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SKANDULV

AN UPDATED SYNTHESIS ON APPROPRIATE SCIENCE-BASED CRITERIA FOR "FAVOURABLE REFERENCE POPULATION" OF THE SCANDINAVIAN WOLF (*CANIS LUPUS*) POPULATION

Assignment from the Swedish Environmental Protection Agency (SEPA)

2015, September 10th

Olof Liberg, Guillaume Chapron, Camilla Wikenros, Øystein Flagstad, Petter Wabakken and Håkan Sand

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GRIMSÖ FORSKNINGSSTATION

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Assignment from the Swedish Environmental Protection Agency (SEPA) Case number NV-03602-15

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The assignment

An updated synthesis on appropriate science-based criteria for "favourable reference population" of the Scandinavian wolf (*Canis lupus*) population

Decision

As a contribution we herewith appropriate 406 800 SEK (260 000 SEK + SLU overhead) to the Grimsö Wildlife Research Station, Dept. of Ecology at the Swedish Univ. for Agricultural Sciences, to be used for your research group carrying out the above-mentioned synthesis.

The report shall be submitted to the Swedish Environmental Protection Agency (SEPA) no later than on August 31.

Background and specification

The Swedish Government has commissioned (Ref M2012/1490/Nm) the Swedish Environmental Protection Agency (SEPA) to entertain an updated synthesis of the existing viability assessments of the wolf (*Canis lupus*) in Scandinavia (i.e. Sweden + Norway) and, on that basis, investigate what is required to ensure that the wolf is considered to have favorable conservation status in Sweden and Scandinavia under the Habitats Directive (the European Union's Council Directive 92/43/EEC).

The Habitats Directive, which states that the habitats and species listed in its Annexes shall have "favourable conservation status" (Article 1e and 1i), has EU Law & Directive Status (http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm), and the wolf is listed in Annexes 2 and 4. The most recent guidelines (Evans & Arvela 2011) for assessing the conservation status of these habitats and species can be found at https://circabc.europa.eu/sd/d/2c12cea2-f827-4bdb-bb56-3731c9fd8b40/Art17%20-%20Guidelines-final.pdf). In this context, it is important to note that Sweden is a Member State of the European Union (EU) and Norway is not.

The report shall include an updated assessment and short review of relevant scientific results for population viability so far, and a synthesis focusing on what would be appropriate science-based criteria for a favorable reference population (FRP; Evans & Arvela 2011) – minimum population size and the minimum genetic connectivity with conspecifics in Finland and/or Karelia – required to fulfill the FRP part of "favorable conservation status" of the Scandinavian wolf population.

The EU Commission guidelines for the management of large carnivores at population level (*Guidelines for Population Level Management Plans for Large Carnivores*, 2008, prepared by the Large Carnivore Initiative for Europe (http://ec.europa.eu/environment/nature/conservation/species/carnivores/pdf/guidelines_for_population_level_management.pdf), and the *Note to the Guidelines for Population Level Management Plans for Large Carnivores*, European Commission, DG Environment, 01.07.2008) were developed due to the difficulties for individual member states to fulfill the Habitats Directive's requirements in the cases of carnivore species with low population densities and cross-border populations These guidelines suggest that the minimum viable population (MVP) shall be defined by the IUCN criterion E (the extinction risk based on a quantitative viability assessment with the criterion < 10 % risk of extinction in 100 years) or criterion D (the number of sexually mature individuals) (http://jr.iucnredlist.org/documents/RedListGuidelines.pdf) and that the population status must monitored by an appropriate method. Linnell et al. (2008) state that where knowledge is available, it is appropriate to conduct a viability analysis to estimate the MVP. Both Linnell et al. (2008) and Evans & Arvela (2011) state that the MVP is by definition smaller than the

FRP. In case of any disagreement between the Evans & Arvela (2011) and Linnell et al. (2008) guidelines, the EU Commission has decided that the 2011 guidelines take priority.

The literature used for the synthesis should foremost be scientifically peer reviewed. Relevant "grey" (not peer reviewed) literature and reports can also be considered/included, but only if their reliability is clearly assessed in the text or in footnotes of the synthesis report.

A feature of the Scandinavian wolf population is that it was extinct in the 1970s and was refounded by 2 wolves in the 1980s plus an additional immigrant in 1991. Not until in 2007-2008 did two additional immigrants reproduce in Scandinavia, even though spontaneous immigration from more eastern populations (Finland and Karelia) does occur; for example, 12 wolves immigrated during the period 2002-2009, i.e. averaging 1.5 per year. It is desirable that the synthesis pays some consideration to this demographic and genetic history and whether or not it should affect the FRP assessment and, if so, how.

There have been a number of PVAs or similar analyses and assessments done already; the most recent one (SEPA report 6639; *in press*) by a senior conservation geneticist, Michael W. Bruford (Cardiff Univ.). It examined the effects of immigration and population size on the genetic diversity and inbreeding coefficient of the Scandinavian population, and will be made available for you. This additional conservation-biological syntheses – addressing and proposing appropriate criteria for FRP for the Scandinavian wolves – shall consider the applicable parts of the Habitats Directive, the EU's Guidelines (Linnell et al. 2008, Evans & Arvela 2011), the relevant scientific literature and information, and also the genetic and demographic history of the present-day wolf population.

A draft of the synthesis report is to be sent to the SEPA contact person no later than on August 14, so that the draft can be discussed at a meeting in Stockholm on August 24. The synthesis report shall be submitted to the SEPA no later than on August 31.

SEPA's contact person is Per Sjögren-Gulve.

To receive the funds, fill in your department's and university's contact and banking details in the enclosed requisition form, have it signed and send it to:

Naturvårdsverket
Ekonomienheten, 2771
Att: Per Sjögren-Gulve
SE-106 48 Stockholm
Sweden

On behalf of the Swedish Environmental Protection Agency,

Maria Hörnell-Willebrand
Head of the Wildlife Assessment Unit
The Research & Assessment Department

English summary

This report provides an updated synthesis on appropriate science-based criteria for "favourable reference population" FRP for the Scandinavian wolf (*Canis lupus*) population and present quantitative values on FRP. The assignment was given by the Swedish Environmental Protection Agency to the SKANDULV research group at Grimsö, SLU, Sweden. A thorough review of the ecology and genetics of the wolf population is provided, including measurements of inbreeding depression in the population. Results from earlier MVP analyses of the Scandinavian wolf population are presented, as are former suggestions of FRP or other management goals for the population. A consensus was not possible to achieve among all involved scientist, the results are therefore presented in two different parts.

OL, CW, ØF, PW and HS suggest that the population value for FRP should be 340 for Scandinavia, and 300 for Sweden. They argue that this Scandinavian sub-population should be connected to a larger meta-population with the minimum size of *Ne*=500, corresponding to approximately 1700 wolves, and the connection should be minimum one immigrant from the large meta-population to the Scandinavian wolf population per generation. They acknowledge a meta-population that includes also wolves living outside of EU territory, as long as there is the stipulated connectivity.

GC evaluated FCS based on a strict interpretation of Habitats Directive informed by previous rulings by the European Court of Justice and documents from the European Commission. He finds that if Sweden cannot include wolves from outside its national territory to fulfill its obligations under the Habitats Directive, FCS will be achieved at 1700 wolves (*Ne*=500) or at the country carrying capacity. If on the contrary Sweden can include wolves living in a separate population from another country to fulfill its obligations under the Habitats Directive, FCS will be achieved at half the country carrying capacity (preliminarily estimated at 1200/2=600 wolves) or more according to the connectivity naturally achieved. Non EU Member States cannot contribute to this meta-population.

There was consensus between all researchers that the target for the population inbreeding coefficient should be 0.2 or lower.

Agreement of independent approaches and authors' contribution

This report provides an updated synthesis on appropriate science-based criteria for "favourable reference population" of the Scandinavian wolf (*Canis lupus*) population. Defining such criteria has been a lasting debate among wolf researchers, quantitative ecologists and geneticists in Sweden. One reason behind this debate is that the concept of Favourable Conservation Status is written in law and is not straightforwardly interpretable in quantitative ecological and genetic terms. Different interpretations can therefore emerge depending on whether one gives more importance to the broader social context of the wolf question or one follows instead a stricter textual interpretation of the Habitats Directive and previous court decisions. Such competing interpretations are not un-common among scientists involved in policy relevant research and SKANDULV – the Scandinavian Wolf Research Project is no exception. We, the authors of the report, have agreed and decided to expose our diverging interpretations of the appropriate criteria for a "favourable reference population" of the Scandinavian wolf population. We therefore provide two parts for the section "Proposed criteria for FRP for wolves". OL wrote the first part, which is endorsed by CW, ØF, PW and HS. GC wrote the second part (with contributions of legal scholars not co-author of the report at Uppsala University) and not other parts of the report. We believe the approach to openly expose how, by following a flexible or strict interpretation of the Directive, we reach different conclusions is more informative and constructive than to force an agreement between irreconcilable interpretations.

Population monitoring, research, colonization history, demography and genetics of the recent Scandinavian wolf population

Methods in research and management

Monitoring

The Scandinavian wolf (*Canis lupus*) population has been monitored annually since the late 1970´s, at first by volunteers and later by professional field personnel (Wabakken et al. 2001). From early 2000´s the responsibility for wolf monitoring in Sweden is at the regional authorities ("länsstyrelserna"), and in Norway with Hedmark University College and with the central authority "Statens Naturopsyn". The monitoring of wolf numbers and distribution is based on snow-tracking (2000 – 4000 km each year), and from 1998/99 also supported with telemetry, and since 2002/03 with DNA-analyses of scats and urine (Liberg et al. 2012a). Annually 400 – 500 DNA-samples are analysed within the monitoring program. Each winter more than 100 professional field workers are engaged full time or part time with snow-tracking and with collection of DNA-samples. Monitoring results are analysed and presented in annual reports (by the Wildlife Damage Center in Sweden and Hedmark University College and Rovdata in Norway), using strict and standardized criteria for determining number of family groups (packs), reproductions, pairs, and single individuals (Wabakken et al. 2006, Liberg et al. 2012a, Wikenros et al. 2014). A detailed description of the monitoring organization and methods is given in Appendix 1.

Research

The Scandinavian Wolf Research Project (SKANDULV) was founded in January 2000, and is a consortium of independent research projects based at seven universities in Sweden and Norway. Research activities and coordinated data are shared within the research project and information is distributed among expert groups, management authorities, and the public. One Swedish and one Norwegian ecological research project comprise the core of SKANDULV, along with associated national projects focusing on genetics, population modelling, veterinary medicine and pathology, sociology and depredation. SKANDULV also has cooperation with a large number of international wolf research groups distributed over Europe and North America (Aronson et al. 1999, Pedersen et al. 2005, Wabakken et al. 2007, 2014).

