Response from Olof Liberg and Håkan Sand to critique on their report on effects of migration and selective harvest of wolves, from Dr Michael Hansen

In a letter to Dr Michael M. Hansen, Århus University, Ann Dahlerus, Svenska Rovdjursföreningen (Swedish Carnivore Association) Stockholm, Sweden has asked for Dr. Hansen' s opinion on a number of questions related to a report by Olof Liber and Håkan Sand to Naturvårdsverket in December 2012 (Liberg, O. & Sand, H. 2012. Effects of migration and selective harvest for the genetic status of the Scandinavian wolf population. A report to the Swedish Environment Protection Agency SEPA (Naturvårdsverket).
Dr. Hansen has in his answer to ms. Dahlerus stated his opinion on the formulated questions which includes a severe critique of the results presented in the report. As the authors of this report we have considered the response made by Dr Hansen on these questions and find much of it to be either misdirected or based on misunderstanding of the results presented in the report. Below we will clarify some of these misunderstandings,

Much of the critics of harvesting wolves have opposed to using genetic improvement as a sole reason for this management action. We agree that improvement of the genetic situation is not in itself a sufficient justification for harvesting any population of wild animals.
However, before responding to the specific points made by Dr Hansen, it is important to consider the wider context in which the report was written as a direct request from the Swedish EPA to the authors.

The currently most serious and acute threat to the viability and a successful conservation management of the Scandinavian wolf population is not genetic problems but the existence of an extensive poaching, a factor that presently is estimated to make up half of its total mortality (Liberg et al. 2008, 2012). The extensive conflicts linked to wolf recovery and the problems with poaching was widely recognized in four different national interrogations on the management of carnivores in Sweden performed during the last 15 years (SOU 1999:146, SOU 2007:89, SOU 2012:22, SOU 2013:60). The reason for this poaching is the extensive conflicts caused by wolves in the local societies with which they coexist (Pyka et al. 2007). So far, there has been very little success in fighting this form of criminality. Neither massive information campaigns, nor increased law enforcement and extended penalties have had much effect. One reason why it is so difficult to fight poaching is the lack of cooperation from the local societies (Pyka et al. 2007). Making broad sections of the concerned rural human population less hostile towards wolves would make it harder for poachers to operate undisturbed.

Several of the interrogations on large carnivores in Sweden have also suggested that one of many important ways to mitigate these conflicts is to control or reduce further growth of the wolf population by harvest once a favorable population status is reached (SOU 2007:89, SOU 2013:60). In this context, a highly relevant question is whether this type of harvest is possible without having a negative impact on the genetic viability of the wolf population, and whether it is possible to design the harvest so that it may even improve the genetic situation. The latter question was exactly what SEPA asked us in their request for a report on alternative ways of harvesting the Swedish wolf population. In our report we stressed that no lasting positive effect on the genetics is possible without a certain degree of migration into the population. But provided we have such an inflow, we show that a harvest where migrants and their offspring are protected will lead to a faster reduction of the inbreeding level, and will also make the population reach a lower inbreeding level than would have been achieved with migration alone, i.e. without harvest.

In conclusion, genetic improvement is not in itself a sufficient justification for harvesting the Swedish wolf population. However, if for other reasons (e.g. conflict mitigation) it is decided that harvest should be a part of the management of this population, and provided that there is a sufficient migration flow into the population, the harvest can also be used to enhance the positive effects of immigration on the genetic status of the population.

Dr. Hansen decided to structure the questions asked to four main questions. These are listed below as are our response to Dr Hansen's answers.

1. Can indiscriminate hunting targeting wolves irrespective of their inbreeding status reduce inbreeding?

Dr Hansen: The answer is a clear no. Indiscriminate hunting can never reduce inbreeding in a closed population such as Swedish wolves. The only possible effect it can have is to reduce the effective population size, which will again increase the rate of inbreeding, Δf, as explained above. The damage done ranges from low (if few wolves are shot) to severe (if many wolves are shot).

Our response: We agree and this is clearly stated in the report.

2. Can hunting targeting highly inbred wolves reduce inbreeding, in the case where no immigration of wolves from other populations occurs?

Dr Hansen: The answer is also no. As stated above, inbreeding can only be reduced by immigration. Removal of highly inbred wolves may be considered equivalent to avoiding mating between closely related individuals, which can delay but not permanently reduce inbreeding. Also, depending on how many individuals are removed, this will further decrease effective population size and thereby increase the rate of inbreeding. So, such an approach will not solve the problem and will instead be increasingly harmful depending on the number of wolves removed.

