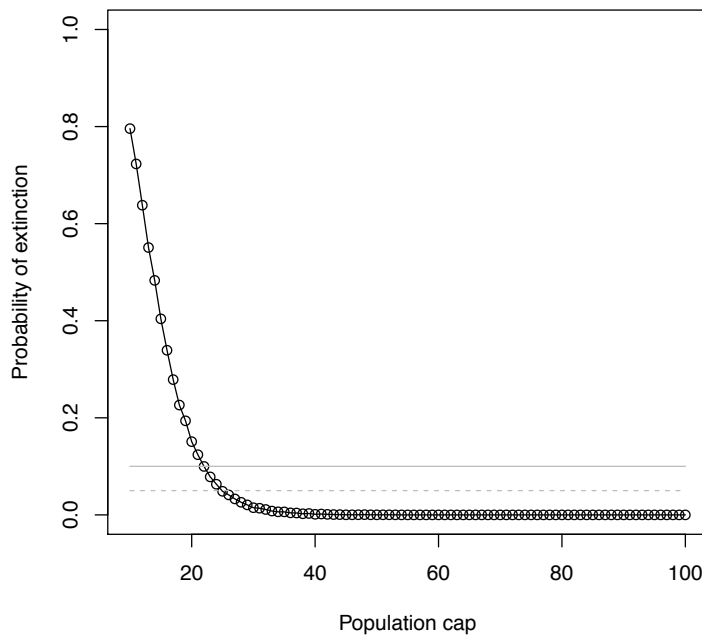
Figure 4: Extinction probability as a function of population cap for a theoretical population having the same parameters (λ = 1.18±0.02) as the ones of the Scandinavian wolf population. Horizontal grey lines are 5% (dashed) and 10% (continuous) threshold of extinction risk.

Future scenarios

The former result is particularly dependent on the limiting assumption that the probability distribution of the population growth rate of the Scandinavian wolf population will remain the same for the next 100 years as it is today. This assumption is unlikely to be true because if there is anything we can be sure of, it is that the future is not going to be exactly like the past. We are not considering possible density dependent effects here – which would be unlikely in such a small population – but rather possible changes in habitat, prey base or simply human attitudes. We can envision two general kinds of changes: gradual ones (change of growth rate and its variation, Boyce 1992) or new events that have never happened before (catastrophes, Albon et al. 2000).

To investigate how the population cap (i.e. the MVP level) needs to be adjusted to these possible changes, we now run simulations but with different values of growth rate and its variation. We consider all cases: growth rates from 1.00 to 1.30 and growth rate standard deviation (SD) from 0 to 0.10. For each λ and its SD, we estimate the required MVP (Figure 5) by running 10,000 runs of a Monte Carlo simulation. The only difference from the previous simulation is that here growth rate is no longer drawn from the distribution we estimated with the hierarchical model fitted to Scandinavian data, but from a normal distribution (excluding negative values as we assume $\lambda > 0$) whose parameters are mean λ and its SD.
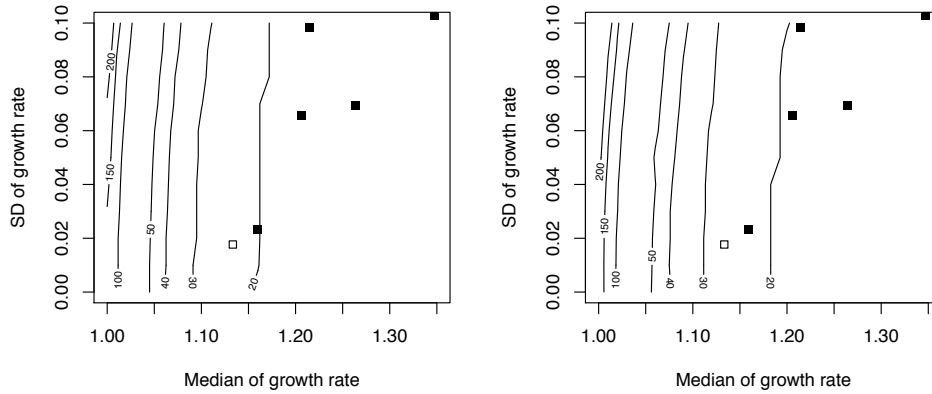
Figure 5. Theoretical MVP contour curves (left panel: with extinction risk < 5%, right panel: with extinction risk < 10%) for an exponential growth model as a function of growth rate λ and its standard deviation. The empty square indicates the actual Scandinavian wolf population (λ = 1.18±0.02), black squares indicate other wolf populations (Wisconsin: λ = 1.16±0.02, Michigan: λ = 1.26±0.07, Montana: λ = 1.20±0.07, Wyoming: λ = 1.21±0.1, Idaho: λ = 1.34±0.1, data from USFWS).

Figure 5 shows that populations experiencing growth rates typical of recovering wolf populations (λ > 1.15 and SD < 0.1) remain viable if they are capped at 30 individuals or more. Considering an acceptable extinction risk of 10%, the parameters at which a wolf population capped at 40 individuals is not viable are for example λ < 1.07 with no variability (SD = 0.0) or λ < 1.09 with a high variability (SD = 0.10). Considering an acceptable extinction risk of 5% instead of 10% generates only small increases in viability levels. Populations appear to be more resilient to increased environmental variation than to decreased baseline growth rate since the contour curves on Figure 5 have a vertical alignment pattern. In other words, a small change on the lambda axis is more likely to require a change in MVP than a corresponding small change on the SD axis is.

Effects of catastrophes

Another way the future can be different from the past is when catastrophes – rare events but with a high impact – occur. There is no obvious satisfying way to model catastrophes as one faces the challenge of estimating the probability of occurrence of an event that has rarely or never occurred before. We circumvent this obstacle by considering many possibilities and adopting an inverse reasoning. Rather than guessing catastrophe patterns, we compute what would be their required frequency and intensity to have the actual Swedish wolf population not viable (with its actual growth rate). We find that a population capped at 30 wolves has an extinction risk lower than 10% even when facing catastrophes from one every decade reducing the population by up to 40% of the population at each occurrence or a catastrophe every century reducing the population by 70% (Figure 6). For a population capped at 100 individuals to not be viable, it would need to face for example one catastrophe every decade reducing the population by more than 60% of the population, or

one catastrophe every century killing almost the whole population (in which case
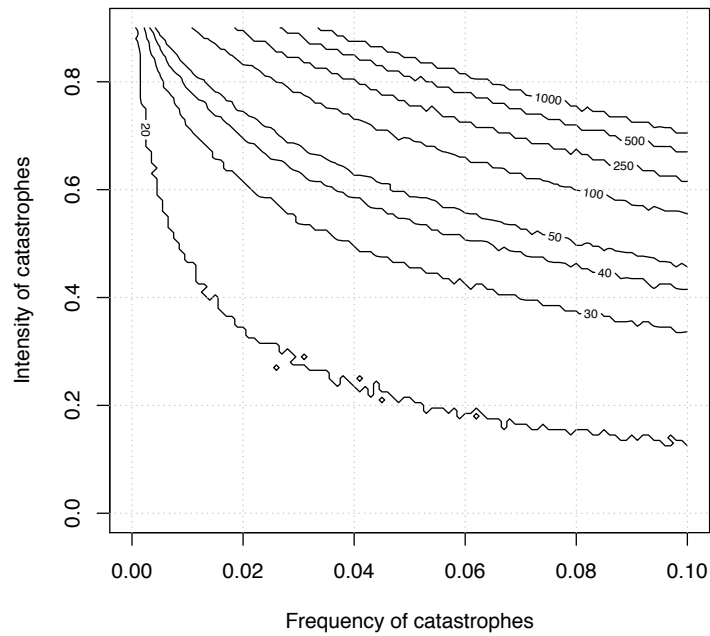no population can actually be viable).

Figure 6: MVP contour curves (with extinction risk of 10%) as a function of frequency of catastro-
phes (one per century = 0.01, one per decade = 0.1) and of intensity (reducing population size by
1% up to 90%) for a theoretical population having the same parameters ($\lambda = 1.18 \pm 0.02$) as the
ones of the Scandinavian wolf population.