Wolf research in Scandinavia includes radio-collaring of wild wolves and have so far included 156 collared wolves, representing 210 ”wolf years" (number of years each wolf was instrumented summed up for all wolves). Research on genetics include samples taken from live-captured and from retrieved dead wolves, but also from faeces and urine found during snow-tracking (Liberg et al. 2005, 2012a). An overall objective (also shared with the monitoring goals) is having DNA-profiles for each year from all territorial wolves (both wolves in established pairs not yet breeding, and both parents in family groups). Analysis of mortality, movements, spacing and other social aspects including predation is based on radio-telemetry. Estimates of reproduction are based on visits at dens for radio-marked packs, counting number of individuals in family groups during snow-tracking supplemented with

DNA-analyses. For further details of research methods, see Bensch et al. (2006), Liberg et al. (2005, 2012a), Sand et al. (2005, 2006b), Wabakken et al. (2001, 2006), and Wikenros et al. 2013.

Colonization history and number of founders

Like in most of the western world, wolves in Scandinavia have been heavily persecuted since early history. When finally the modern 20th century view of nature and its preservation also came to embrace the wolf in Scandinavia, with total protection in Sweden in 1965 and in Norway in 1972, it was too late. The last confirmed breeding occurred in 1964, in northernmost Sweden (Wabakken et al. 2001). By 1970, the wolf was regarded as functionally extinct in Scandinavia, and also for most of Finland, except possibly a few packs living close to the Soviet/Russian border. In the Soviet Union, which at that time also encompassed all the Baltic countries, there still existed a large wolf population, from which dispersers repeatedly established in eastern Finland, and occasionally some even reached northern Scandinavia.

In the late 1970´s reports of wolf sightings increased markedly including the south-central part of the Scandinavian Peninsula, and in 1983 biologists recorded the first litter (Wabakken et al. 2001). DNA-analyses later revealed that the wolves in this breeding pair were immigrants from Finland/Russia (Figure 1; Vilá et al. 2003, Liberg et al. 2005). The same pair continued to produce litters until 1985, and incestuous breeding by a sequence of various constellations of wolves continued within this pack until 1991, when the first reproduction outside the original territory was observed 250 km north-east. A reconstruction of the DNA-profiles of the two breeding wolves in this new territory by samples obtained from their offspring showed that the male in this pair was a new immigrant from the east (Liberg et al. 2005). After 1991 the number of breeding pairs increased rapidly (Figure 1) with five breeding packs in1997 and 19 in 2007. The number of individual wolves in 2007 was estimated to 188 ± 22 (Wabakken et al. 2008). At that time the entire population was founded by only three individuals. A detailed record of how the origin and relationships among individual wolves in this early phase of the wolf colonization of Scandinavia is given in the Supplementary Material in Liberg et al. (2005).

After 1991, another 20 immigrant wolves have been recorded by DNA in Scandinavia. Most of these immigrants were recorded in the reindeer area in northern Scandinavia, where typically they were either legally killed due to depredation on reindeer, or contact was lost after a short time. A small number of these wolves managed to reach the breeding wolf range in central Scandinavia, and only four of them successfully bred (Figure 2). Two males arrived in 2006/2007 and both started breeding in 2008. By 2014, twenty offspring (called F1) from these two immigrants had bred successfully. In late 2012 another two migrant wolves from the Finnish/Russian population established as a pair in northern Sweden. As this was inside the reindeer husbandry area, the authorities decided to translocate them to southern Sweden. This was done in February 2013, and the wolves accepted their new environment and established a territory around the releasing point. They reproduced already the same spring (2013), and again in 2014 (Figure 2). By winter 2014/15 no offspring from this pair has

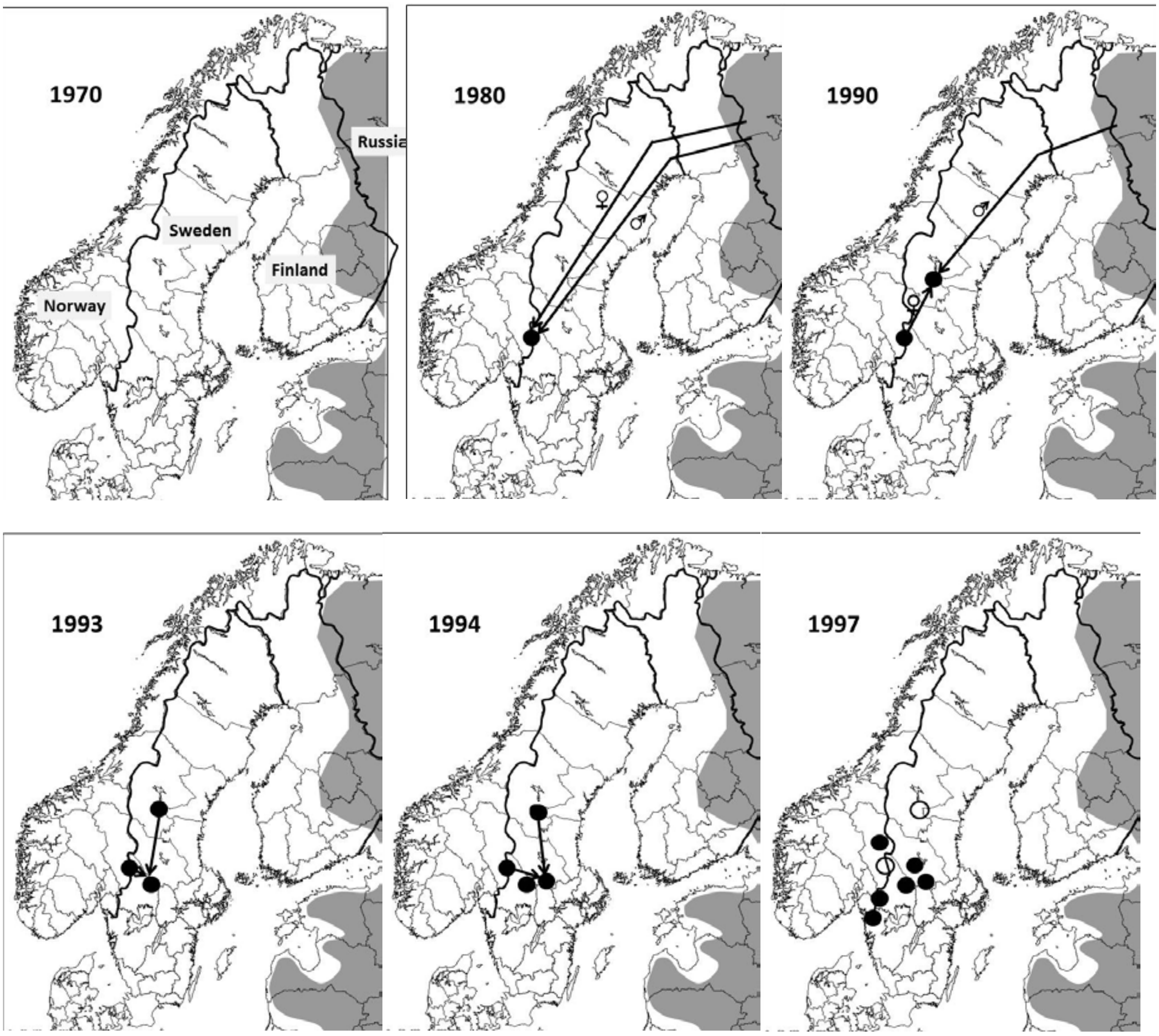
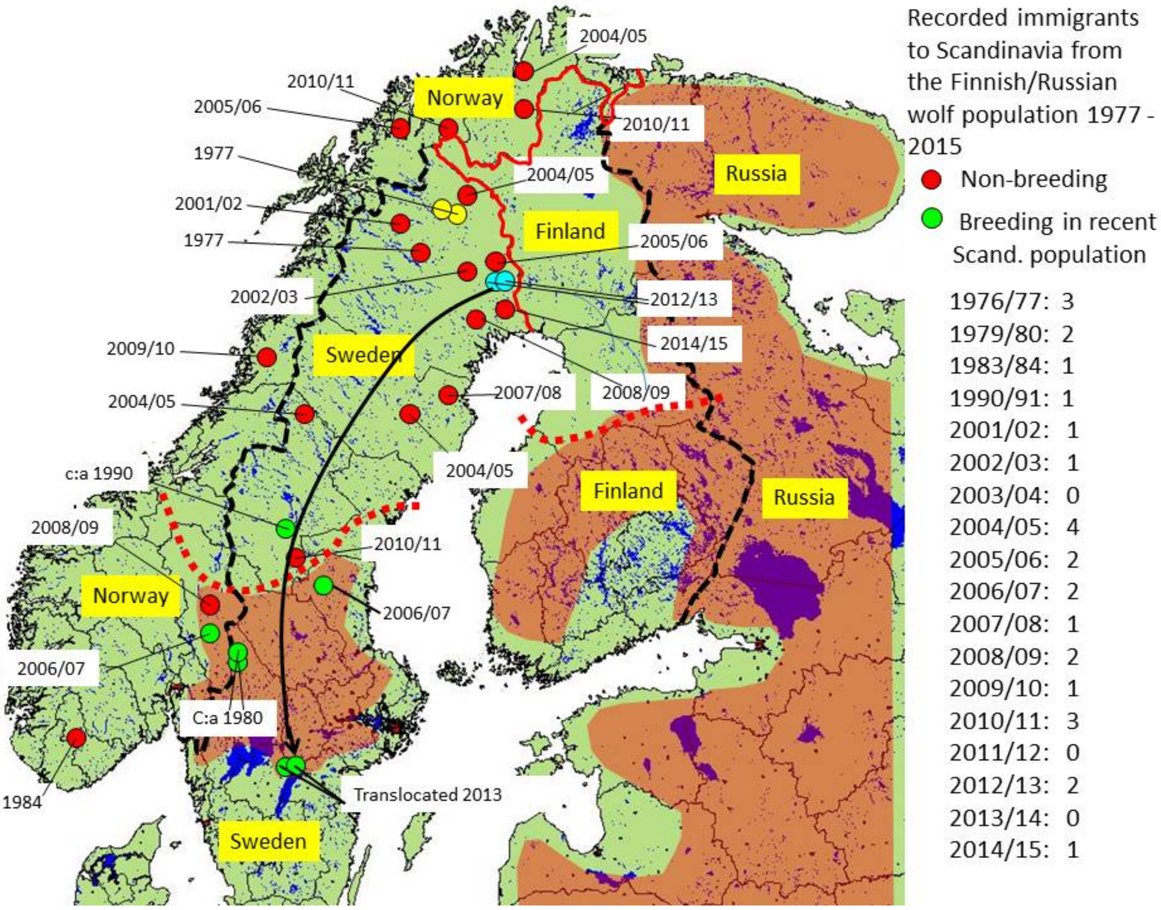


Figure 1. The recolonization of the Scandianvian Peninsula by wolves from the eastern population in Finland and Russia and establishment of new breeding territories in Scandinavia during the 1980´s and 1990´s. The eastern wolf population is denoted in dark gray. Filled rings are breeding territories, unfilled rings are former territories no longer active. Arrows go from natal population/territory to establishement territory (not shown for 1997 map).

yet bred, and therefore this new pair cannot yet be included as founders of the recent Scandinavian wolf population in addition to the first five wolves.

