Critique of Swedish FCS assessments

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For any kind of killing of endangered or threatened species, and indeed for any kind of hypothesis testing, it is paramount that one err on the side of caution. If you are going to hold a population of an endangered species down at low levels for an extended period of time through repeated mass culling you ought to be extremely conscientious in your assessment that you are not jeopardizing the viability of the population. This calls for conservatism at every level where you are making choices about model formulation and implementation, parameter values, their ranges and variances, factors included, data input, and so on. Under no circumstances should you push the envelope to the limit to see how little conservation you can get away with.

The authors of the reports that Naturvårdsverket bases its claim of an FSC (reference level) on, consistently treat model outputs and estimates as if they were truth, ignoring uncertainties, variation around the estimates, and the absence of key factors for consideration, and using them as inputs in further models and assessments. Some of these models are outright bad, and, not least, inappropriate for practical management purposes.

None of these authors are qualified population dynamics experts or population geneticists that can say anything about viability. It would be much better to listen to a real expert, like Nils Ryman, who has occasionally got a chance to give a statement buried in the annex somewhere of a Swedish government report (without being given any weight in the synthesis. E.g. Liljelund 2011, 2012, Naturvårdsverket 2009 (Bilaga 4).)

The authors themselves all blame time constraints for not being able to provide a better analysis.

Even the researchers that got to give a statement for these reports do not agree, and certainly they should have consulted more qualified and relevant scientists.

Would you get on a plane if you were told that it has a less than 10% risk of crashing? What if you knew the models used to assess that risk might underestimate the risk?

The managers cherry-pick the parts of the scientific basis that suits their purpose of getting away with managing the population at absolute rock bottom population levels. Scientists who provide statements or analyses to managers have to be cognizant of the many ways in which the recipients might misconstrue, misuse, misunderstand, cherry-pick, or outright abuse the inputs they receive. Consequently, they need to make all limitations of their analyses explicit and unavoidable, and state outright how the analysis can and cannot be used in practical wildlife management. Models that might be fine in a strictly academic exercise and in a very particular and circumscribed sense, may be entirely inappropriate to apply to the justification of culls of a particular endangered species or small population. (Or to defend maintaining such a population at a very low level over time.) Unfortunately these scientists are themselves routinely commenting and providing "analyses" far beyond their own areas of expertise. There is a tendency for both scientists providing input and managers to forget about caveats and critical assumptions of the models.

No real population dynamicist and/or population geneticist would conclude that 300-350 individuals constitutes a favorable conservation status. Certainly not for a population that is already critically inbred, with extremely low genetic variation (frequency of rare alleles or heterozygocity) and suffering from inbreeding depression, like the wolf population(s) in Norway and Sweden. And if one did, one certainly couldn't argue that the "FCS" they speak of is a much higher population level than the Minimum Viable Population (MVP), or a population size that gives a low risk of extinction. In any case, exceeding the MVP, or the FCS, does not mean that the risk (probability) of extinction within a given time horizon is negligible. Granted, wolves have some advantages going for them in that they are a species with high litter sizes, and that can reproduce every year. Consequently, they can have high maximum population growth rates at low density, if left unmolested by humans. On the other hand, they are social, cooperative animals which need their experienced individuals, and only one pair breeds in any family group. Hence packs are the reproductive units rather more than the individuals. As such they may also be subject to Allee effects.

According to EU documents (Evans and Arvella 2011, p. 8), the conservation status will be taken as 'favourable' when:
a) population dynamics data on the species concerned indicate that it is maintaining itself on a long-term

basis as a viable component of its natural habitats, and
b) the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and
c) there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis; (Article 1i)

"Population dynamics data" cannot really indicate anything about whether a species is "maintaining itself on a long-term basis as a viable component of its natural habitat". Unless you interpret "population dynamic data" extremely broadly, to include all the parameters that would go into a realistic simulation of future population development, including the population genetic data and a realistic link between the population genetics and the population dynamics. This is a statement about the future. Consequently, what you need is a prediction of the future, or a "forecast", and for that you need a realistic simulation model. A snapshot of current population dynamic data, or past trends, is in no way adequate for statements about the future, especially given the history and population genetic situation of Scandinavian wolves.