Bayesian model

Model description

While the strength of the previous model was its relative simplicity, its drawback was its limited use of available data. During the past 13 years, the Scandinavian Wolf Project has been able to collect one of the most comprehensive dataset of wolves in the world. This data can be instrumental in leveraging our understanding of wolf population dynamics and consequently in estimating possible levels of MVP. The second model we develop is therefore a model whose strength relies on its ability to merge multiple sources of data and prior information in a streamlined way. This model belongs to the family of integrated hierarchical Bayesian state-space models and is actually an extension of the previous model. We modify the first model to include other available data and then run similar computations. While the previous model considered that population at year $t+1$ was the population at year t minus harvest at year t multiplied by growth rate λ, this new model considers that population at year $t+1$ is the outcome of births and deaths occurring during year t. This is also a very general model as any population of individuals experience births and deaths at any time step and the result becomes the updated population. We did not include density dependence in this model (see previous model). The model can be written:

$$N_{t+1} = (1 - m) \cdot N_t + f \cdot R_t - H_t$$

where m is mortality rate, f is litter size and H_t is harvest at time t. We can infer growth rate from the model with $\lambda = (1 - m) + a$ where a is per-capita reproduction rate estimated from f. The model is also written in a hierarchical way, similar to the previous model and also considering observation errors. The additional data we include compared to the first model is annual number of reproductions R_t. We also include prior knowledge in the model by giving informative priors to parameters. We run a Kaplan Meier analysis to compute annual mortality from radio-telemetry data and use the median mortality estimate ± SD as an informative prior to mortality m. From reproduction data, we calculate a median litter size estimate ± SD and use it as an informative prior to litter size f.

We estimate the posterior distribution of each parameter – in particular m, f and a – by running Monte-Carlo Markov chains, implemented in JAGS (Plummer et al. 2003) with R (R Development Core Team 2009). Three chains were initialized with different sets of parameter values chosen within biologically plausible bounds. After an initial burn-in period of 100,000 iterations, we obtained 1,000,000 iterations of each of the chains, thinning each by 10. We successfully checked for convergence using the Heidelberger & Welch stationarity and half-width tests with the CODA package (Plummer et al. 2006).

As with the first model, we need to run simulations that will project the population dynamics into the future to compute MVP. We do this by considering that during the next 100 years, mortality and per-capita reproduction rates are going to be

drawn from the same probability distributions as the one they have been drawn from during the past 10 years. We model both demographic and environmental stochasticities by a binomial distribution for survival and by a Poisson distribution for reproduction. Since we want to infer about a MVP, we cap the population at a ceiling K (considered as a maximum population size implemented by harvest) and we run Monte Carlo simulations (100,000 trajectories) with various values of K (K being constant during each simulations) and compute each time the resulting probability of extinction. The smallest value of K that leads to an extinction probability lower than 10% (or 5% when indicated) is the MVP.

Model assessment

Simulations indicate that our data supports the most a mortality rate $m = 0.24\pm0.02$ and a (winter) litter size $f = 4.29\pm0.47$, which corresponds to a per-capita reproduction rate $a = 0.42\pm0.05$. When converted into a population growth rate, these values indicate the population has had an annual growth rate of $\lambda = 1.18$ which is exactly the same value obtained with the independent first model.
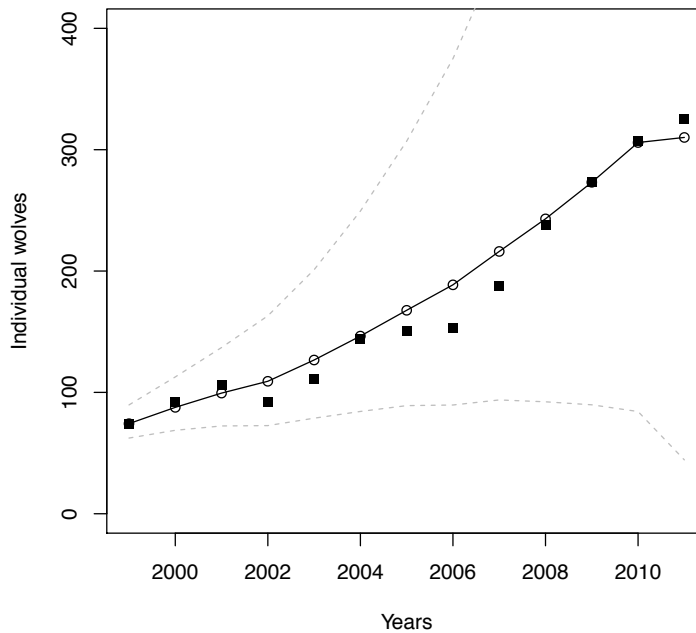

Figure 7: Forecasting simulation starting from 1999 with the Bayesian model ($m = 0.24\pm0.02$ and $a = 0.42\pm0.05$). The black squares are annual census data of the Scandinavian wolf population, the open circles are the median population size predicted from the model and the dashed lines indicates ± standard deviation of our model predictions. Notice how this standard deviation becomes extremely large after just a few years of simulation.

Simulations starting with the size of the wolf population in 1999 as initial population and running for 12 years until 2011 are able to correctly match the data (Figure 7). However, and same as with the previous model, we find that there is a large standard deviation of our predictions (shown by the dashed lines) and that the fur-

ther the simulation moves forward in time, the less precise its forecast becomes. While the second model uses more data and considers wolf population dynamics at a finer scale (i.e. deaths and births rather than only growth rate), we still have a wide uncertainty when predicting population size a few years ahead, and this uncertainty can only become much larger when predicting one century ahead.

Computations of MVP

When capping population sizes, stochastic simulations show that a wolf population with the same annual mortality rate and per-capita reproduction rate as the ones of the Scandinavian population has an extinction risk less than 10% (resp. 5%) if it is capped at 33 individuals (resp. 42 individuals) (Figure 8). In other words, culling all surplus individuals above a threshold of 33 or 42 individuals does not lead to an extinction risk higher than 10% or 5% according to this model and its assumptions. The difference of values between the current and the previous model arises from the fact that the current model describes the wolf population dynamics with finer details by discriminating between two stochastic processes (i.e. survival and reproduction).
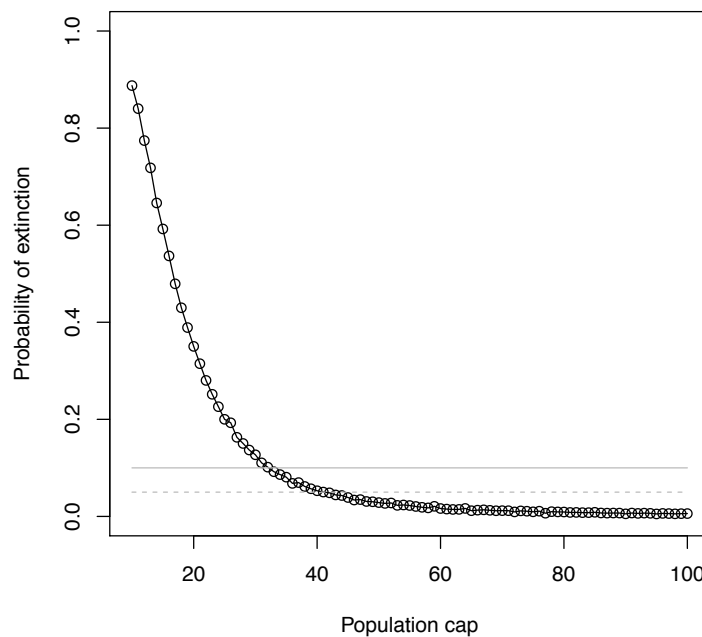

Figure 8: Extinction probability as a function of population cap for a theoretical population having the same parameters (m = 0.24±0.02 and a = 0.42±0.05) as the ones of the Scandinavian wolf population. Horizontal grey lines are 5% (dashed) and 10% (continuous) threshold of extinction risk.