Demography

The Scandinavian wolf population is expanding in an environment that is favourable concerning resources (space and prey) but hostile concerning human tolerance. These aspects, as well as genetic problems, both exert influence on the demography of the population. Below we give a brief description of the basic demographic and genetic characteristics of the population as based on the more than 15 years of research performed.



1976/77:	3
1979/80:	2
1983/84:	1
1990/91:	1
2001/02:	1
2002/03:	1
2003/04:	0
2004/05:	4
2005/06:	2
2006/07:	2
2007/08:	1
2008/09:	2
2009/10:	1
2010/11:	3
2011/12:	0
2012/13:	2
2013/14:	0
2014/15:	1

Figure 2. Recorded immigrants to Scandinavia from the Finnish/Russian wolf population 1977-2015 (n = 27). Immigrants that have managed to breed and contribute to the recent Scandinavian wolf population are marked in green; immigrants that have failed to breed before death/disappearance are marked in red. Two immigrants that bred in 1977 but did not contribute to the recent population are marked in yellow. Two immigrants that established as a pair in the reindeer area in northern Sweden in 2012 but were translocated to southern Sweden in winter 2013 before their first breeding are marked with blue in their first established territory and with green in their final territory. The translocation route is marked with black arrow. The approximate breeding ranges of the Scandinavian and the eastern Finnish/Russian wolf populations are marked with transparent red. The border between Scandinavia (Norway + Sweden) and Finland/Russia is marked with a continuous red line. The southern borders of the Scandinavian and the Finnish reindeer husbandry areas are marked with dashed red lines.

Number of family groups, reproductions and litter sizes

The number of wolf family groups (packs) in Scandinavia (see Liberg et al. 2012a for definition) has increased from one in the winter 1990/91 to 49 in 2014/15. The number of wolf packs where reproduction has been confirmed is for some years slightly lower, but has increased from one in the winter 1990/91 to 46 in 2014/15 (Figure 3). Total number of individuals has not been counted in both Sweden and Norway since 2003, and has since 2011

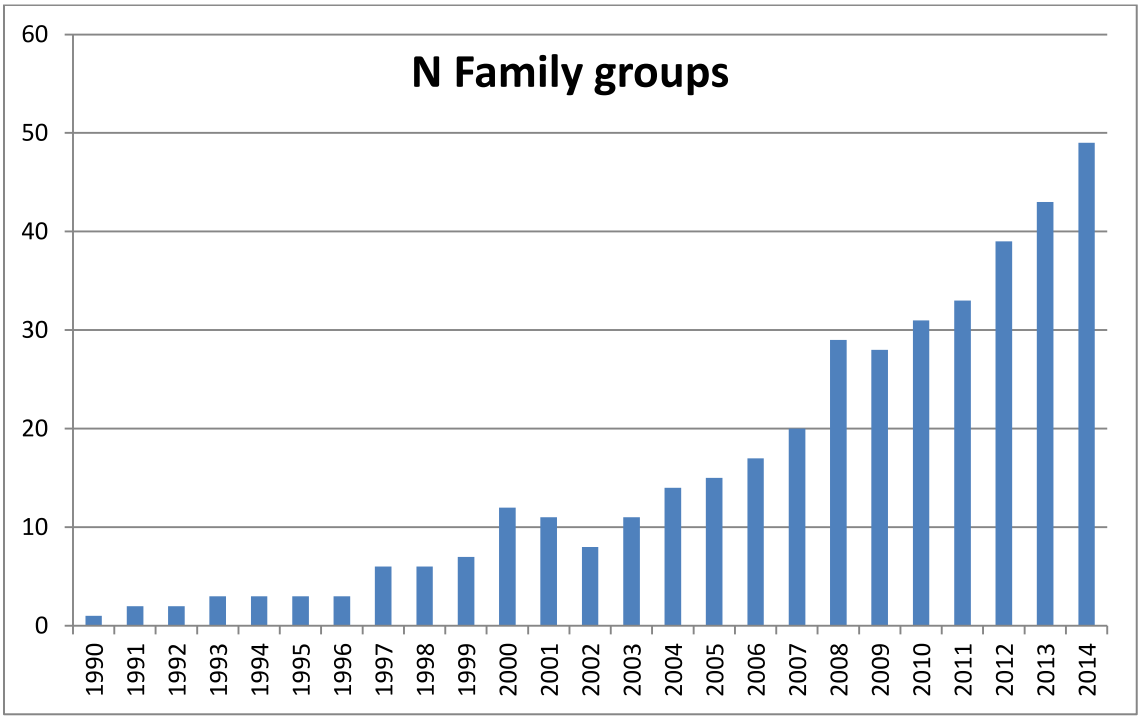


Figure 3. Number of family groups in early winter in the Scandianvian wolf population 1991-2015. The year denoted on the x-axis refers to the first part of the winter. i.e. 1990 represents for the winter 1990/91.

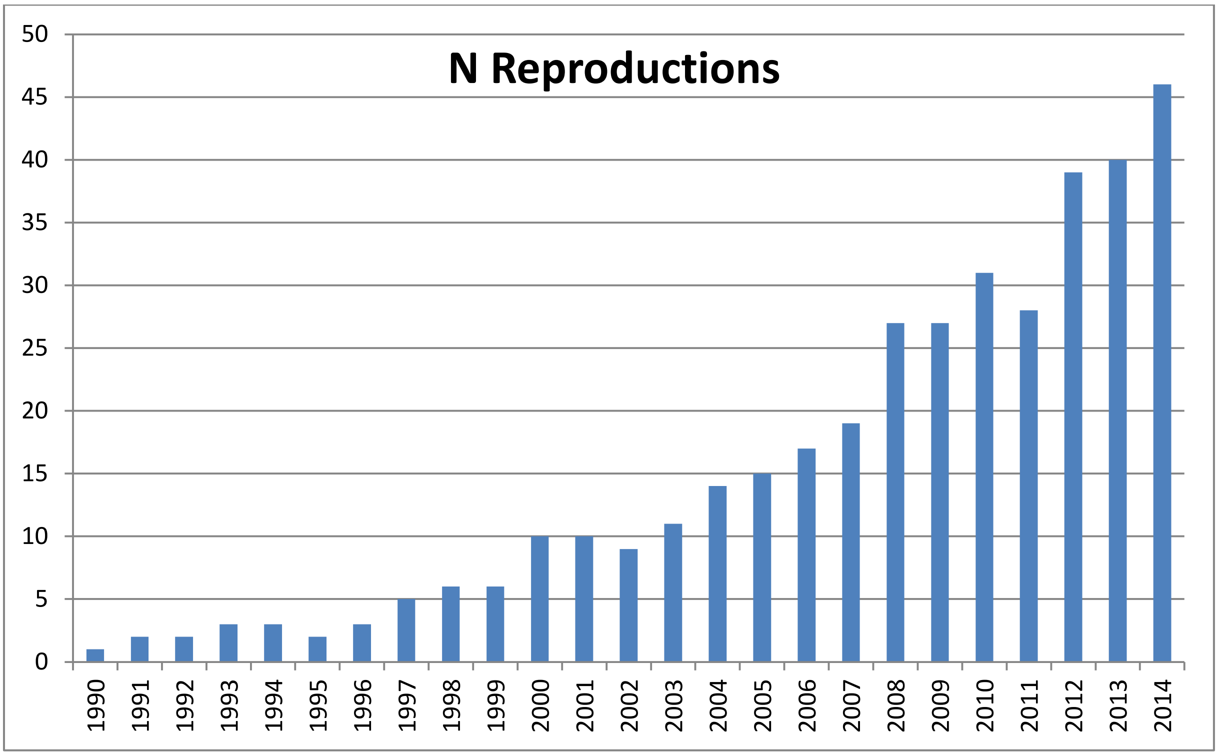


Figure 4. Number of reproductions in the Scandinavian wolf population 1990-2014.

been calculated based on number of reproductions. For the winter 2014/15 population size was estimated to 460 with a minimum of 364 and a maximum of 598 (Anon. 2015).

Litter sizes are recorded on snow during winter. We limit our estimates to first-born litters (primiparous) only, as it is impossible to differentiate between tracks from pups of the year and older siblings in packs that have bred more than once (multiparous). For the 1983-2011 period (total number of animals in each pack was not recorded in the same strict way after 2011 in Sweden) the average winter litter size was 3.6 (CI ± 0.3, range 1 – 8). During 1991-2001 the average winter litter size was 4.1. Thereafter, the average litter size declined to 3.5 during 2001-2005, and later to 3.2 for the 2006-2007 period. This decline could be a result of ongoing inbreeding depression (Liberg et al. 2005), but none of these changes in litter size have yet been statistically confirmed. After the two new immigrants started breeding the mean litter size has again increased to 3.6 in 2008-2009 and 3.4 in 2010-2011. This is similar to the average winter litter size of 3.6 in the Finnish wolf population for the period 1998-2011 (I. Kojola, pers. com.).

Winter pack sizes have averaged 6.0 wolves (range 3-11, pairs not included) for the entire study period, which corresponds well to the average reported for a large number of North American (Figure 5) wolf populations living on deer and moose (Fuller et al. 2003), and is well above the size of packs reported for another newly established expanding wolf populations (Wydeven et al. 1995).