Our response: Here we also agree with Dr Hansen. On a short term scale (1- 10 years) a harvest excluding immigrants and their offspring may result in a small and temporary decrease of the population inbreeding level. As Dr Hansen points out, this however will be increasingly harmful depending on the number of wolves removed. We would not recommend such an action in absence of migration into the population. This is also stated clearly in the report.

3. Can hunting targeting highly inbred wolves reduce inbreeding, in the case where natural or assisted immigration of wolves occurs from other populations?

Dr Hansen:

Theoretically, I find it plausible that inbreeding can be reduced in the manner described (but see my response to question 4 concerning other effects of this approach). This appears to be a simple dilution effect where unrelated individuals are continuously supplied to a population, and the smaller the population size, the faster the dilution will be.

However, the specific population size and rate of assisted immigration that is required depends entirely on the parameters assumed in the model. How robust are the results to deviations from the parameters assumed, for instance the critical assumption that migrants have the same probability to survive and breed as native animals? A detailed sensitivity analysis would seem important in order to assess the robustness of the quantitative results.

Response: This critique raises an important point, but we think the concern expressed by Dr Hansen here is already considered in the report. The fitness parameters used in our simulation model are based on the assumption that immigrants are reproducing and surviving at the same rate as native wolves, which is a reasonable and a rather moderate assumption. In fact, empirical data on individual demographic parameters from our population show that immigrants and their offspring have a considerably higher fitness than non-immigrants (Åkesson et al. in prep.). Therefore the model results actually may be conservative in term of the effects of selective harvest and immigration on the level of inbreeding in the population. However, we do agree that it would be desirable to perform a full sensitivity analysis of the model and suggest that this would be a priority for the extended analyses that was actually recommended in the report.

Most importantly, however, the results depend crucially on the assumption that the immigrants are derived from a very large source population and are unrelated. It seems unrealistic that this assumption of the model can be fulfilled in practice.

In total, other concerns set aside it does not appear realistic that inbreeding can be reduced to the level suggested by the simulations by Liberg and Sand, as it would require assisted immigration by unrelated individuals from a large source population. It is not pointed out in the report by Liberg and Sand how this requirement can be fulfilled in practice. A more suitable analysis would therefore have consisted in simulations, where assisted immigration took place from a small population, e.g. similar to the Finnish wolf population, consisting of individuals that are also inbred, albeit inbred within a different population.

Response: We agree that this may be an important and relevant extension of the analyses. However, there are several factors that indicate that the results received from the simulation are indeed appropriate for the questions asked. First, analyses on the genetic structure of Finnish wolves show that these still contain much genetic variation that we do not have in the Scandinavian wolf population, and therefore are expected to contribute with new genetic material for a number of wolf generations (Åkesson, unpubl.). Second, analyses of the genetic composition of immigrating wolves indicate that several of them are not coming from genetic lines present in the Finnish core population but from some to us unknown genetic lines for which we lack reference material, e.g. northern Karelia or the Kola peninsula (Åkesson & Bensch 2009, Åkesson, unpubl.) Third, analyses of the genetic structure of wolf populations in NW Europe have shown that historically there has been substantial genetic exchange between wolf populations in Finland, Russian Karelia, Baltic countries and also further east in Russia, and these data also show that there still is at least some connection (Jansson et al. 2012, Baltrunaite et al. 2013). Finally, if this gene flow still should prove to be insufficient and/or population sizes too small to achieve a favorable long-term genetic population status in Scandinavia in the future (in some 30-50 years from now), actions could still be taken to increase connectivity with more remote populations.

4. What are the general conservation implications of an approach where hunting is combined with natural or assisted immigration?

Dr Hansen:
A procedure involving a fixed upper population size of, say 200 individuals, hunting of individuals exceeding this limit and assisted immigration of wolves from a different population could be considered akin to creating a "source-sink" system. This means a system where the Swedish wolf population becomes a "sink" with a negative growth rate (due to hunting), which is compensated by immigration from a "source" population. In other words, population dynamics data do not indicate that the population is maintaining itself on a long-term basis.