Future scenarios

With this model, we also consider how changes in demographic and environmental conditions may affect population viability. We investigate how MVP levels need to

be adjusted to changes in mortality by running simulations but with different values of mortality rate. We only studied the effect of mortality, as changes in mortality rate has the largest impact on growth rate for large carnivores, i.e. long-lived species. For normally distributed mortality ranging from 0.1 to 0.5 and with the same SD as the one of the posterior distribution of m, we estimate the required MVP by running 10,000 runs of a Monte Carlo simulation for each mortality rate (Figure 9). We find that no population can be viable (for 100 years) if its mortality rate is 42% or higher – extinction is then deterministic. Note that mortality rates slightly smaller than 42% are still likely to lead to extinction, these simulations do not show this because some populations have not yet gone extinct within 100 years. For the Scandinavian population, having a mortality rate of 24%, a population cap of 30 individuals is sufficient to keep extinction risk below 10%.
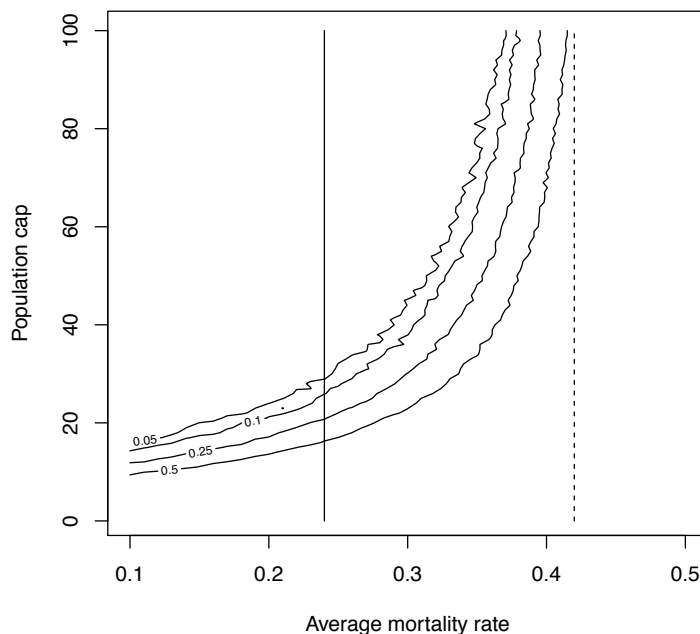

Figure 9: Extinction probability contour curves as a function of mortality rate and population cap (MVP). The actual mortality rate of the Scandinavian population (m = 0.24) is shown by the continuous vertical line. No population is viable if m > 0.42 (dashed vertical line).

Effects of catastrophes

When simulating catastrophes, we find that a population capped at 30 wolves has an extinction risk lower than 10% even when facing catastrophes from every decade and reducing the population by up to 15% of the population at each occurrence or a catastrophes every century reducing the population by 40% (Figure 10). For a population capped at 100 individuals to not be viable, it would need to face for example one catastrophe every decade reducing the population by more than 60%, or one catastrophe every century removing almost all the population (in which case no population can actually be viable).

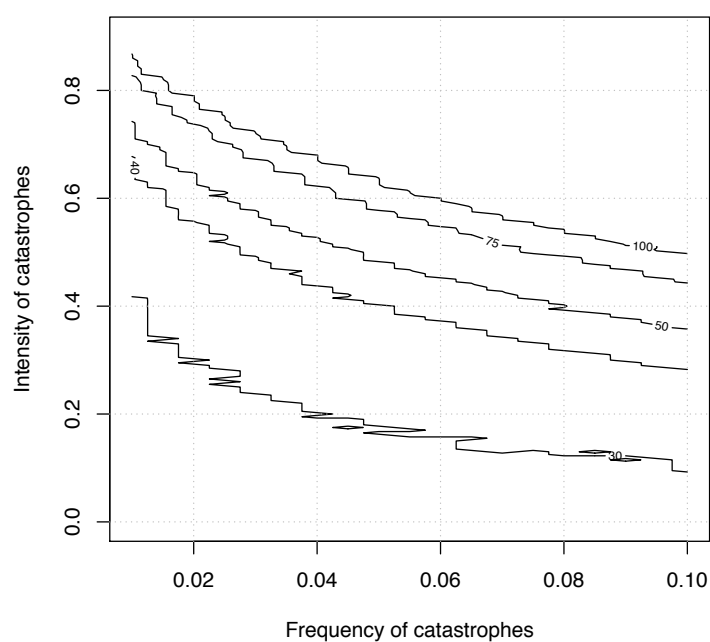Figure 10: MVP contour curves (with extinction risk of 10%) as a function of frequency of catastrophes (one per century = 0.01, one per decade = 0.1) and of intensity (reducing population size by 1% up to 90%) for a theoretical population having the same parameters (*m* = 0.24±0.02 and *a* = 0.42±0.05) as the ones of the Scandinavian wolf population. Irregular patterns are stochastic artefacts.

Individual-based model

Model description

General approach

The two previous models were not wolf specific and could have been used to model the viability of any population. Any population has a growth rate and experiences deaths and births of individuals. The only wolf specific elements in these models were parameters that we estimated by Bayesian inferences. Another method to address viability questions in ecology is to develop more realistic models – based on high quality data – which try to capture with some degrees of realism what actually happens in the lives of animals (Case 2000). These models can be age-structured where one describes the survival and reproduction rates for age-related classes of individuals. This is the basis of Leslie matrices and is the approach also followed by the packaged model VORTEX (with demographic, environmental and genetic stochasticities further included, Lacy 1993 & 2000). More realism can be brought by considering stage-structured models where classes of individuals can consider for example social status. However, the field of viability modelling has recently benefited from a conceptual and methodological improvement with the introduction of rule-based models – more often termed individual-based models (Grimm et al. 2005). Because the model is ruled-based, it can have the individual (or a pack or a pride) as its functional unit and this allows consideration of more explicit biological realities. Individual-based models can consider much more than random events in survival or fecundity since individuals or packs can be tracked during the whole simulation with dynamically varying parameters such as spatial aspects, behaviour, or social mechanisms. Because the model considers mechanisms at the individual or pack level, the demographic consequences of these mechanisms are population level emerging properties of the model and are not predefined by equations as in more traditional population models (as they were in the previous two models).

Using an individual-based model, as opposed to traditional age-class models, is a particularly relevant choice when modelling wolf population dynamics. The wolf is a social animal living in packs, which is in fact the functional unit of a wolf population. Events at the individual and pack levels – e.g. dispersing from a natal pack, founding a new pack – shape the overall population dynamics. In addition, killing individuals has different effects if this individual is a pack breeder or a non-breeding animal. We have developed a wolf specific rule-based model where every wolf is described as an "object" (in a computer programming sense) and characterized by its biological "attributes" (sex, social status, pack, age, etc.) and where every pack is also described as an "object" with attributes (breeding male and female, litters, etc.). The rules governing how individuals and packs react to events have been constructed and parameterized from the long-term biological data of the Scandinavian Wolf Project. Also in this model, we did not include density dependence (see above). The model is coded in Objective-C and compiled with CLANG

in Xcode 4.3. It uses the GNU Scientific Library for probability arithmetic, libdispatch for multi-threading and the Mersenne Twister random number generator.

Algorithms

The model runs Monte Carlo simulations by repeating 10,000 random trajectories, each of them starting by the creation of a fixed initial number of packs containing each a dominant couple. The time step in the model is one month and wolves in the simulated population go through particular events according to their sex, status, pack membership or age. Every month, all individuals survive or die following a Bernoulli trial drawn from a monthly survival probability normally distributed with same shape parameters of the posterior distribution of survival rate estimated in the previous model (mortality rate $m = 0.24\pm0.02$). In this way, we include both demographic (Bernoulli trial) and environmental stochasticities (posterior sampling). Non-reproducing individuals in packs (i.e. young of previous year litters) disperse to become transients or remain in their pack following a Bernoulli trial drawn from a monthly dispersal probability estimated from empirical data of the Scandinavian wolf population (Wabakken, unpubl. data). When the breeding couple in a pack dies, all other members of the pack automatically disperse to join the pool of transients and the pack ceases to exist and is removed from the population. Every month, transients will try to find a transient mate of the opposite sex and to settle on a vacant territory. Transients also try to settle in packs where a same sex breeder is missing. Production of litters in packs is modelled by sampling from a Poisson distribution, whose parameter is itself drawn from a normal distribution of litter size with same shape parameters of the posterior distribution of litter size estimated in the previous model ($f = 4.29\pm0.47$). Similar to survival, we include in this way both demographic (Poisson trial) and environmental stochasticities (posterior sampling). Winter population count is implemented one time per year (in December).

Simulations

Except for the simulation to evaluate whether the model can match well the observed Scandinavian wolf population growth, we include a population ceiling, which is the MVP. We define the MVP in individuals and any individual above the ceiling is automatically removed. When removing individuals, all adult wolves have a probability to be removed and random Bernoulli trials are performed until the population is back at its ceiling.