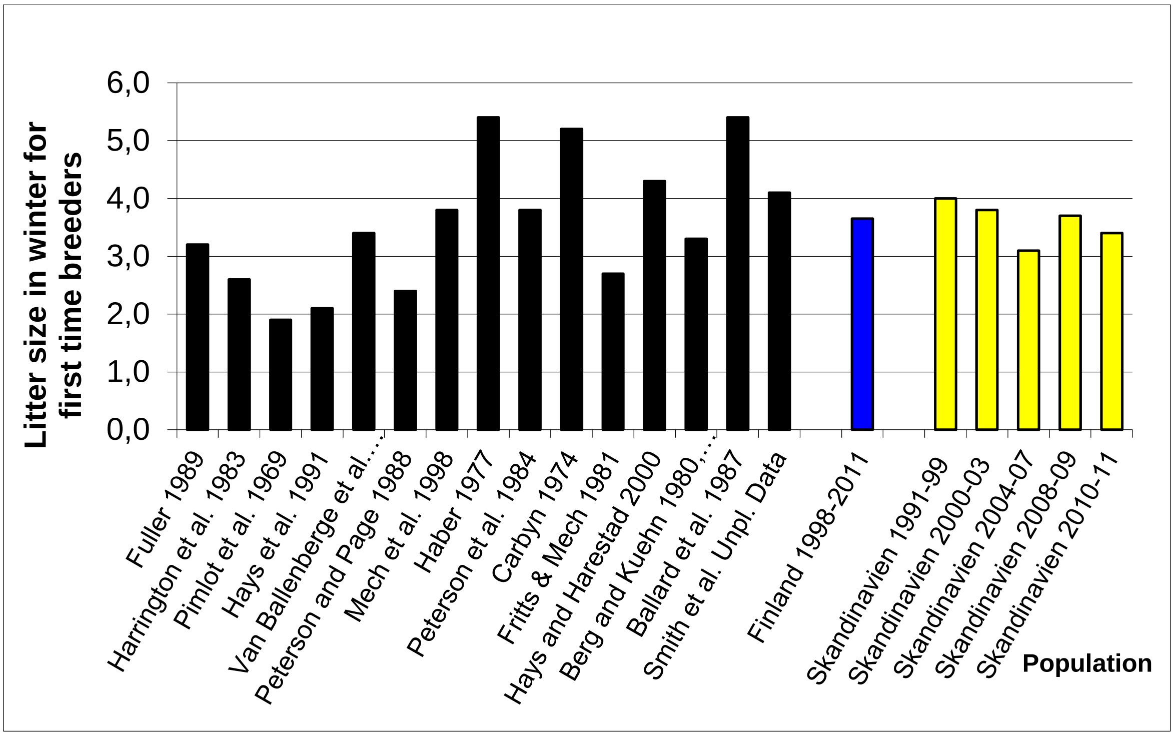


Figure 5. Litter size (mean number of pups in packs in early winter) for a number of North American wolf populations (black, Fuller et al. 2003), for the Finnish wolf population in the period 1998-2011 (blue. I. Kojola pers. comm.) and for the Scandinavian wolf population during five different time periods (yellow).

Survival and mortality causes

Poaching has been found to be the strongest single mortality cause in the Scandinavian wolf population (Liberg et al. 2008). A large part of that is due to what we have termed "cryptic poaching", i.e. a poaching that is not verified with the help of a dead body or other physical evidence (Liberg et al. 2012b). This makes poaching difficult to quantify but this problem can be overcome with the help of a sophisticated modelling technique including multiple sources of data, including both radio telemetry (104 radio marked wolves, representing 141 "wolf years") and monitoring data (Liberg et al. 2012b). According to this analysis total annual mortality between 1998 and 2009 was 0.29, which corresponds to a survival of 0.71. Poaching accounted for no less than 51% of the total mortality, and two thirds of this was classified as cryptic poaching (for information on variance and other details, see Liberg et al. 2012b). It was also possible to demonstrate the effect of this mortality on population growth. In the period 1999-2009 the population increased from 74 individuals to 263 with an annual growth rate of 13.5%. A population simulation with all poaching excluded between 1999 and 2009 gave a population in 2009 of 990 instead of the actual number of 263 (Figure 6). Although it is quite possible that other mortality causes would have increased in such a scenario, e.g. legal harvest or density effects, this simulation demonstrates the dramatic effect of poaching on the potential for population growth.

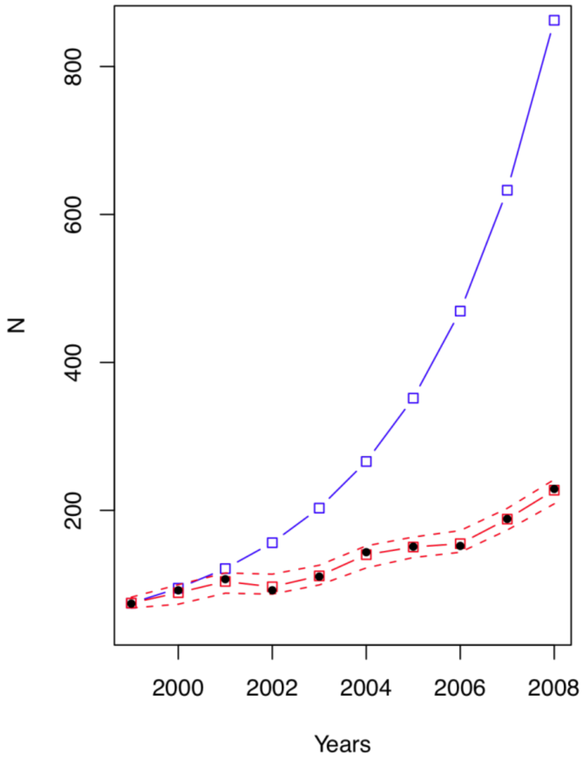


Figure 6. Census estimates of the wolf population in Scandinavia (filled black squares) and modelled population with poaching (red squares and lines, 95% credible interval shown by dashed lines) and without poaching (blue squares and line) during 1999-2009. From Liberg et al. 2012b.

The results of the Liberg et al. (2012b) report do not deviate much from unpublished results based on a larger data set, covering the whole period from 1998 to early 2015 (SKANDULV unpubl. data). This dataset includes 149 radio-marked wolves, representing 198 "wolf years (Table 1). Seven wolves that have been marked in the reindeer area are excluded from this dataset. Overall survival for this whole period was 0.74, which is close to the earlier estimate of 0.71. Territorial animals had a survival rate of 0.79, whereas subordinate adult pack members had a survival of 0.61 and survival of dispersing animals was as low as 0.41. The proportion of the mortality caused by poaching was almost identical to the earlier results (52% vs. 51%). Legal killing comprised 23%, traffic 9% and natural causes (disease, age, trauma) another 17% of total mortality. Total annual survival rates of 0.75 correspond well with the average for many wolf populations in North America (Fuller 1989, Fuller et al. 2003, Adams et al. 2008, Smith et al. 2010). This is somewhat lower than what is typical for non-harvested wolf populations (Ballard et al. 1987, Hayes and Harestad 2000) but well above the level typical for declining populations (Ballard et al. 1987).

Table 1. Cause specific annual mortality rates (%) for the period 1999-2014 among radio marked Scandinavian wolves split up on age- and social classes. For total mortality also 95% confidence intervals are given. Observe that the same wolf individual can occur in different classes as it is growing and changes from one social class to another. Therefore the figure for "All wolves" is smaller than the sum of all individuals split up on categories in column "N radio marked".

				Cause specific annual mortality rates					
Category	N radio marked	Wolf years	N dead	Natural	Traffic	Leg harvest	Confirmed illegal	Prob. legal	Total mortality
Terr.males	50	72.0	14	5.0	0	2.7	2.6	8.8	17.9±9.6
Terr. females	49	77.8	20	2.5	2.5	6.6	0	13.6	23.5±10.4
Subord. pack adults	27	14.1	4	22.2	0	0	20.0	0	38.8±14.4
Dispersers	44	20.3	17	4.2	12.5	22.4	22.6	17.7	59.2±9.3
Pups	54	14.2	2	2.1	1.9	0	0	0	4.0±5.1
All wolves	149	198.3	57	4.8	2.6	6.5	4.3	10.9	26.3±6.1

In another report Liberg et al. (2011), demonstrated a significant reduction of poaching and of total mortality in Sweden during the 2006-2011 period, compared with the 1998-2005 period. No corresponding change could be detected in Norway. Unfortunately, no more recent analyses have been performed on this aspect.

Population growth

The Scandinavian wolf population has had a positive growth almost every year since the third founder started breeding in 1991 (Figure 3 and 4). As all categories of individual wolves have not been recorded in all of Scandinavia since 2003, we do not here present rates of increase based on individuals, but on the number of family groups and reproductions. As these two parameters follow each other rather closely, the growth rates based on them also do so. For family groups, the intrinsic rate of increase (*r*) between 2003 and 2014 (early winters) was 0.132 resulting in a lambda 1.14 (14% annual increase; Figure 7). For reproductions corresponding figures were 0.125 and 1.13 (13% annual increase; Figure 8).

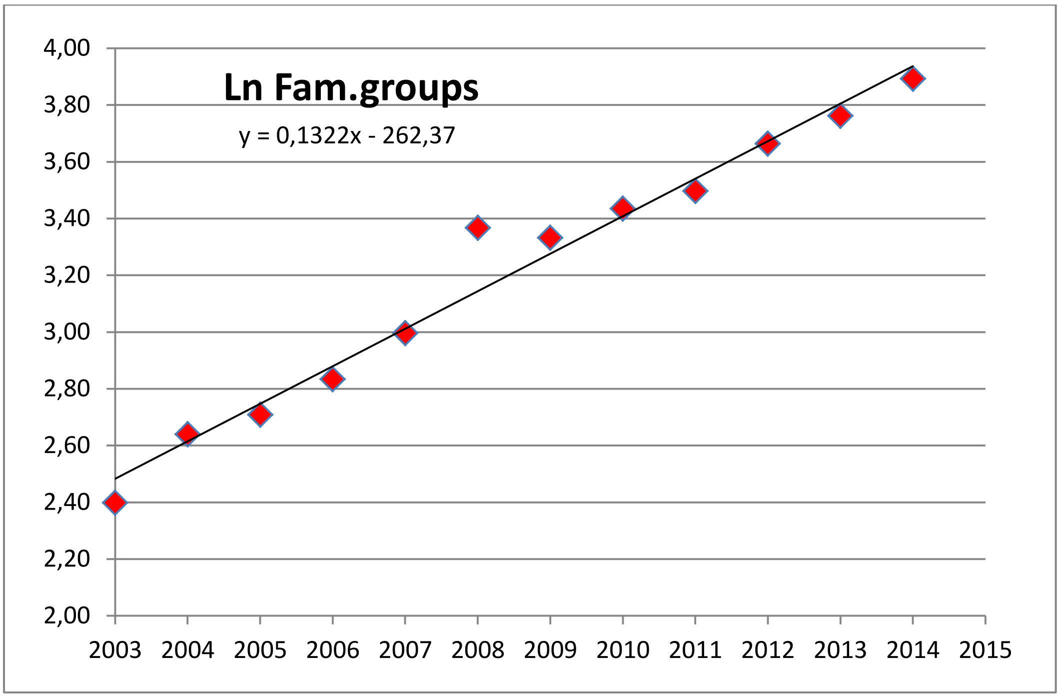


Figure 7. Trendline of population growth for family groups (transformed to natural logaritms) in the Scandianvian wolf population 2003-2014. Intrinsic growth rate (r) for the total period = 0.132. lambda = 1.14. The years on the x-axis refer to early winter. e.g. 2003 refers to the winter 2003/2004.