Our response:
The example with a maximum of 200 wolves, given by Hansen is of less interest. Based on recent management decisions, the population size in the future will be a minimum of 300 wolves and most likely higher. To be controlled at this level, it is true that a regular harvest of the population will be necessary, but this will not make the population a demographic sink. Demographically it will be self-maintaining. It is unclear what Hansen means when he writes "*population dynamics data do not indicate that the population is maintaining itself on a long term basis".* The growth rate presently is positive and high, with an annual average of approximately 15 % during the last six years, and the population size is now four times larger than it was 10 years ago. Even if this population is stabilized at a certain level through a regulating harvest, it will demographically continue to be self -maintaining and not dependent on any subsidies from the outside. In this case growth rate over time will not be negative, but zero. A regulating harvest that will take the annual surplus and stabilize the population around e.g. 350 wolves will be equal to removing 50-60 individuals per year. The main function of the few natural migrants or trans-located individuals needed (one per year or less), is not to compensate numerically for this harvest, but to maintain genetic connectivity with adjacent populations. Neither is the population a genetic sink in the sense that it will only receive migrants and not produce any in return. It has been shown that wolves already now migrate in the other direction (Wabakken el al. 2007), and it is a reasonable assumption that this dispersal will continue. Also, just as artificial trans-location into our population can be used as a last resort if the natural migration rate during some period is judged too small, it is of course possible to perform trans-locations also in the opposite direction.

Dr Hansen:
A second problem from a long-term conservation perspective concerns the ability of Swedish wolves to adapt to future environmental change. If the population size is reduced to 200, then this would correspond to an effective population size of 80, assuming an Ne/N ratio of 0.4 (as explained previously). This is much below the recommended minimum effective population size of 500 to ensure adaptation in the long term [Franklin et al. (1980) Evolutionary change in small populations. In: Conservation biology: an evolutionary-ecological perspective, pp. 135-150]. Moreover, such a low effective population size combined with continuous one-way

migration from a source population would make it difficult to adapt to local environmental change."

Our response:
In our report we clearly state that population connectivity and immigration from other adjacent populations is vital for the conservation status of the Scandinavian wolf population. If immigration rates occur similar to the rates used in the analyses of the report, it will become part of a large meta-population of wolves, which is actually what Dr Hansen himself is recommending, both in his present critique letter and in an earlier report (Hansen et al. 2011). The problem with adapting to local changes will be the same for all parts of this meta-population. We again stress that the issue is not 200 wolves in the Scandinavian population, but rather $\geq$300. This will give an effective population of $\geq$120 wolves assuming N_e to be 0.4. This is better than 80, but still too few to ensure local adaptations on a long term basis. However, those adaptations will have to occur within the whole meta-population. After all, the wolf habitats in Scandinavia, Finland, and NW Russia are very similar and the effects of climate change will be similar over the entire area. New epidemics will also spread over the whole meta-population, given the degree of genetic connectivity assumed.

Dr Hansen:
A third problem concerns the failure to address what is really at the heart of the conservation problems of wolves in the region, i.e. fragmentation and the associated problems with low effective population size and lack of gene flow. In other words, an inbred Swedish wolf is not "genetically worthless". It can be valuable if it interbreeds with, for instance, a Finnish wolf that is also inbred. Therefore, removing inbred Swedish wolves and substituting them with one-way gene flow from a different population represents, at most, a short-term solution and does not contribute to conservation of the species as a whole in the region."

Our response:
There is already evidence for migration from the Scandinavian wolf population to the Finnish/Russian population (Wabakken et al. 2007). However, because of the special situation with the Scandinavian and the Finnish reindeer country, the flow both from the eastern populations to Scandinavia, and the flow in the opposite direction, is limited. That is why artificial translocations should not be excluded from possible future management actions concerning Scandinavian wolves (one artefact, the reindeer husbandry, is countered by another, translocation). If and when judged necessary, wolves can be trans-located not only from the east to the west, but also in the opposite direction.

Further, there seems to be a misunderstanding by Dr Hansen that inbred Scandinavian wolves should be "substituted" with an equal number of Finnish wolves. As stated above, the needed inflow of wolves will be at most one or two per year, while the harvest to control the population at 300 will be at least 40 wolves annually. Still, there will be several hundred of "genetically worthless" wolves left in the population (we have never argued that inbred wolves are "genetically worthless"). We believe that this type of harvest will not impoverish the genetic variation that is contained within the present wolf population. In fact, it is very hard to imagine that we would lose some unique genetic material through an annual harvest of 40-60 wolves, when there is 300 or more other wolves left that have an extremely high degree of genetic similarity to the lost ones. Even if some unique and valuable genes would be lost in this way, there is a good prospect that they will be brought back through the flow of immigrants. After all, all the genes that our inbred wolves carry originate from the same eastern populations (Åkesson and Bench 2009), that will be the donors also of future migrants to Scandinavia.