Model assessment

We evaluate the model by confronting it with summary statistic of several wolf populations in the world. We run simulations to compute the growth rate of wolf populations with median mortality rate ranging from 0.15 to 0.75. We compare the simulated growth rates with values obtained for field studies of several wolf populations (note that contrarily to the two previous models, we do not fit this model to these data, because cannot write its likelihood). We find that the model captures well the dynamic of most wolf populations (Figure 11). All of them (except for low

mortality) are within the 95% confidence interval. The model predicts larger growth rates for low mortality rates than the empirical data and this is likely due to the fact that real-wolf populations were close to carrying capacity, which is not the case for simulated data.
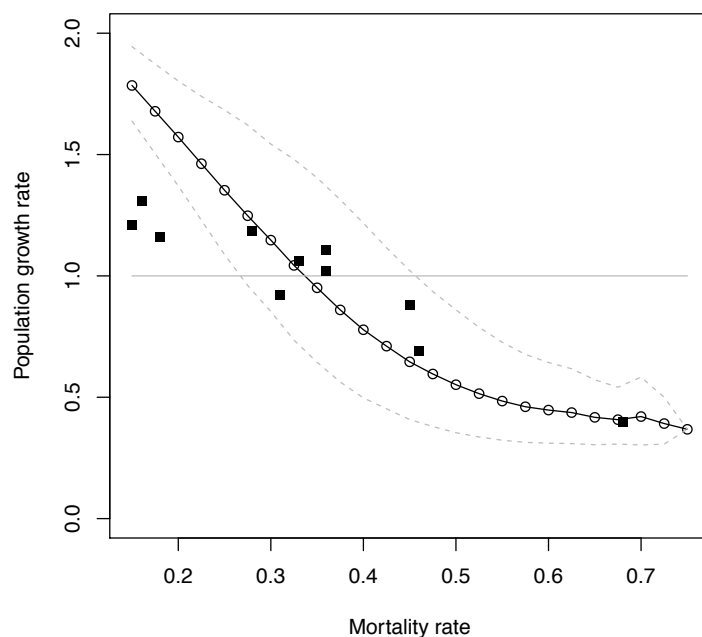

Figure 11: Population growth rates computed by the model as a function of mortality rate (which is the same for all wolves). Continuous black line is median of simulations, dashed is ±SD and black dots are data from different wolf populations worldwide (see Marescot et al. 2012 for details).

We also simulate for 32 years the trajectory of a wolf population starting with 1 pack. We find that the model matches relatively well the observed growth of the Scandinavian population from 1980 to 2012 (Figure 12). The model does not fit the data as well as the previous models because here we cannot run MCMC simulations, the model being individual-based, writing its likelihood is intractable. In addition, the model does not consider harvest events.
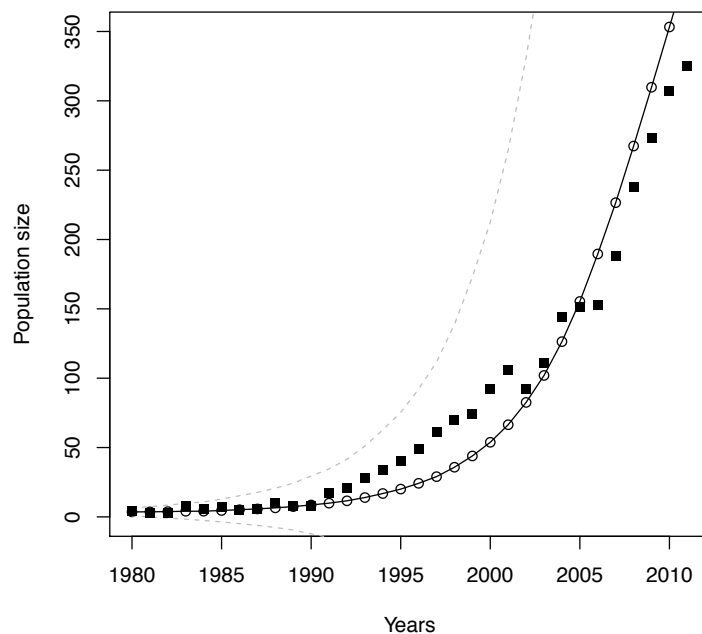
Figure 12: Forecasting simulation starting from 1980 with the individual-based model. The black squares are annual census data of the Scandinavian wolf population, the open circles are the median population size predicted from the model and the dashed lines indicates ± standard deviation of our model predictions. As with previous models, notice how this standard deviation becomes extremely large after just a few years of simulation.

Computations of MVP

When capping population size, stochastic simulations show that a wolf population with the same annual mortality rate and per-capita reproduction rate as the ones of the Scandinavian population has an extinction risk less than 10% (resp. 5%) if it is capped at 38 individuals (resp. 41 individuals) (Figure 13). In other words, culling all surplus individuals above a threshold of 38 or 41 individuals does not lead to an extinction risk higher than 10% or 5% according to this model and its assumptions. These values are remarkably similar to the much simpler previous models.
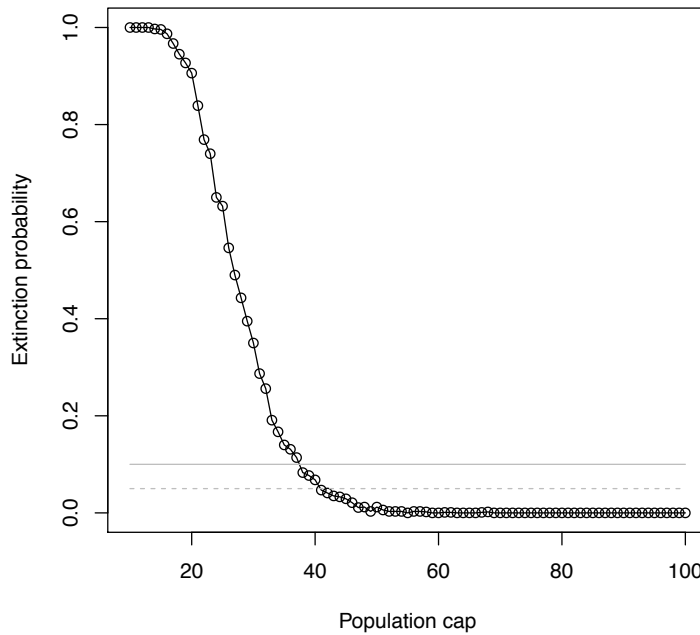
Figure 13: Extinction probability as a function of population cap for a theoretical population with parameters (m_{pack} = 0.24±0.02 and f = 4.29 ±0.47) obtained from the Scandinavian wolf population. Horizontal grey lines are 5% (dashed) and 10% (continuous) threshold of extinction risk.

Future scenarios

We investigate how MVP levels need to be adjusted to changes in mortality by running simulations but with different values of mortality rate. For mortality ranging from 0.1 to 0.5, we estimate the required MVP (Figure 14) by running 1,000 runs of a Monte Carlo simulation. We find that no population can be viable during 100 years if its mortality rate is 39% – where extinction is deterministic. Note that mortality rates slightly smaller than 39% are still likely to lead to extinction, these simulations do not show this because some populations have not yet gone extinct within 100 years. For the Swedish population, having a mortality rate of 24%, a population cap of 30 individuals results in an extinction risk below 10%.
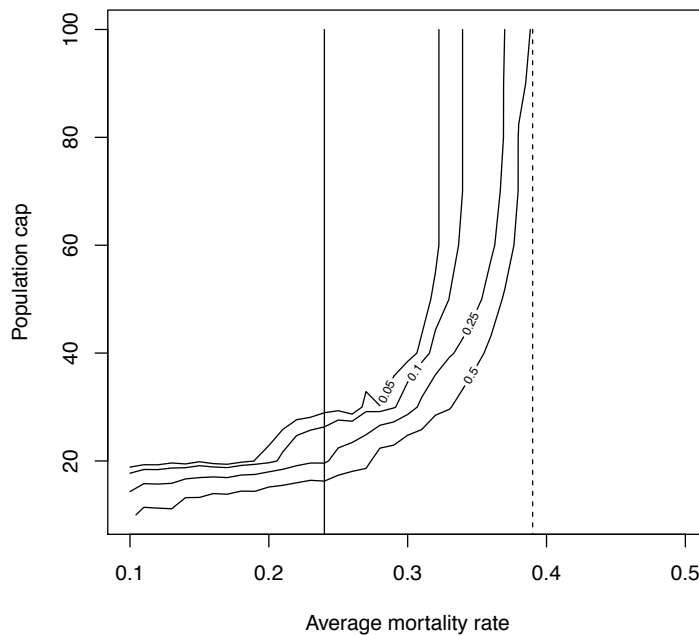
Figure 14: Extinction probability contour curves as a function of mortality rate and population cap (MVP). The actual mortality rate of the Scandinavian population (*m* = 0.24) is shown by the continuous vertical line. No population is viable if *m* > 0.39 (dashed vertical line).