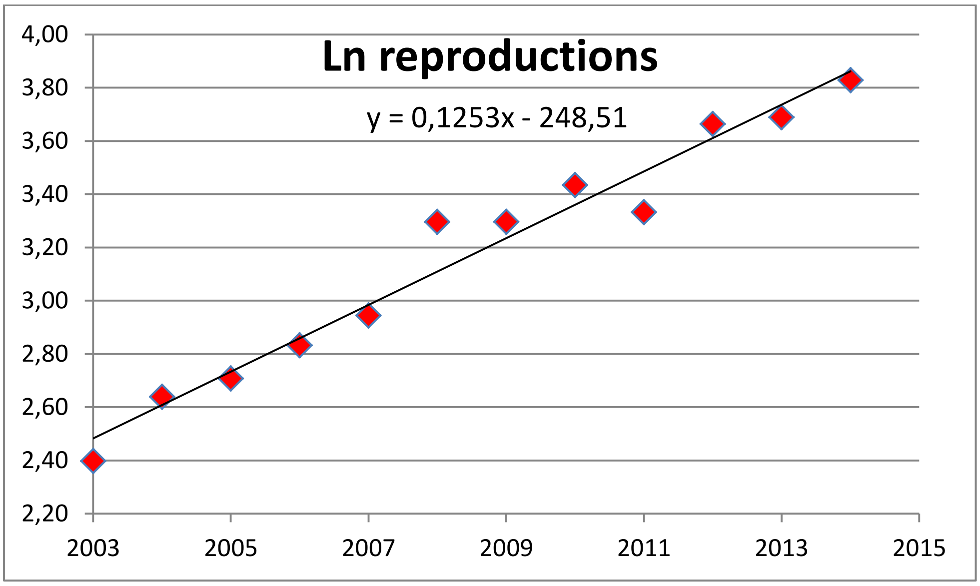


Figure 8. Trendline of population growth for number of reproductions (transformed to natural logaritms) in the Scandianvian wolf population 2003-2014. Intrinsic growth rate (r) for the whole period = 0.125 with lambda = 1.13.

Distribution

The present breeding range of wolves in Scandinavia covers a continuous area in the southern boreal zone of south-central Scandinavia (Figure 9 and 10). Including gaps within the range, it covers approximately 120,000 km^2 of which 100,000 are in Sweden and 20,000 in Norway. This wolf distribution area covers approximately 25% of Sweden´s total land-area. Most of Sweden, excluding the reindeer area, with the highest suitability for wolves as determined by Karlsson et al. (2007), is now occupied by wolf territories (Figure 9). But vagrant wolves and stationary single wolves are recorded in increasing frequency all over the country outside the breeding range, both in the reindeer area which covers almost half of Sweden, and in the south (Figure 10). Every year young wolves try to establish both in the reindeer area and in the south, but are either killed legally in control operations due to depredation on livestock and domestic reindeer, or they simply disappear from the area which may have multiple potential explanations, where poaching likely constitutes the major candidate. In the south also traffic kills takes a heavy toll (Table 1).

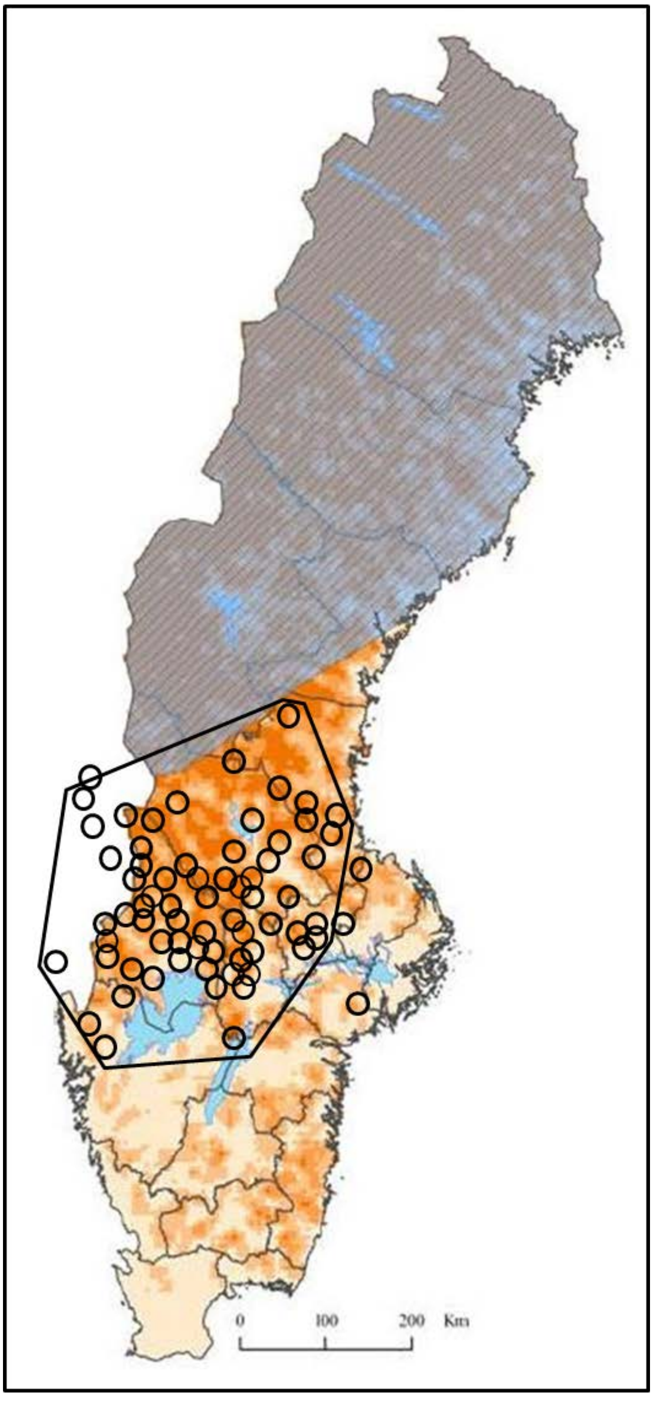


Figure 9. Wolf habitat suitability and distribution of wolf territories during the winter 2014/15 in Sweden. Also wolf territories in the Norwegian part of the wolf breeding range are denoted. The Scandinavian wolf breeding range in 2014/15 is denoted with thick black line. Territories with family groups or pairs are denoted with circles. The reindeer husbandry area in northern Sweden is shaded in gray. The background colors of southern Sweden mark the suitability for wolves with darker red/brown showing higher suitability. Developed from Karlsson et al. 2007.

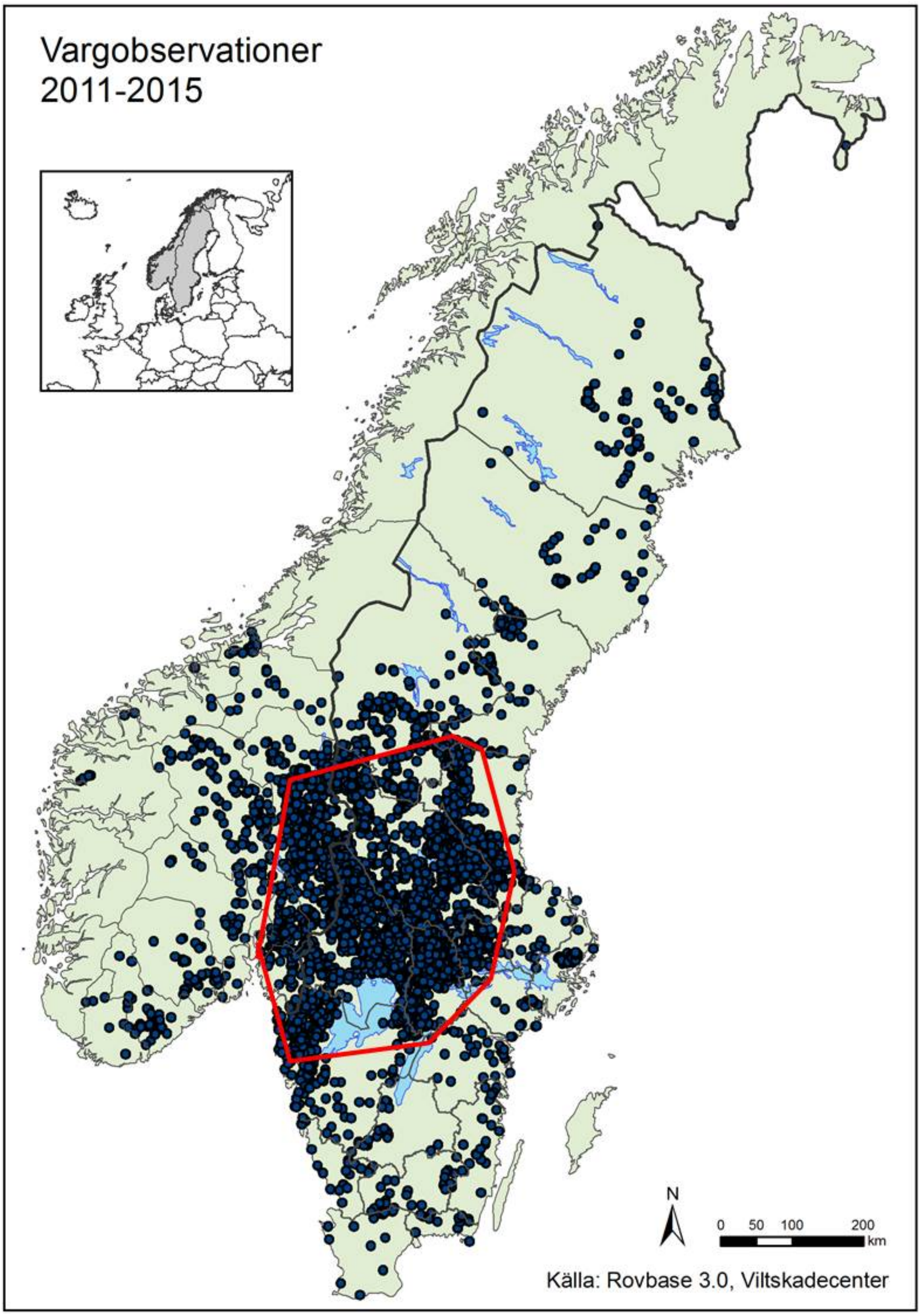


Figure 10. Confirmed wolf observations in Scandinavia from January 2011 to June 2015. The Scandinavian wolf breeding range in 2014/15 is denoted with a red line.

Dispersal

Out of 42 Scandinavian wolves radio-marked as pups between 1998 and 2010, 81% dispersed from their natal territory. Average straight-line dispersal distances from the natal territory to the place where they finally settled was 89 km for females and 139 km for males, but the variance was large, and some wolves dispersed very far. In Figure 11 we present straight-line dispersal distances for 25 wolves that moved further than 400 km. Many of these died during dispersal meaning that the real dispersal distance for those would have been even longer. The longest dispersal distance we have measured concerns a female born in 2002, who moved from SE Norway (the Gråfjell territory) to northern Finland where she established with a male close to the Russian border. The straight-line dispersal distance was 1092 km, but it was estimated that she totally had moved more than 10,000 km (Wabakken et al. 2007). Recently we have recorded a similarly long dispersal from a male born in in SE Norway in 2012 that have dispersed to northern Karelia in Russia.