Perhaps if you have a species that is genuinely doing well, and you have no reason to think that it is not "maintaining itself" long term, a realistic simulation is not strictly needed. But for a species as marginal as, say, the wolf population in Norway, or in Sweden, or in Norway and Sweden combined, a snapshot or a representation of trends from the past, is in no way adequate. Or even very relevant. This is about what will happen to the population in the future, not about past trends. For the aforementioned wolf populations, you also need to consider the population genetics, not merely the population dynamics. In a small population these are all probabilistic phenomena, and no particular realization of potential population trajectories in the past or present tell you much about how things will go in the future, or whether management has been living up to their responsibilities.

"A viable component" means that a viability analysis is required. For a threatened or endangered species this sets high demands for the realism of the simulations required—unless you are prepared to concede offhand that the species or population in question is *not* in favorable conservation status. If a population is obviously doing well, the requirements for data analysis would not be so stringent.

b) and c) hardly apply in the case of Scandinavian wolves, as it is not the "natural range", nor habitat availability, that is the limiting factor on wolf population dynamics, population genetics, or viability. It is the constant killings by humans that is the limiting factor on wolf viability and where it is found. (And to some extent (in a critical case like this), the rate of immigration, but this too is primarily determined by the constant killing by humans.)

Wild animal populations can experience patchiness and density dependence at multiple scales, and with regard to many different demographic or behavioral parameters. These will affect estimates of future population dynamics, genetics, and viability. A realistic simulation would therefore have to be spatially explicit, and with due consideration of density dependent factors at all relevant levels. Failing that, a model that is to be applied to a controversial question of a threatened or endangered population would have to be —**beyond any conceivable contention**— *clearly conservative*. The fact that we are even discussing this means that the analysis done to date has not been conservative enough.

Making assumptions about population growth rates remaining positive in the future, as done in Naturvårdsverket's documents (e.g. Bilaga 4, p. 20-21), is not appropriate.

Norwegian and Swedish "wolf management" is *de facto* setting a cap on the size of the population, this becomes a ceiling for population sizes in simulations that the population is not allowed to increase beyond, instead of any carrying capacity given by the habitat quality, availability and variability, the natural range, or the availability of food sources.

If management wanted real answers they could have called in some truly qualified experts in population dynamics, population genetics, stochastic processes, simulations, and philosophy of science. Yet they don't, choosing instead people who have worked on wolf monitoring, and particularly people associated with Skandulv, which is also largely funded by the government bodies seeking inputs.

Using basic models simply to conclude that immigration rates is more important than population size is stupid and useless. It presupposes that the models and the data inputs are adequate and realistic, but, moreover, because population size is something you have much more control over than you have over the

immigration rate. Eliminating all legalized culling would likely allow the population to expand rapidly. Needless to say, this is what one should do under the current circumstances, if one were serious about improving the conditions of either the Norwegian population, the Swedish population, or the combined population.

A metastudy of minimum viable populations across a range of taxa (287 populations and 211 species, Traill *et al.* 2007) produced a range for "standardized" MVPs of 3577-5129 (95% confidence interval). It is therefore eye-popping that the one study referred to by these people, for wolves, appears to make the claim that 100 individuals constitutes an MVP for Scandinavian wolves. And that it is by far the *lowest* estimate in the metastudy's sample of analyses for wolves. Standardizing these estimates, however, still put them in the interval from 5513 to 8753 individuals. Standaridization is done to correct for the absence of factors that should be incorporated in an MVP analysis, and differences in the viability criteria used. They standardized MVP estimates to represent the population size needed to provide a less than 1% probability of extinction within 40 generations. The median value for standardized MVPs among mammals was 3876 individuals (95% confidence interval: 2261–5095).

In light of this, and a solid understanding of stochastic processes, population dynamics and population genetics of small populations, and philosophy of science, it is clear that anyone claiming that an FCS of such a critically inbred population can be anywhere near 300 individuals should be required to supply some pretty sophisticated and realistic modelling to substantiate their claim.

Chapron et al. (2012) were given *one month* by Swedish authorities to conduct a MVP analysis. And the results bear clear witness to the imposition of this time restraint. The terms of reference also explicitly called for the analysis not to include any population genetics. It goes without saying that any influence of further deterioration of the population genetics upon the population dynamics (or the interaction between population genetics and population dynamics in general) also were excluded from this analysis. They do state explicitly that their results must be interpreted extremely cautiously, and point out some of the model's limitations themselves, yet the people who rely on this study to justify wolf culling clearly are not extremely cautious.