Effects of catastrophes

When simulating catastrophes, we find that a population capped at 40 wolves has an extinction risk lower than 10% even when facing catastrophes from every decade and reducing the population by up to 30% of the population at each occurrence or catastrophes very century reducing the population by 60 %. For a population capped at 100 individuals to not be viable, it would need to face for example one catastrophe every decade reducing the population by more than 60% of the population, or one catastrophe every century removing almost all the population (in which case no population can actually be viable).

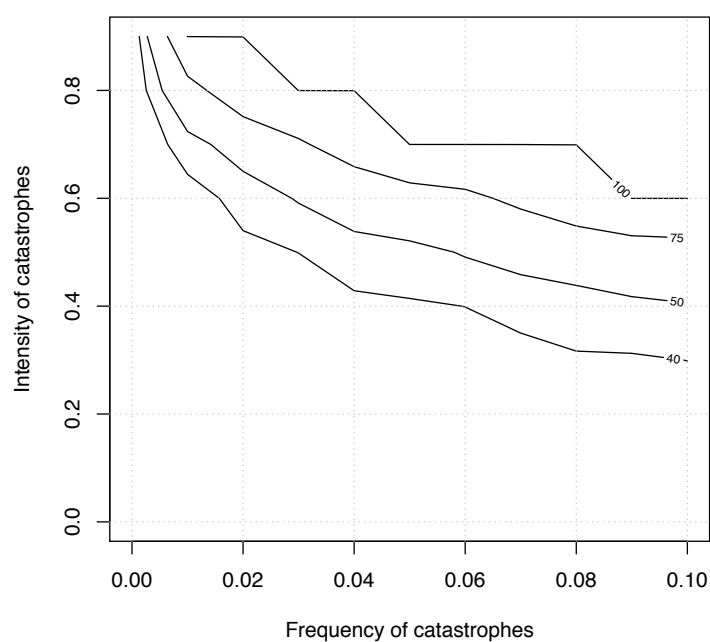Figure 15: MVP contour curves (with extinction risk of 10%) as a function of frequency of catastrophes (one per century = 0.01, one per decade = 0.1) and of intensity (reducing population size by 1% up to 90%) for a theoretical population with parameters (m_{pack} = 0.24±0.02 and f = 4.29 ±0.47) obtained from the Scandinavian wolf population. Irregular patterns are stochastic artefacts.

Discussion

Synthesis

Population viability analysis is an example of how scientific advances – in this case model-based inferences – may be used to answer questions for which they have not been designed and should not be used, e.g. determining minimum population sizes (Reed et al. 2002). In fact, a recent review of the issue concluded that "population viability analysis is an inexact science and there is no single 'magic' population size that guarantees population persistence" (Flather et al. 2011). Still, a strong demand from decision makers and the lack of suitable alternative tools result in that, whether this is recommended or not, models will be used to make number-focused predictions. The responsibility of scientists working with applied research questions is then to find approaches and methods to answer questions asked by the management authorities and to use models in an appropriate way. Reviews on PVA have found that relying on a single software may lead to misleading conclusions and that keeping track of uncertainty is fundamental (Reed et al. 2002). Based on these recommendations, we used three different models, each relying on a different set of assumptions.

The first two models had very general assumptions and could have been used for any kind of species. On the contrary, the third one was developed on purpose to model wolf demography. In all three approaches, uncertainty was accounted for. The first two models were hierarchical where uncertainty in count data was explicitly quantified. The second model relied on Bayesian statistics and made use of prior knowledge in wolf parameters (i.e. mortality and reproduction) – incorporating the part of unknown, which remains in these parameters estimates. The third model is the one for which handling uncertainty is the most challenging as the definition of rules makes it less possible to include what is termed "process errors". Still, this model used parameters including uncertainty and not point estimates. For any one of our three models we did not include density-dependence because there is plenty of space and wild ungulate prey sufficient for a much larger wolf population on the Scandinavian Peninsula (Karlsson et al. 2007), and both Sweden and Norway have some of the highest moose / wolf ratios in the world (Sand et al. 2012). Because of the one-month time frame given to conduct the analysis and write this report, we did not have the possibility to conduct a full sensitivity analysis. The use of the first two models may appear superfluous since the third model considers much finer details of wolf population dynamics, but scientific evidence points rather towards the opposite. In a review paper on the use of demographic models of population viability in endangered species management, Beissinger & Westphal (1998) recommended to use simple models rather than more complicated ones. While it has also been advised that model structure should be detailed enough to use all the relevant data – and the more data the better (Akçakaya & Sjögren-Gulve 2000), Ellner et al. (2002) found that increasing the complexity of a model parameterized with the right amount of data would not produce more correct extinction risk estimates. In fact, one of the first textbook on applied population dy-

namics and uncertainty (Hilborn & Walters, 1992) stated that: "*General knowledge about a stock (including distribution, longevity, and growth) is not a reliable guide to the best model representation for a particular policy purpose. Ludwig and Walters (1985, 1989) have recently shown that the best model choice can even be one that is known to be unrealistically simple. Ludwig and Walters generated simulated data sets using an age-structured model (so they knew the "correct" model for the entire data set), and then showed that there are conditions under which the simulated population could be better managed by fitting data from it to a simpler biomass dynamics model than by fitting to the model that was used to generate the data in the first place. Generally, they concluded that simpler models are likely to outperform the correct (biologically more complex and realistic) model in situations where there has been little informative variation in harvest patterns over time; in these cases, parameter estimation performance for the simpler models was much better than for the realistic model.*" Even if an exponential model would alone not have been suitable to estimate a MVP for the Scandinavian wolf population, we believe it was important to include a simple and general model in our analyses. Despite we return MVP as point estimates, all our models keep track of uncertainty as computations are done with the posterior distribution samples returned by the MCMC. This posterior distribution includes all uncertainty inferred by merging the mechanistic population model, the data and the prior information in a Bayesian framework. The Bayesian approach is particularly suited to handle uncertainty as its results can be interpreted as degrees of belief rather than as outcomes of an infinite series of trials under identical conditions. While Ludwig (1999) and Ellner et al. (2002) found that small changes in input parameters may lead to large differences in estimated MVP we believe adopting a Bayesian approach (also recommended by Ludwig 1996) makes suitable the use of models with more structural uncertainty than model 3.

We did not use "canned" packages such as VORTEX (Lacy 1993 & 2000), which have contributed to the widespread use and acceptance of PVA (Beissinger 2002) despite a relevant interpretation of simulations results is often dependent on the ability to write one's own model (Jonzén *in litt*.). The generality of canned software precludes the tuning to specific questions. This is particularly important when modelling population for which a social unit – the pack – is the functional unit of the population. Because incorporating social structure cannot be properly done with these generic models, their usefulness to model social canid population dynamics is problematic (Heinsohn 1992) and would deliver speculative results. Finally, and while we could have validated our models against a generic software, we decided not to do it. We believe that having three different models, all handling uncertainty, was a more appropriate approach than to use a canned package as a reference point, for which different versions have been shown to return different results (Mills et al. 1996) or to underestimate extinction risk despite being commonly used (Lindemayer et al. 2000).
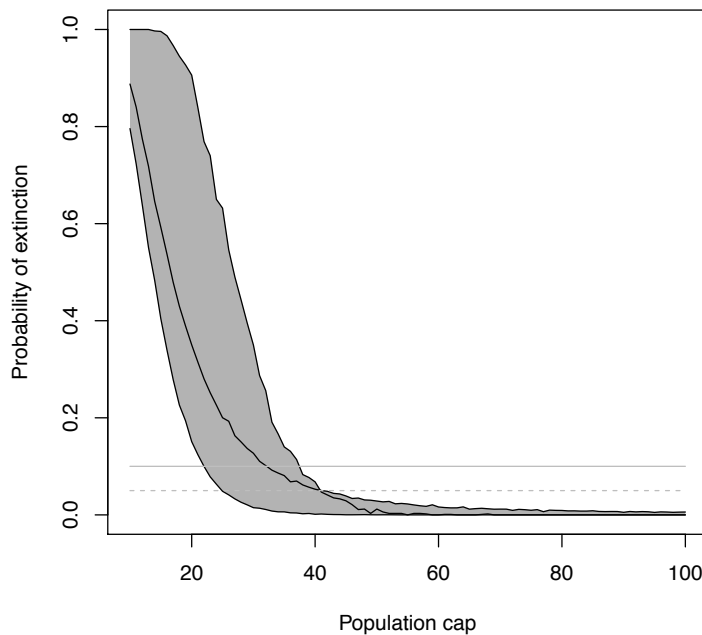
Figure 16: Summary estimates of extinction probability as a function of population cap (in individuals) for a theoretical population with parameters obtained from the Scandinavian wolf population (and therefore without catastrophes). Continuous black lines are median estimates returned by each of the 3 models (see Fig. 4, 8 and 13). The grey area shows extinction probabilities for each population cap that are included within all 3 model estimates. Horizontal grey lines are 5% (dashed) and 10% (continuous) threshold of extinction risk.