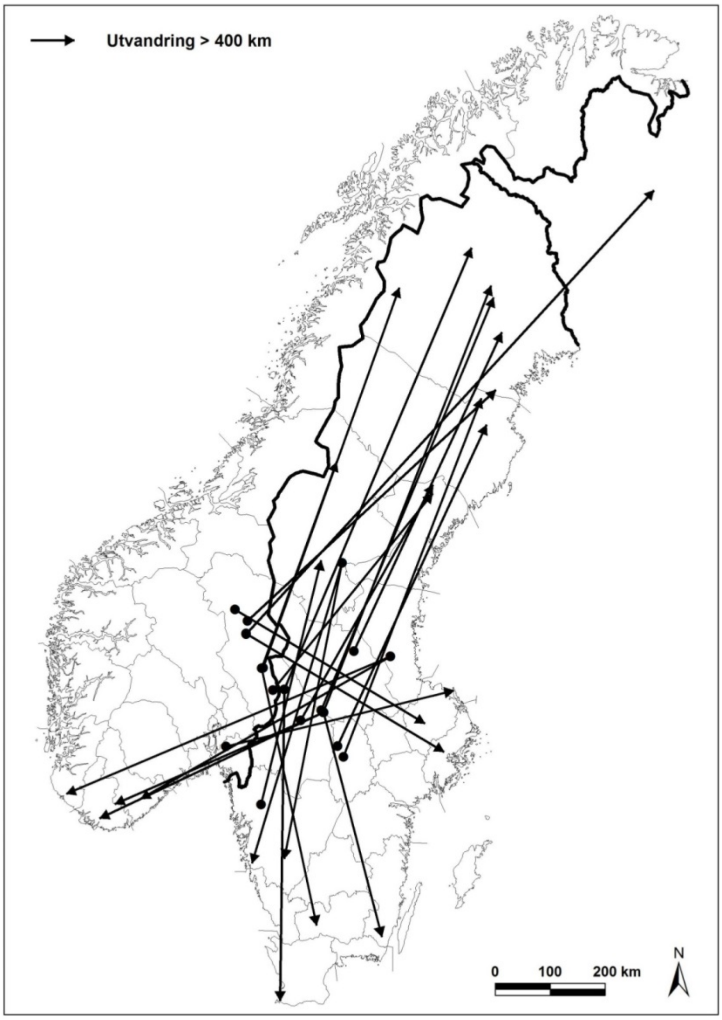


Figure 11. Dispersal distances for 25 wolves that moved more than 400 km from their natal territories in the period 1984 – 2013 in Scandinavia. The origin for each wolf is based either on radio marking or DNA analysis of wolves found dead. End-point of arrow either shows the last radio position or the place where the wolf was found dead.

Genetics

The Scandinavian wolf population has some typical characteristics for being in a critical genetic situation. It is small, isolated, and has a narrow genetic basis. Up to 2007 when the population size was close to 200 wolves, it was based on only three founders. An expected consequence of this situation was a rapid increase of inbreeding levels, and evidence of inbreeding depression has been demonstrated (Liberg et al. 2005, Bensch et al. 2006, Räikkönen et al. 2013). Recently, the situation has improved since two new wolves entered the breeding population in 2008 by natural immigration, and another two were artificially translocated from the Swedish reindeer range in 2013. These new migrants have halted the increase of the inbreeding level, and even depressed it somewhat (Figure 12). To continue this decreasing trend however, more genetic input from outside is needed.

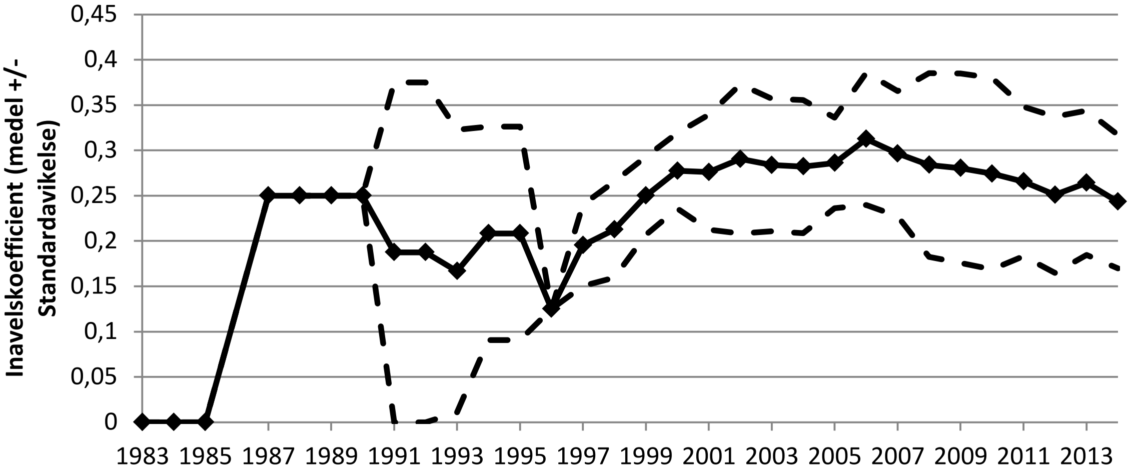


Figure 12. Average inbreeding coefficient (F) for family groups 1983-2014 (SD dashed lines).

Fortunately there exists a very good knowledge of the genetics of this population. The core of this knowledge is a near complete pedigree of the population, going back to the first founder (Liberg et al. 2005). The reasons for that this pedigree (Figure 13) could be constructed are partly the same as is causing the genetic problems for the population, namely few founders and a small population. The recent origin of the population, and the small number of founders entailed that enough DNA-samples from the early phase of the population´s history allowed a reconstruction of its complete pedigree, from the first two founders up to present (Liberg et al. 2005).

Material and analysis methods

For identification and parentage analysis we have used between 19 and 36 microsatellite markers. The markers used depended on the year of analysis where more markers were used from 2010 and onwards in order to increase information content and to increase the comparability between analysis made by Swedish and Norwegian laboratories (Grimsö Wildlife Research Station, SLU and NINA, Trondheim, respectively). Samples for microsatellite analyses were derived both from dead and live-captured radio-collared wolves, and noninvasively, primarily from scats, and less frequently from hair and blood in snow. For description of the laboratory methods, see Liberg et al. 2005 and Åkesson et al. (in review).

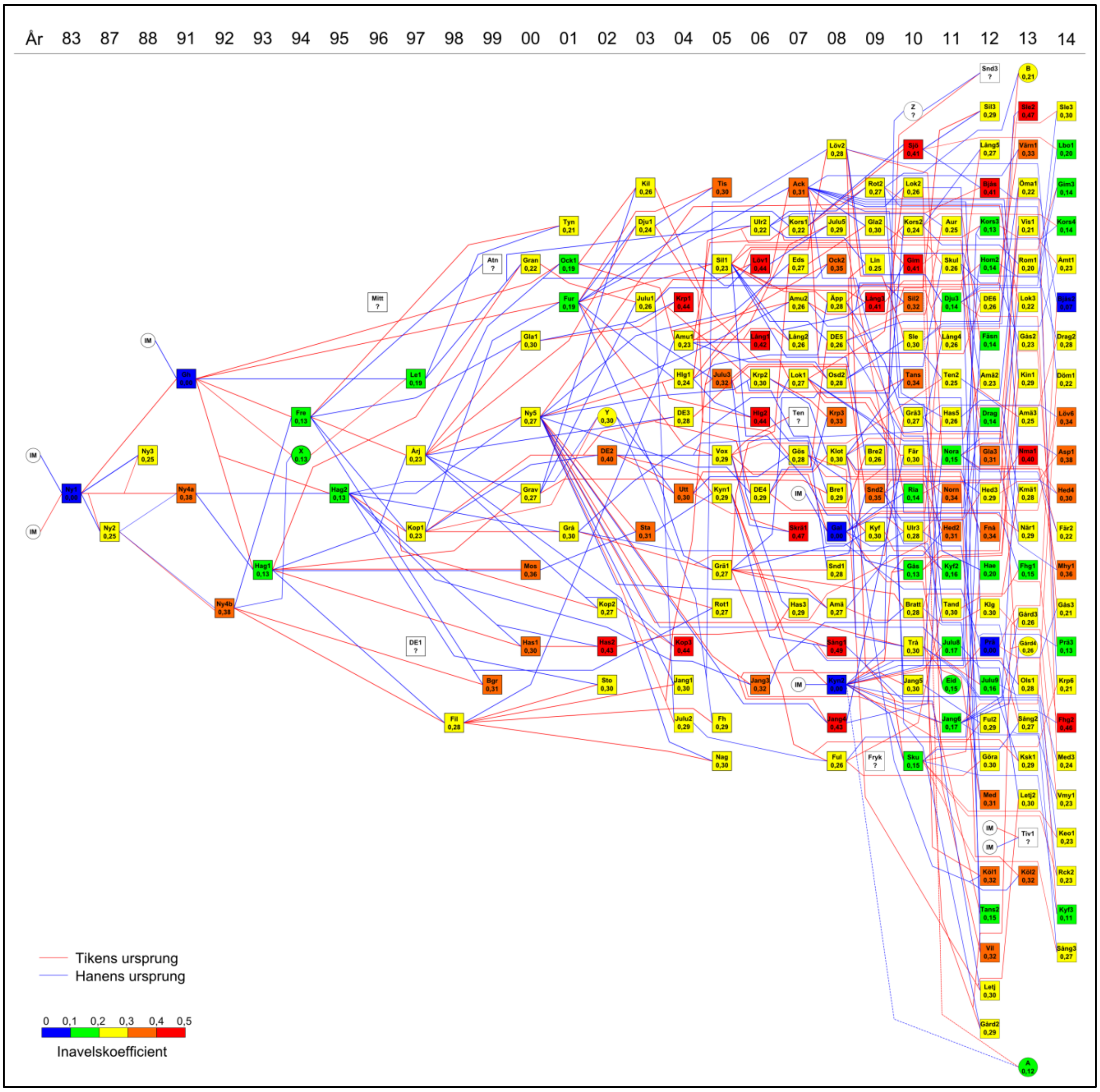


Figure 13. Pedigree of the Scandinavian wolf population for reproducing pairs during 1983-2014. Pairs are visualized from left to right in the order of year they first reproduced. Below each pair is the inbreeding level (F) denoted for their offspring. IM represents individuals with an origin outside the Scandinavian wolf population. Pairs denoted by a circle have not been able to link to any known reproducing pack in the population. The abbreviations of each pair are further explained in Table 1.

The number of samples analyzed per year has increased with the growing wolf population. Recently between 1500 and 2000 samples are sent in to the two laboratories each year, of which approximately 1000 are analyzed. The ambition is that at least all the territory marking animals in packs and pairs should be identified each year. In our database there are now 1445 different individual DNA-profiles, which correspond to between 85 and 90% of all wolves > 6 months old that have ever existed in this population since it was founded in 1983. The pedigree contains 199 different breeding pairs, of which complete genetic relationships has been possible to reconstruct for 192 pairs (Åkesson and Svensson 2015).