Both diseases/epidemics and environmental "catastrophes" are phenomena that intermittently reduce natural populations to low levels where they, for a while, will be vulnerable to extinction through stochastic processes (if they don't die out deterministically and directly from such an incident). Both kinds of events can in principle have effects spanning several years, even generations. And continued loss of, or low levels of genetic variation makes a population increasingly exposed to and vulnerable to such events.

Another factor that is always left out is the possibility of environmental variations (including "catastrophes") with effects extending beyond a single year. For instance, if an external factor severely depressed the food supply of wolves, one could imagine that it might take several years for the availability of moose prey items, for instance, to rebound.

Realistic integration of the interaction between the population genetics and the population dynamics is also required to capture the effect of an epidemic hitting a population of severely inbred wolves with little genetic variation.

The models are commonly calibrated with historical data from the same population. These are populations that for a while were growing rapidly from an absolute minimum of one or two pairs. It was a time period where no significant diseases occurred, either in the wolves themselves or their prey, and the area has enjoyed the highest density of moose in the world. Little attention seems to have been given to the question of whether the resulting parameter estimates will prove representative for a simulated population in the future. Using past means and variances of population parameters may severely underestimate the amount of critical stochasticity the population faces in the future. There has been no convincing sensitivity analyses for the models presented and their assumptions.

I will provide just one quote from Naturvårdsverket's own report: "For example, density dependence – including both the specified carrying capacity (K) and the functional form used to describe density dependence (eg ceiling, logistic, Allee) can vastly affect the outcomes of PVA predictions, causing different PVA models to have widely divergent predictions even when the input data (eg vital rates and their variances, population sizes and age structure, etc.) are identical for the different models (Mills et al. 1996)." (Naturvårdsverket 2015, Bilaga 4, p. 9).

The old rule of thumb that population genetic variation can be maintained with one immigrant per generation is based on the assumption that the source population is infinitely large. In the case of wolves in Norway and Sweden, Aspi et al. (2006, 2009) have shown that the likely source populations in Finnish and Russian Karelia and the Kola region are each of a magnitude effective population size around 40. Inherent to this is showing that Russian wolf populations are not panmictic, and exhibit patchiness at various scales. As such the source populations will themselves exhibit limited genetic variability.

Furthermore, this old rule of thumb is for the *maintenance* of genetic variation in a population. This however, is a population that is already suffering from founder effect, loss of rare alleles, extreme inbreeding and inbreeding depression. Hence the proper focus is on *increasing* the genetic variation, not simply maintaining it. The one-migrant-per-generation rule has also come under general criticism from population geneticists, as being inadequate in many cases (Mills and Allendorf 1996). In another Swedish government report, which is *not* cited, they recommended that the inbreeding coefficient should be reduced to 0.1 (Hansen et al. 2011). They thought it necessary to set a deadline 12 years into the future to alleviate the genetic problems in the population, and to reestablish the wolf population in a larger region. Furthermore, Laikre og Ryman (2009, in Liberg et al. 2009) concluded that "The intense inbreeding should be resolved urgently. The effort should be made to, as soon as possible, bring the average inbreeding level down to 5-10%. In our opinion, this ought to happen within the next few wolf generations (5-20 years). Until this reduction has been achieved, it is not reasonably that any immigrant wolves be shot. […] We recommend the goal be to achieve long term genetic viability for an "international" total population within 5 to 25 years. Such long term viability is achieved at effective population sizes of 500-5000." (my translation).

Even where the authors have fastened on the "1 successful immigrant per generation" as the result of a model, the reliability of such a rule is subject to the limitations and peculiarities of the model.

Most of the talk of genetic variation has been focussed on the mean level of heterozygosity. Little analysis is included regarding the consequences of the loss of rare alleles. One key consideration of management actions taken, or not taken, today, may be the effect they have on the effects of an epidemic hitting the population some time in the future.

The weighting of the harmonic mean when you have population fluctuations causes time spent at low population sizes to have a disproportionate effect on the genetic effective populations size, and populations need to grow out of a genetic bottle neck like this *as quickly as possible*. Artificially and deliberately maintaining the population at such low levels is conservation malpractice.

For the ratio N_e/N_c in wolves we see various calculation ranging from around 1/3 to 1/10. Yet these authors routinely chose the least conservative of the options. This even while the least conservative options are themselves caused by the high rate of wolf killings by humans, where large, successful family groups are shot out, many pair formations are quite recent and without young members in the pack, etc.—though unestablished vagrants will be discounted too.