We ran similar simulations for all three models and found that they all return very consistent results and this increases the level of confidence in our conclusions (Figure 16). We find that small wolf populations (< 100 individuals) are large enough to escape stochastic extinctions and only extremely small wolf populations (< 40) are not viable. In agreement with empirical evidence (Fuller et al. 2003), we also find that no wolf populations can be viable if their mortality rate is > 35%, a value at which extinction is deterministic. Based on data from recovering wolf populations in Europe and North America, there is no evidence that increased environmental fluctuations may seriously affect wolf viability. We addressed catastrophes by asking what would be the their frequency and intensity which would require much larger MVP than the one of the Scandinavian wolf population. We find that such catastrophes should be quite severe and frequent to impose a much larger MVP, a pattern that so far remains unsupported by data on catastrophes for any wolf population in the world. In short, a wolf population with the same size and growth rate as the ones of the current Scandinavian wolf population is undoubtedly demographically viable under IUCN Red List criteria E (i.e. risk of extinction is smaller than 10% over 100 years). As stressed in the introduction, our models excluded genetics and we remind readers that our conclusions can only be valid under the assumptions that genetic issues faced by the Scandinavian population have been solved.

Comparison with other wolf models

This report is not the first contribution to estimating what is an MVP for a wolf population and several wolf PVAs have been published in the peer-reviewed literature. For the Scandinavian wolf population, Ebenhard (2000) used VORTEX to estimate the extinction risk for wolves under several different scenarios. For the scenario (growth rate of 1.20) that was closest to the development of the Scandinavian wolf population so far (growth rate of 1.18), Ebenhard (2000) found that a population cap of 25 wolves had an extinction risk of 5 % (Table 4, scenario L in Ebenhard 2000). Decreasing the growth rate increased the MVP (Figure 1 scenarios A-G in Ebenhard 2000) in a similar way as the results in this paper (Figure 5). In Ebenhard's simulations, without genetic effects, a population cap of 100 was viable (extinction risk 7 %) even with as low growth rate as 1.02 (Figure 1, in Ebenhard 2000), which is very similar to the result in this report (Figure 5, $\lambda = 1.02$, SD = 0.05). Nilsson (2004) also used VORTEX to estimate the extinction risk for wolves under several different scenarios. Nilsson (2004) focused on long-term (1000-year perspective) genetic effects, which is very different from the aim of this report. However, Figure 1 in Nilsson (2004) indicated that a population cap of 100 individuals had an extinction risk of < 10 % after 100 years (the bar at 120 years is less than 10 %). A more recent model (Bull et al. 2009) focused on the Norwegian side of the population (which was assumed isolated from the Swedish one) but run simulations for the Scandinavian population for comparative purpose. The authors found that the extinction risk was strongly correlated with illegal mortality (i.e. triggering a deterministic extinction after a certain rate). When illegal mortality was kept low, Bull et al. (2009) also found that low extinction rates similar to the ones of Nilsson (2004). Chapron et al. (2003) studied the viability of wolf populations in general and developed an individual-based model to evaluate how extinction risk was affected by different management strategies. They found that under favourable demographic scenarios, wolf populations capped at 4 packs would have a low extinction probability (2%) in 100 years. In North America, Vucetich et al. (1997) simulated the wolf population on Isle Royale and concluded that a population of 50 wolves only had a 30 % chance to survive beyond 100 years. However, their model was particular as they simulated the abundance of moose (the main wolf prey) as a statistical autoregressive process and made it affect the wolf population dynamics in a density dependent way that resulted in a carrying capacity of the wolf population around 50 individuals (i.e. the maximum number of wolves observed on Isle Royale). In their simulations the growth rate was high when then the number wolves was low and number of moose was high, for example from year 0 to year 9 in a simulation the number of packs increase on average by 20 % per year (Figure 2b in Vucetich et al 1997; $\lambda=1.20$). Furthermore, in a simulation the number of wolf packs decreased after year 9 due to a decline in the moose population (Figure 2b in Vucetich et al. 1997). Other wolf population models have been developed and published but they address questions that are different from the one discussed in this report (Cochrane et al. 2003, Haigh & Mech 1997, Haigh et al. 2008, Theberge et al. 2006, Patterson & Murray 2008, Marucco & McIntire 2010).

Except for the very specific case of Isle Royale, all literature consistently concludes that (i) wolves have a high potential growth rates and (ii) small wolf populations can be viable.

Conclusions

It is not possible to come with a single absolute value of what is a MVP for any population. We believe the opposite would be a lack of scientific rigor. First, the wolf population dynamics remains vaguely understood like any biological process as many confounding factors can results in multiple feedbacks. Second, PVA relies on the assumption that it is possible to infer about the future by explaining the past. While this is possibly correct to some extent, it is also certainly wrong in absolute terms. With major influences of human activities on wolf population dynamics, landscapes and ecosystems and, last but not least, global patterns of natural phenomena, no reliable inferences on the future population dynamics of wolves in Scandinavia can be made. As explained at length earlier, we should not give an exact number of what is a wolf MVP, however, we can indicate what is not a wolf MVP. Based on our three models, we conclude that a wolf population capped at less than 40 individuals is not viable under IUCN Red List criteria E (i.e. risk of extinction is smaller than 10% over 100 years). Furthermore, a wolf population is not viable if its annual mortality rate exceeds 0.35. Environmental fluctuations and catastrophes require larger MVP and we find that a population capped at 100 wolves is not likely to go extinct in light of the available empirical data about catastrophes. A wolf population with the same size and growth rate as the ones of the current Scandinavian wolf population is undoubtedly demographically viable under IUCN Red List criteria E. Readers of this report should bear in mind that all our models presented here relied on the assumption – as stated by the assignment – that genetic issues – including their demographic consequences – have been resolved, which is not yet the case. Genetic considerations have often been ignored in conservation planning (Laikre et al. 2009) but our report ought not be interpreted as a further attempt to sidetrack genetics. Full consideration of demo-genetic issues for wolf conservation in Scandinavia is a question deserving particular importance and which we are currently addressing for the years to come. Finally, we want to stress that the use of a single estimated MVP-value or a single value for Favourable Reference Population, cannot, and must not, replace a continued updating of relevant demographic and genetic parameters, as warned by Flather et al (2011). The best guarantee to keep the wolf population viable in the future is not a "magic number" but an adaptive management that has access to a continuous updating of the population status.

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Appendix 1: Assigment

Genomföra en kvantitativ (endast demografisk) sårbarhetsanalys avseende varg i Sverige. Sårbarhetsanalysen ska tydliggöra minsta livskraftiga population av varg baserade på IUCN:s kriterium E. Analysen ska bygga på senast dokumenterade kunskaper om den skandinaviska vargstammen, förutsatt att de genetiska frågorna har lösts. Uppdraget ska utföras efter konsultation beträffande metodik och resultat med relevant nationell och internationell forskningskompetens. Dokumentation av konsultation och sammanställning av inkomna synpunkter ska ingå i redovisningen såväl som hur synpunkterna omhändertagits. Rapporten ska innehålla en populär-vetenskaplig sammanfattning på svenska.

Appendix 2: Comments

We circulated a preliminary report to scientists who we believed could provide relevant insights on our work. In this Appendix, we include all the answers we have received. Note that because of the short timeframe of the assignment, we could not give more than 72 hours to people for commenting on the report, and some other scientists had not the possibility to comment. The comments received illustrate that the use of PVA remains very much debated in the scientific community. There is clearly no firm agreement on how to best proceed when dealing with questions similar to the one we have been asked and a convergence of opinion is unlikely to be reached in one month. Some people strongly suggest not answering the question, while others recommend giving the most accurate answer possible. The approach we adopted in this report – which several comments find appropriate – was to develop separate and independent models relying on novel statistical tools to adequately handle uncertainty. In the final version of the main report, we have included or discussed as many of the comments as we could, given the extremely short timeframe we had between receiving the comments and delivering the main report (36 hours). We heartedly thank all scientists who were able to send us comments, which are included below.