Development of inbreeding and genetic variation

During the 1980´s and early 1990´s the average inbreeding coefficient F (calculated as the mean of F for offspring to all breeding pairs for the respective year, not weighted for variation between pairs regarding number of offspring) varied largely due to small number of breeding pairs (Figure 12). From the mid-1990´s, the inbreeding coefficient increased steadily until it peaked in 2006. After that the increase has been halted, and there even has been a small decline during the following eight years. This decline has also been expected because in 2008 the two new migrants started breeding and later also their F1 and F2 offspring have entered the breeding section of the population. The possible positive effect of the latest migrants in the Tiveden territory has not been included in this analysis yet, as the genetic relation between the partners in this pair is not yet resolved.

Also the genetic variation, measured as multi-locus heterozygosity in 30 microsatellites, has been affected by the new migrants and their offspring. It decreased until 2007, after which it has stabilized or even shown a small increase (Figure 14). Also the number of alleles in our sample of microsatellites decreased through genetic drift in the early phase of the population, but after the third migrant arrived in 1991, it has increased steadily with each immigration event (Table 4). On a sample of 30 microsatellite loci, the total number of alleles has increased from 88 in the first breeding pair in 1983 to 147 in 2014. A total of 151 alleles have been brought to the population by the seven founders (including the Tiveden couple). Eleven alleles have been lost through genetic drift, but of these 7 have been restored later by immigrants.

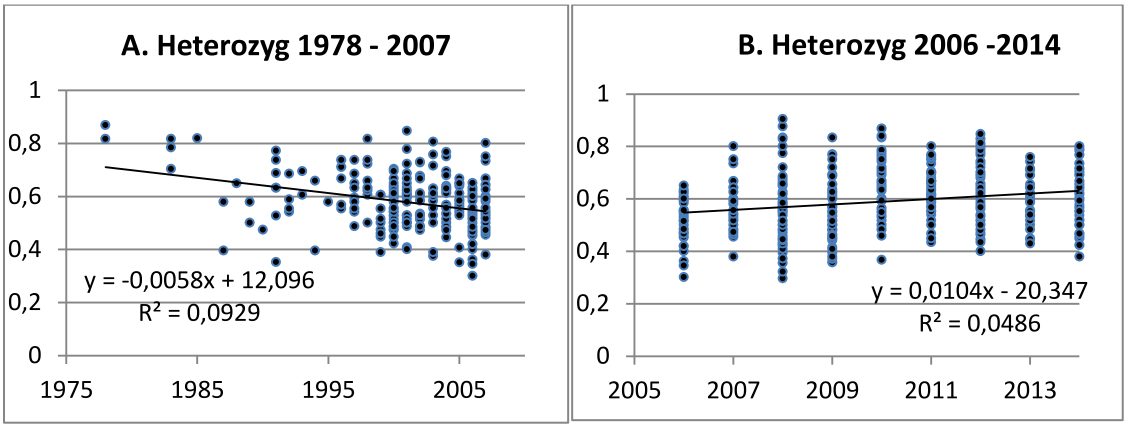


Figure 14 a and b. Development of multi-locus heterozygosity MLH in 650 wolves with known year of birth in the Scandinavian wolf population from 1978 to 2014. Each wolf is assigned to its year of birth on the X-axis.

Table 4. Contribution of new alleles on 30 microsatellite loci by the founders of the Scandinavian wolf population, number of these alleles lost by drift, and number of those lost that have been restored by later immigration.

Year/ Period	**Founders**	**New alleles**	**Lost alleles**	**Lost alleles restored**	**Tot alleles in pop**
1983	Nyskoga pair	88			88
1983-1991			9		
1991	Gillhov male	21		1	101
1991-2008			2		
2008	Galven + Kynna males	30		5	134
2008-2013					
2013	Tiveden pair	12		1	147
Total		151	11	7	

Evidence of inbreeding depression

Already in 2005 a negative effect of inbreeding was demonstrated on winter litter sizes in the Scandinavian wolf population (Figure 15; Liberg et al. 2005) in an analysis that covered the first 20 years of the population´s existence (1983-2002). This negative effect remains using an extended data set reaching up to 2013 (Figure 16), but the relationship has been weakened (linear regression: r^2 declined from 0.39 to 0.20).

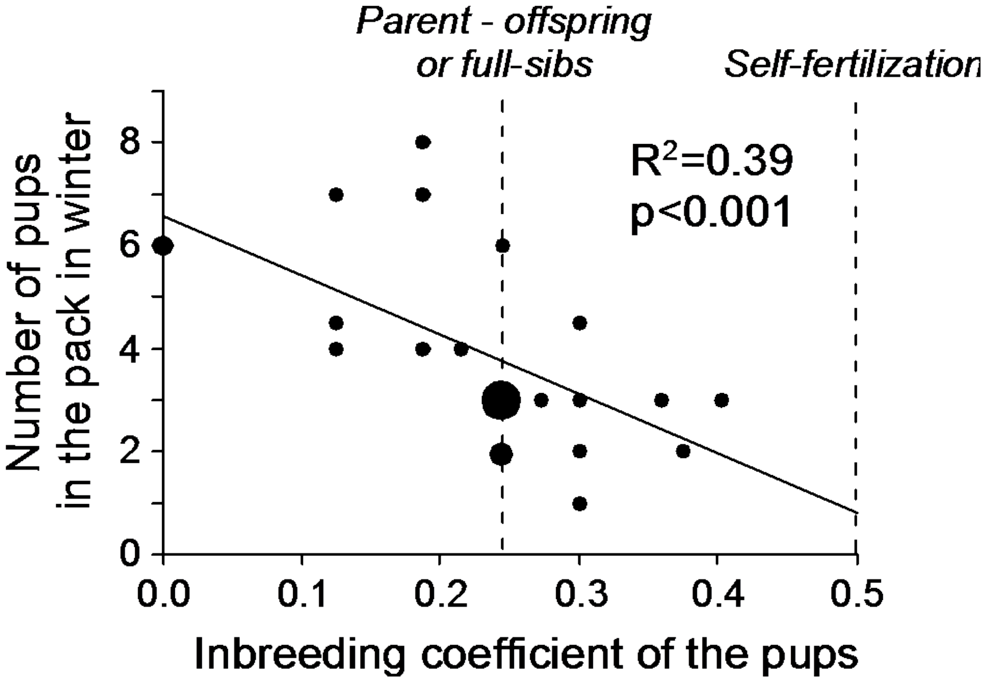


Figure 15. Litter sizes in early winter for first born litters in relation to the inbreeding coefficient of the pups in the Scandinavian wolf population in the period 1983-2002. Small dots refer to one data point each, medium-sized to two data points and large to four data points. Inbreeding levels corresponding to parent-offspring or full-sib mating and self-fertilization are indicated (From Liberg et al. 2005).

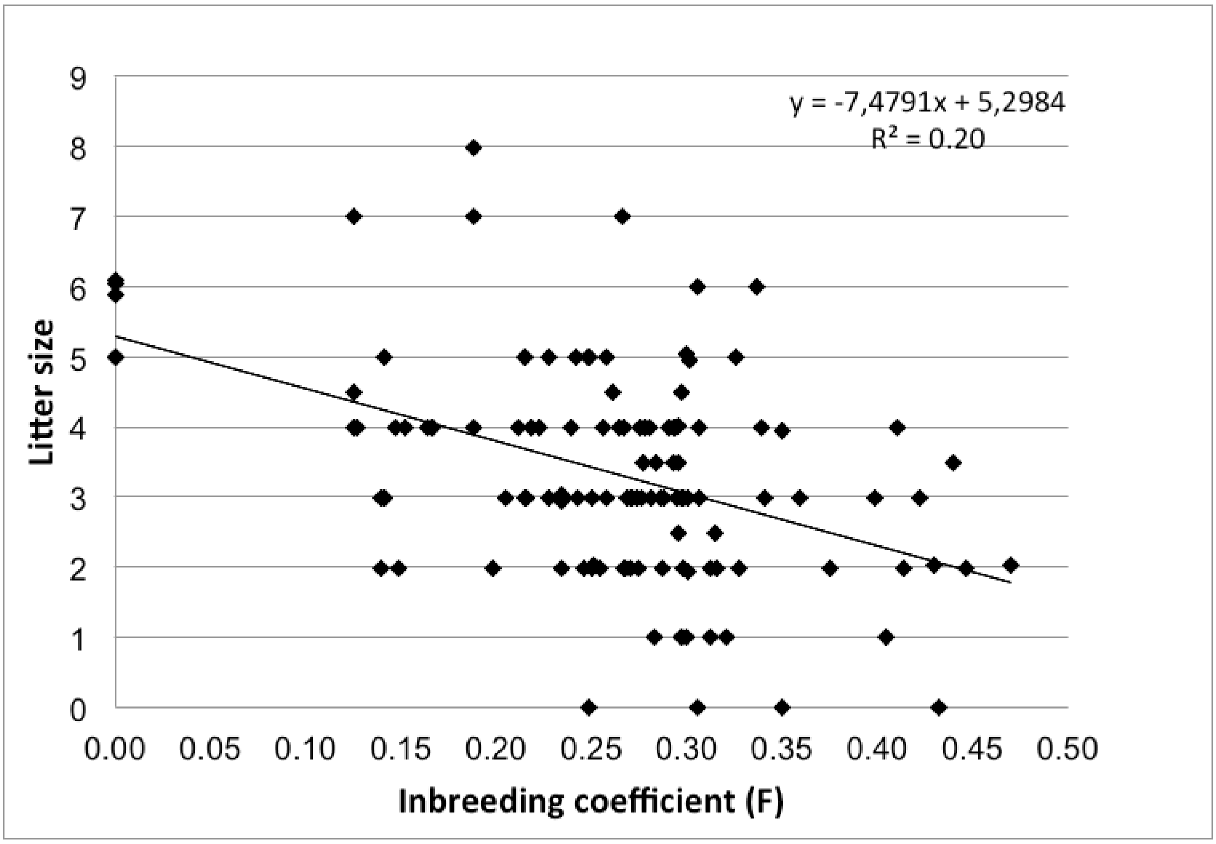


Figure 16. Same as in Figure 15 but with data extended over a longer period (1983-2013).

There has also been demonstrated an increase in the frequency of congenital malformations with time in the Scandinavian wolf population, that has been claimed to be connected to the simultaneous increase in inbreeding level in the population (Räikkönen et al. 2013). In a sample of 171 necropsied Scandinavian wolves born between 1978 and 2011, all kinds of malformations were found, but vertebrae and teeth were examined in deeper detail. A total of 63 cases of malformations (37% of all examined) were found, with 50 occurring in vertebrae and teeth and 13 in soft tissue. Frequency of malformations increased from 13% to 40% during the period (Figure 17).