Finally, we would like to finish with a reflection on harvest as a conservation tool. We know that there is a large resistance among conservationists and geneticists in general to accept human harvest under any circumstances as a management tool in conservation. Harvest of small populations is so beyond the basic instincts of conservation ecologists and geneticists that this instantly seems to call for skepticism and criticism. This is of course not very surprising, considering that overharvesting and poaching often has been the main reason for populations and species to go extinct. We also agree that in most cases harvesting would cause more harm than benefit to a threatened population. But sometimes it can be necessary to question conventional thinking. We think conservation of wolves in inhabited landscapes where they are supposed to coexist with humans is such a case. There is a generally intense and widely recognized potential for conflict with humans almost everywhere where wolves share their habitat with humans, and this becomes especially sharp when wolves colonize or re-colonize formerly vacant areas (Fritts et al. 2003), which is the case for Scandinavia. We are thus convinced that conservation and management of the Scandinavian wolf population is extremely challenging and needs to consider population recovery in a multi-disciplinary perspective including social, economic, psychological, ecological, and genetic aspects, and sometimes also a little unconventional thinking.

Also we should not forget that the most typical characteristic of the wolf is not genetically fixed local adaptations, but an ecological flexibility that has made it one of the world's most widespread, adaptable and successful mammal species (Mech and Boitani 2003).

Literature cited

Baltrunaite, L., Balčiauskas, L., and Åkesson, M. 2013. The genetic structure of the Lithuanian wolf. Population. Cent. Eur. J. Biol. 8, 440-447.

Fritts SH, RO Stevenson, RD Hayes and L Boitani 2003. Wolves and Humans. In: Mech, L.D. and Boitani, L. 2003 (eds). Wolves. Behavior, Ecology and Conservation. The University of Chicago Press. Chicago and London.

Hansen, M.M., Andersen, W., Aspi, J. & Fredrickson, R. 2011. Evaluation of the conservation genetic basis of management of grey wolves in Sweden. Rovdjurens Bevarandestatus, Delbetänkande av Rovdjursutredningen, SOU 2011:37, Bilaga 3, Stockholm, Sweden.

Jansson, E., Ruokonen, M., Kojola, I and Aspi, J. 2012. Rise and fall of a wolf population: genetic diversity and structure during recovery, rapid expansion and drastic decline. Molecular Ecology (2012) 21, 5178–5193

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. and Sand, H. 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc. R. Soc. B, 7 March 2012, vol. 279, no. 1730, pages 910-915.

Liberg, O. & Sand, H. 2012. Effects of migration and selective harvest for the genetic status of the Scandinavian wolf population. A report to the Swedish Environment Protection Agency. SEPA (Naturvårdsverket)

Mech, L.D. and Boitani, L. 2003. Wolves. Behavior, Ecology and Conservation. The University of Chicago Press. Chicago and London.

Pyka, M., Nyqvist, A., Monstad, T. et al. 2007. Illegal jakt på stora rovdjur. Konflikt i laglöst land (eng. ”Illegal hunting on large carnivores. Conflict in lawless country”). Brottsförebyggande rådet Brå, Rapport 2007:22. (in Swedish).

SOU 1999:146. Sammanhållen rovdjurspolitik. ISBN 91-7610-73-5. Stockholm 1999.

SOU 2007:89. Rovdjuren och deras förvaltning. ISBN 978-91-38-22847-0. Stockholm 2007.

SOU 2012:22. Mål för rovdjuren. Slutbetänkande av rovdjursutredningen. ISBN 978-91-38-23712-0. Stockholm, 2012.

SOU 2013:60. Åtgärden för samexistens mellan människa och varg. ISBN 978-91-38-23999-5. Stockholm 2013.

Wabakken P, Sand H, Kojola I, Zimmermann, B, Arnemo J M, Pedersen H C, & Liberg O. 2007. Multistage, long range natal dispersal by a Global Positioning System–collared Scandinavian wolf. J. wildl. Manage. 71: 1631-1634.

Åkesson, M. & Bensch, S. 2009. Analys av den genetiska populationsstrukturen i Skandinavien, Finland och Ryssland. Bilaga 2 i Liberg O. m.fl.: Förslag på åtgärder för att stärka den genetiska situationen för den svenska vargstammen. . Redovisning av regeringsuppdrag (Dnr 429-8585-08), rapport från Naturvårdsverket.