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This report is an excellent example of the optimal way to use science to answer a management question. The question is very simple but the answer is scientifically extremely difficult, to the point that serious scientists admit that there is no clear answer. In spite of the excellent quality and quantity of data available on the study population, the simulations performed through three models of increasing complexity are not enough to bring any conclusive number as the threshold for survival for the next 100 years. Models are the only way to simulate populations' trajectories in time and space but, no matter their complexity, they remain an imprecise representation of reality, necessarily built on several assumptions and forced to ignore unknown amounts of uncertainty in the number of parameters and their values. Within these huge conceptual and operational limitations, the proposed models still produce some results that can be useful to managers: first in organizing the thinking on the potential key parameters influencing population persistence, second in indicating some bottom-line thresholds produced under their simplistic scenarios. The authors of the report are very clear in calling the attention to the critical assumptions that limit the applicability of the results, including the solution of the genetic issues, the persistence of current environmental conditions, and the unavoidable simplifications used in the biological rules applied to the third model. Therefore, I strongly urge managers not to dismiss those caveats and avoid taking

the numerical thresholds as reliable base for management. There is no magic number for any animal population, and even less so for the highly structured and adaptable wolf populations.

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You are to be congratulated on accomplishing this PVA simulation study in such a short time. I know of several PhD theses that didn't accomplish as much even though the student had 5 years to do it! Although I would be the first to champion an analysis like that you've done, I also find it ridiculous that the European Community would hold stock in such a subjective method. PVA is useful as an exercise to hypothesize how you think that the system works, but one cannot have any confidence in the numerical results emerging from such an analysis (e.g., the 10% probability of extinction threshold). Structural inadequacies in the ecological model, and inability to estimate parameters make such analyses useful as academic exercises, but they are much too easily manipulated to be objective criteria for making management decisions. Furthermore, PVA is inherently about probabilities and stochastic processes that can be difficult to summarize succinctly, and attempting to hang a result on a single number like a MVP or the 10% probability threshold is dangerous ground. As you said you would do, I suggest some key references be cited reinforcing strong caveats that must go with any analysis of this sort. Most notably you've neglected the effective assault on PVA and MVP by Don Ludwig. His work was extremely critical of analyses such as you've produced, and I'm surprised that you've not cited these seminal works (e.g., Ellner et al. 2002. *Cons. Biol.*; Ludwig 1999. *Ecology* 80:298-310; Ludwig *Ecol. Appl.* 6:1067-76). Assumptions about model structure, density dependence, and poor estimation of parameters makes every PVA that has ever been attempted a hypothetical exercise at best. For the model to be complex enough to do a reasonable job of capturing interesting ecology (e.g., predator-prey interactions) we need too many parameter estimates to imagine that we can estimate the probability of extinction for any real-world population (especially for a species at risk where population size is seldom large enough to yield the sample sizes necessary for reliable model parameterization). In some ways working with simpler models is worse because we know that the performance of the model is so strongly tied to structural assumptions in the model; although certainly simpler models make the modelling easier and with more reliable projections (Ludwig 1999). My contention is that the model must reflect basic features of the ecology of the population or it is not reasonable. For example, basing a PVA on an exponential growth model for a species like the wolf is simply not useful for conservation applications, as in the first of the 3 models estimated. From a conservation perspective, a demographic model that is independent of habitat covariates is not useful or reasonable. We cannot forecast well with demographic models, but we can anticipate future habitat management

reasonably well (why else would major timber corporations retain forest model-lers?). Therefore, the real hope for PVA is this link with habitats and conservation of places where wolves can persist (see Boyce et al. 2001. *IBA Monograph*). Wolves are NOT randomly distributed throughout Sweden, and there are good reasons why they are abundant in some areas and absent in others. Wolves occupy a wide array of habitats and forage on a large number of prey. But this does not imply that all habitats are equally important for wolves, and as true in essentially all conservation issues, habitat is crucially important. Likewise, I have strong reservations about the Young et al. (1994) paper for a number of reasons that we articulated in the Erb and Boyce (2001) paper that is attached. Doing a substantive job of estimating variances for all of the parameters used in your analysis is an onerous task, and the downfall of most PVAs given how sensitive PVA can be to variances in the system. This problem is not resolved by using Bayesian methods. Indeed, Bayesian methods are highly controversial because of underlying assumptions, and I look forward to an exchange between you and Subhash Lele on this topic at the meeting this summer in Evenstad. As I've explained in previous publications, we should never be making management decisions based on the outcome of a PVA and I have contempt for the IUCN guidelines that "formal PVAs" should be required. Such guidelines jeopardize our credibility as scientists. Generally I do not disagree with the conclusions that you make, but when management issues are at hand, I would suggest that justification should be based on the empirical evidence and not the modelling results. I am sorry that I cannot provide a more favourable assessment of your population viability analysis. As a modelling exercise, you did a commendable job. But limitations of the method and the objectives render demographic PVA a process that is useful for research reference, but I caution against using it to base management decisions.

Prof. Tom Hobbs, Colorado State University

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I have read this engaging, well-prepared report. My general conclusion that the authors have done an unusually credible job of addressing one of the hardest problems in conservation biology–advising decision makers on actions required to protect a rare species from extinction. The general approach of viability analysis has roundly criticized in the scientific literature, which speaks to the difficulty of the problem. However, the Bayesian state-space methods employed here are novel, and to some extent overcome the flaws of traditional viability analysis. The novelty arises from separating process variance from observation error, thereby allowing true forecasts-that is, estimates of the future population size accompanied by rigorous credible intervals. This approach allows the authors to predict the probability that the population will be above or below a given threshold in a way that is entirely credible. The concept of process variance is key to understanding this prediction.

Process variance includes all of the variation that the population experienced since its return but that is not specifically accounted for by the model. So, as long as the sources in the future resemble those in the historic data used to estimate process variance, the forecasts of the model are sound. This represents a fundamental improvement over predictions of earlier viability models. The use of multiple types of models is notable strength. The fact that of these models arrived at qualitatively similar conclusions reinforces those conclusions. I think it is important to conclude by saying how I think these results should be used. They are quantitatively, state-of-the-art, but that doesn't mean that policy makers should view them as anything more that the best approximations at hand. We all know that the future is uncertain and that past data and experience have limited value in reducing that uncertainty. Thus, it is my belief that the results here should be seen as the best possible guidelines and that decisions should incorporate them alongside societal values, which of course, must ultimately enter all policy decisions. That said, I do not believe that addition analysis, different models, or consultation with experts would give results that are meaningfully different from those offered here. In the end, if the values of Swedish citizens seek to assure the viability of wolves, then decision makers should view the modeling results as optimistic and set population targets that exceed thresholds for viability, thereby increasing the likelihood that the wolf population will persist.

Docent Niclas Jonzén, Lund University

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The Scandinavian Wolf Project (Skandulv) has received an assignment from the Swedish Environmental Protection Agency to "*Conduct a quantitative (demographic only) viability analysis for wolves in Sweden. The viability analysis will clarify what is the minimum viable population of wolves based on the IUCN criterion E. The analysis shall be based on the most up-to-date scientific knowledge of the Scandinavian wolf population, and under the assumption that genetic issues have been resolved.*" In the Swedish version of the summary (please add this also in the English version), it is explicitly stated that by taking on this assignment, one is actually infringing the scientific convention of not conducting VPA to arrive at a population extinction risk. For good reasons, the scientific community advices against using VPA to estimate extinction risk (unless put in a decision-oriented framework where alternative management actions are compared in the face of uncertainty about the true state of nature). My opinion here is no different and has been well described by others. If I may be so bold as to cite Ludwig (1999):

"It is understandable that biologists, when confronted by the requirement to make recommendations based upon limited data and resources, may use "the best information available" to generate predictions, even though these may depend upon computer models that have quite limited validity. Such an approach is encouraged by legislation and regulations based upon the expectation that scientists will be

able to arrive at well-founded conclusions based upon the data and resources that are available. Legislators and management agencies are encouraged in such beliefs by scientists who are anxious to promote better decisions in critical situations. But such an exaggeration of our capabilities carries a high risk of failure and subsequent disillusionment. It would be better to be more modest about our understanding and achievements, and to help decision makers understand the complex, realistic arguments that pertain to most conservation decisions (Doak and Mills 1994)." Given that I am sceptical against this exercise in the first place, mainly because I'm afraid that it can be mis-used and it gives a false impression of how much we really know about extinctions, I would like to support the authors choice in presenting and analysing a range of alternative models differing in complexity and realism. I think they have done a great job by contrasting three interesting model alternatives, and it is indeed encouraging that the three alternative models give similar results. I think, however, that it should be stressed even further (it is mentioned at least once in the report) that the analyses rest on the assumption that prey density is not limiting. Moose density ought to be the most important part of wolf habitat quality. If prey become limiting we may expect density dependent effects and possibly spatio-temporal changes (due to social structure dynamics) that may give rise to non-linearity in a non-spatial model not accounting for such complexity. It is not clear to me whether the rule-based model actually captures that.