Even the generation time of wolves is being shaped by anthropogenic killings. The mean age of reproduction of female wolves is forced down by the fact that these wolves don't live very long, because they get killed by humans, either illegally or through decisions made by management. When breeding females are killed, increasingly younger individuals replace them, lowering the age at first reproduction and further lowering the generation time. Wolves in Norway and Sweden live such short lives that the generation time was initially reduced to five years, and have now reached a level as low as the 3-4 year range (Flagstad pers. comm.). Again, this means that saying one successful immigrant per five year period (old estimate for generation time), is to not be conservative.

The routine mass killings of wolves is itself what is limiting the range and available habitat for the population. Hence points b) and c) of the definition of FCS (above) become irrelevant for wolves in Norway and in Sweden.

Management cannot hide behind the claim that immigration is more important than population size, as long as they are not doing more to ensure the influx of fresh genes from outside and their maintenance in the population over time. (Such as by restricting killing of individuals trying to move through the reindeer herding regions in the north, eliminating the shooting or poisoning of immigrants and their recent descendants, or transplantation of individuals into the population.)

The burden of proof should be on anyone claiming that a given cull (or repeated culls keeping the population down at a low level) does not jeopardize the viability of the population, or that a given population size is adequate for favorable conservation status.

In addition to the factors mentioned above, for the analyses to be realistic and conservative they ought to
- not use a predesigned software package like Vortex, but the models should be written *de novo* to ensure that one completely understands exactly what the model does, and how, and it is tuned to fit the particular circumstances and biology of the population(s) in question.
- be spatially explicit (assuming panmixia, where all individuals are equally likely to meet, interact, and form pair bonds is obviously not realistic or conservative)
- incorporate or rule out (evidence based) patchiness (in the population structure and interactions)
- incorporate realistic or conservative density dependence at the necessary levels and scales
- rule out or allow for the possibility of Allee effects in the population dynamics
- realistically model the interaction between population dynamic parameters and the population genetics. For this one would want to have detailed information, for instance, regarding the prevalence of lethal and sublethal alleles (or generally, the prevalence of deleterious alleles), their effects on population dynamic variables, as well as the same for the potential source population for immigrants. (Alternatively one could make clearly conservative/pessimistic assumptions)
- incorporate the possibility of "catastrophe" with effect potentially beyond a single year
- realistically implement the potential for epidemics, both in the population itself and its prey, with adequate interactions on how this could pan out in a critically inbred and genetically impoverished population
- ensure that the sum of the decisions made about model implementation, coding, and parameters does not result in a simulation with a very slight effect of stochasticity.

More critiques of modelling efforts to date could be raised, but any one of these (or subset of them) should suffice to critique the notion that 300 individuals constitute an FCS, or even an MVP. Even where some of these have been discussed in one or more analysis, they are not all addressed in interaction in any given conclusion.

Guillaume Chapron has claimed that there is no natural population density dependence in the Norwegian or Swedish wolf populations. And, indeed, at the moment, the ceiling on populations is set by regular culls, and that is the only density dependence included in these models. But, of course, biological populations exhibit density dependence in a variety of variables and at a variety of scales—even if a particular set of scientists has not detected it in the way they have been looking for it, or in the time period in which they have been looking for it.

If you use a model that underestimates extinction probabilities, you cannot use it to claim that extinction risk is low. Especially not if, at point of departure, it can be expected that the extinction risk is high, and you are responsible for ensuring that it does not die out.

Wolves should be modelled as structured populations consisting of packs and pairs, and solitary individuals, where only one pair in a pack reproduces, and packs cooperate in hunting, rearing of young, etc. Ideally the models should be spatially explicit in a way that captures the population(s) in question, and of course the unit of simulation should be individually represented individuals with age and sex characteristics, incorporating both genetics and population dynamics, risk of epidemics and "catastrophes" that may impact populations over several years. It is imperative that such models, if they are to be applied to real populations, should have realistic feedback between the genetics and the population genetics—and of course "conservative" environmental variation. Perhaps even explicit modelling of predator-prey interactions.

Barring this, one should build in huge safety margins, but this is not done either. Instead they push and push and push to try and justify "management" at the lowest possible population levels.

It is also worth noting that Norwegian authorities (I am less familiar with the discourse in Sweden) made exactly the same claims regarding the viability of the population (and the effect of licensed culls upon it) long before any of these analyses had been conducted.

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