Prof. Linda Laikre, Stockholm University

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The time frame for commenting on this report is very short, and coincides with several other commitments of mine (as has already been pointed out to the Swedish Environmental Protection Agency). Therefore, I will not be able to provide in depth comments on this work. Brief comments:
Both the assignment from the Swedish EPA and the present report seem to rest on the idea that the IUCN Red List criterion E deals with extinction risks over 100 years using demographic data only. This is not correct. The Red List criterion E is defined as an analysis that estimates the extinction probability making "full use of all relevant available data" (IUCN 2001). Therefore, a PVA that deals only with demographic and environmental stochasticity while ignoring other available information of relevance to extinction risk is not consistent with this criterion.
The fact should be stressed in the report, both in the Summaries (Swedish and English) and in the main text.
It should be stressed even more clearly that Favourable Conservation Status (FCS) requires larger population sizes than an MVP, requires population viability over much longer time frames than 100 years, and needs to include conservation genetic considerations. This should be pointed out both in the Summaries (Swedish and English versions) and in the main text.

Life table data and all parameter values that underlie the analyses should be presented.

The phrasing "We stress our results should be interpreted cautiously because they rely on the assumption that genetic issues have been solved" may provide the reader with the false impression that genetic considerations can be ignored if they have been "solved". But genetic considerations should always be included when assessing extinction risk, providing estimates of MVP, assessing FCS, etc. This needs pointing out in the report (summary and main text).

The statement "We would like however to point out that genetic issues are more dependent on diversity and connectivity between populations than on population size alone" can be interpreted as if the census size of a population is not of direct concern from a conservation genetics perspective. On the contrary, the population size is of direct relevance for rates of inbreeding and genetic drift, and thus the potential for harbouring genetic diversity. This is one of the reasons why MVPs estimated from PVAs that do not include genetic considerations is not recommended (e.g. Allendorf & Ryman 2002 in "Population Viability Analyses", edited by Beissinger & McCullough and published by the University of Chicago Press). Similarly, demographic characteristics are often directly linked to and affected by the genetics of a population e.g. through inbreeding depression. Therefore, dealing only with demographics without taking into account how it is affected by genetics is not biologically meaningful. This should be stressed in the summary and in the main text.

Dr. Eric Marboutin, ONCFS

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The report demonstrates how MVP of wolves in Scandinavia can be estimated in a robust way, and provides, as a result, sound estimates of related numbers. The authors made use of 3 complementary and independent approaches that all gave convergent results. Such a kind of cross-validation process means that their conclusions should be considered as valid ones both from a methodological point of view and the conservation biology point of view. The effect of possible catastrophes (and demographic stochasticity) is properly embedded in the analytical procedure, as well as that of measurement errors and biological uncertainty. Well-accepted (in the scientific community) levels of extinction risks have been used, and the limits of the results obtained are honestly stressed (especially regarding the differences between MVP and FCS). Overall this report can be regarded a key contribution towards a better understanding of how PVA should be conducted and how large a wolf MVP should be from a demographic point of view.

Dr. Torbjörn Nilsson, Länsstyrelsen Värmland

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I have read the preliminary version of your report with great interest. Here comes an attempt to summarize my most important comments and suggestions:

1. I think it is very good that you have mentioned both in the Swedish and English Summaries and in the main text that FCS requires a larger population than a MVP. Also very good, and even more important, is the mentioning that FCS requires population viability in a longer time frame than the 100 years analyzed in the present study; this I think should be put clearly in the Summaries as well. Furthermore, it would be good to mention more explicitly, both in the main text and in the Summaries, that population range (FRR) is also an aspect of FCS, which has not been covered by the present study.

2. The IUCN Criterion E does not exclude effects of genetic problems on extinction risk. Hence, since the assignment said that only demographic aspects should be included in this study, the results of the study cannot correspond directly to the IUCN Criterion. This I think should be clearly explained in the Summaries and at relevant places in the main text. Consequently, all sentences where conclusions are drawn about wolf population size in relation to Criterion E should be omitted.

3. The most problematic aspect of the preliminary report, I think, is its complete absence of quantification of the uncertainty of the MVP estimates presented. As mentioned, keeping track of uncertainty is essential in performing and interpreting PVA. This may be done by using confidence limit input values, or other input values with a statistically described probability, and find out what the model outcome would be if those values were the true ones. (The use of three alternative models is not an appropriate substitute for putting confidence intervals or similar uncertainty measures to the MVPs estimated.)

4. As pointed out, a major advantage of quantitative PVA is that it is transparent (in contrast to e.g. expert assessment). However, this transparency is only achieved if input parameter values as well as model structure are clearly specified when reporting a PVA. Therefore, I suggest that in the final version of the report, all relevant parameter values should be listed in tables.

5. In some places, you state that there would exist a general consensus that PVA models should only be interpreted qualitatively, without inferring any quantitative conclusions. I think this statement is incorrect. There has been considerable scientific debate on this topic, but the criticism against quantitative conclusions from PVA has been repelled. PVA modeling has its shortcomings, but its methods are transparent and subject to continuous improvement, which makes it strongly preferable over intuitive expert guessing. Before conservation biologists began to estimate population sizes needed to meet various viability criteria, many people intuitively thought like Noah: "save one male and one female, and you have saved the species". An effect of conservation biologists calculating MVP estimates - and claiming them to have relevance for management - is that today, quite many people realize that there may be needed hundreds or thousands of individuals to give a

population a good chance of persisting for a long time. This is an important step forward. If conservation biologists refrain from drawing quantitative conclusions about extinction risks and MVPs, the "Noah approach" to conservation management will probably become more prevalent again. Therefore, I think it is important to put forward the insight that the quantitative output of a PVA is much better guidance than sheer intuition is. Equally important, however, are two lessons that can be learned from the criticism against quantitative PVA: a) that PVAs intended for use in an applied management context should as far as possible account for all factors that may have a significant effect on extinction risk, and b) that PVAs intended for use in an applied management context should keep track of uncertainty and clearly quantify how moderate uncertainty of input values leads to much greater uncertainty of the MVP estimated.

6. In several places, I think you over-emphasize the lack of documented really severe die-offs in wolf populations. Such catastrophic events are not only rare, they are also generally unlikely to be documented in a way that quantifies mortality or population decline. Therefore, the summarized knowledge about catastrophic die-offs among wild mammals in general, and among wild canids in particular, may be a better knowledge base for assessing the risk faced by wolf populations.

7. Population viability analyses are designed and performed for various purposes. Some analyses are designed to estimate which population size meets certain viability criteria; such analyses should be as realistic as possible, and especially they should as far as possible take into account all kinds of factors likely to influence extinction risk. Other analyses are designed to explore general relationships, which apply to many kinds of species under various conditions; in such analyses simplicity and robustness are to be strived for. The latter type of analyses should not be used in applied contexts such as determining minimum population sizes. In this perspective, the two simpler models used in your study (the exponential growth model and the Bayesian model) are less relevant than the individual-based model. Therefore, I suggest putting the descriptions of the two simpler models and their results in an Appendix and omitting them from the Summaries. The two simpler models do not improve our insights about the wide uncertainty in the results of the study. On the contrary, there is a considerable risk that bringing up the results of the two simpler models gives many readers a false feeling of confidence in the result of the third and most realistic model, hence leading readers to intuitively misunderstand the uncertainty of all the presented model outcomes. The main benefit of performing the analyses with two simpler models is, I think, that they confirm the general pattern that more simplified models tend to give lower MVP estimates than more realistic models. Scientifically, it may be interesting that this is found also in the current study, but addressing this issue is not within the purpose of the assignment. Therefore, they may deserve an Appendix and / or a short mentioning somewhere in the main text, but should not be put forward as if they were equally relevant for management purposes as the individual-based model.