However, a draw-back with this study was that malformation frequency was not correlated directly with inbreeding coefficients, but with time, using the assumption that inbreeding increased with time. In a sample of 282 wolves necropsied at the Swedish National Veterinary Laboratory between 1978 and 2014 where 59 malformations in 52 different individuals were reported (18%), failed to support a correlation between the frequency of malformations and inbreeding coefficient (Figure 18). This is puzzling and an indication that some of the strong conclusions drawn by Räikkönen et al. (2013) might have been premature. The two data sets are not identical, but the overlap is large. There was a higher frequency of anomalies in vertebrae and teeth found in the sample of Räikkönen et al. (2013) due to their deeper and more detailed analysis of these organs, while SNVL-sample was larger covering a period up to 2014. The ratio between anomalies in hard tissue (vertebrae and teeth) and soft tissue

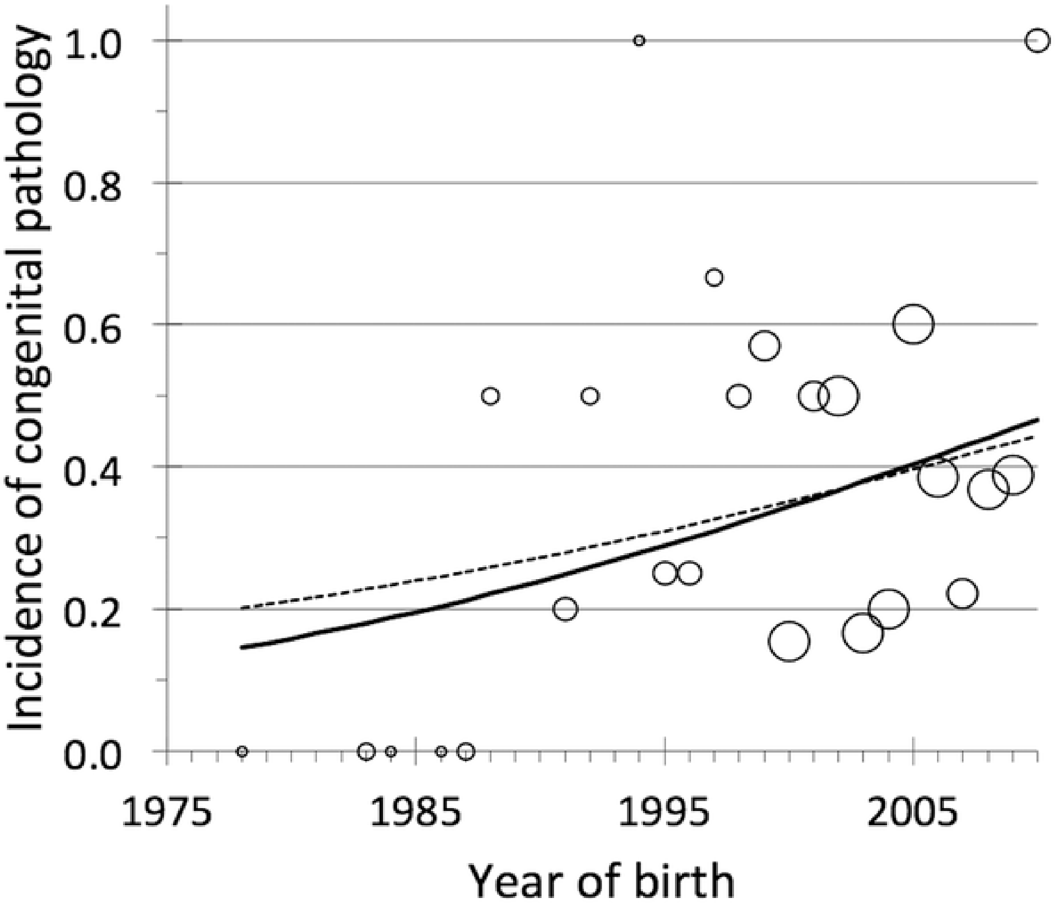


Figure 17. Relationship between year of birth and incidence of congenital pathology in Scandinavian wolves born between 1978 and 2010 (n=171). The wolf born in 1978 is the founding immigrant female. The solid line is the predicted logistic regression line which includes an estimate for the slope and intercept. The dashed line is the weighted average of two models, the model that includes an estimate of the slope and intercept and a model including only an intercept (i.e. assumes no trend). Each circle is the proportion of wolves observed for a particular year with some kind of congenital pathology. The size of each circle represents the number of wolves observed each year. There are five sizes of circles representing sample sizes of 1, 2-3, 4-6, 7-9 and 9 to 19 (from Räikkönen et al. 2013).

(aorta, heart, kidneys and testis) in the latter sample was 35 to 24, as compared to 50 to 13 in Räikkönen et al. (2013). When the two types of anomalies were split up in SNVL-sample, there was a tendency for soft tissue material to correlate with inbreeding coefficient, but no such trend were find for hard tissue (Table 2). This could indicate that some of the anomalies of the latter type indeed are not congenital or are ubiquitous in the population with no or little natural selection against them. The trivial nature of some of these anomalies with little or no effect on fitness, as also pointed out by Räikkönen et al. (2013), might support the latter interpretation.

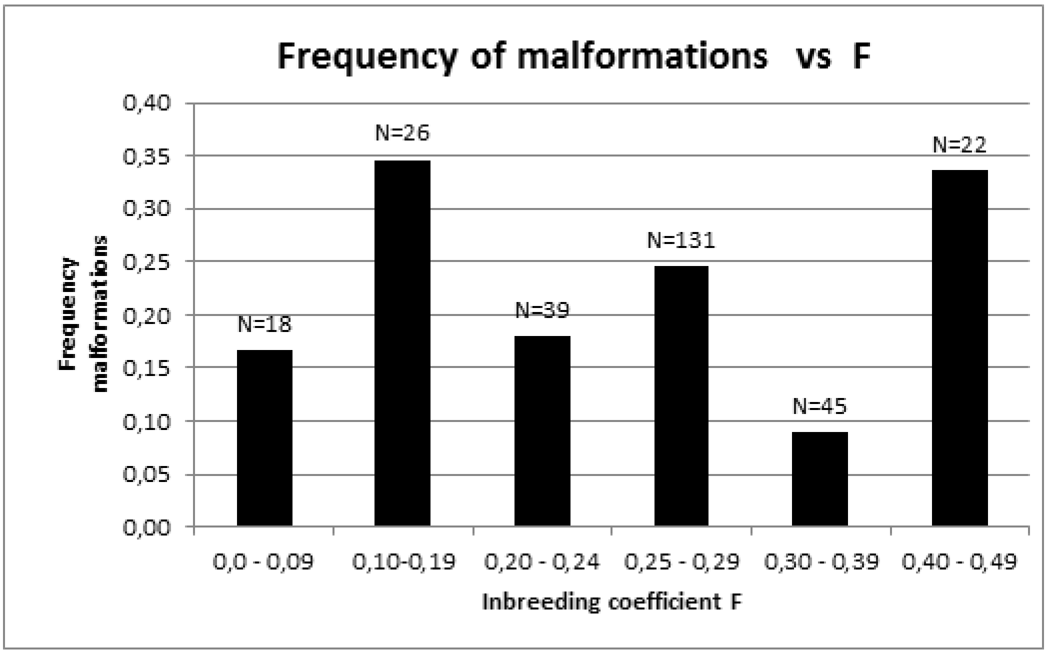


Figure 18. Frequency of all recorded malformations found in 282 wolves necropsied at the Swedish National Veterinary Laboratory in the period 1978 -2014 at different levels of inbreeding. Chryptorchism and testis anomalies that only can occur in males are weighted for the proportion of males in respective sub-group (SKANDULV unpubl.).

Irrespective of how well or poor the malformations in the Scandinavian wolf population correlate to the inbreeding coefficients, their total frequency still is relatively high which makes it difficult to completely dismiss some link to inbreeding (Figure 18). However, when comparing frequencies of single types of anomalies in the Scandinavian wolves with those in other strongly inbred carnivore populations, like the Florida panther (Roelcke et al. 1993) and the wolves on Isle Royale (Räikkönen et al. 2009) they are still rather modest (Table 3).

Table 2. Frequencies of anomalies in two types of organs at two different inbreeding levels (F) found in 282 wolves necropsied at the Swedish National Veterinary Laboratory in the period 1978-2014.

	F= 0.0-0.24		F=0.25 - 0.45	
	N necropsies	N Malformations	N necropsies	N Malformations
Soft tissue	83	6 (7 %)	199	25 (12 %)
Hard tissue	83	12 (14 %)	199	20 (10 %)

Table 3. Frequencies of three types of morphological malformations in three different large carnivore populations. LSTV stands for "lumbo-sacral transitional vertebrae", a malformation in the hip region of the spine. References within parentheses are: SKANDULV unpublished data (1); Roelcke et al. 1993(2); Räikönen et al. 2009 (3).

	Scandinavian wolves (1)	Florida panther (2)	I. Royale wolves (3)
Heart/aorta	0.7% (1)	18% (2)	
Kryptorchism	7% (1)	80% (2)	
LSTV	10% (3)		33% (3)

Pairing and breeding success of migrant offspring compared with inbred offspring

Interestingly, the first generation offspring (F1) of the two migrants that started breeding in 2008, had a significantly higher pairing and breeding success than their contemporary inbred counterparts (Åkesson et al. in review). Among the 28 migrant offspring that were born between 2008 and 2010 and that were not legally shot before reaching pairing age (1.5 years), 18 (64.3%) managed to find a partner, which is a significantly higher proportion than the 33 of 93 (35.5%) inbred offspring, also born between 2008 and 2010, that managed to form a pair ($\chi^2 = 7.32$, p = 0.007).

The difference was even larger concerning how many succeeded to breed. Among the 27 migrant offspring that were not legally shot before reaching breeding age (2 years), 14 (51.8%) managed to breed, compared with 17 of 85 (20.0%) inbred offspring ($\chi^2 = 10.38$, p = 0.001). This disproportionate success of the migrant offspring has contributed significantly to the decrease in average inbreeding coefficient seen in the population after 2007. After only one wolf generation, these two migrants together contributed with some 15% of the genetic variation in the population. In winter 2014/15 there were 68 family groups or territorial pairs in the Scandinavian wolf population, of which 38 (56%) contained at least one migrant, or an F1 or F2 migrant offspring.

Earlier viability analyses of the Scandinavian wolf population

There has been produced a number of viability analyses of the Scandinavian wolf population between the second half of the 1990´s and 2014.

Ebenhard and Johnsson 1996-2000

Johnsson & Ebenhard (1996), Ebenhard (1999) and Ebenhard (2000) used the computer programme package Vortex (Miller and Lacy, 1999), to simulate the development of the population 100 years into the future. As there were very little hard data on the demography of the Scandinavian wolf population available at that time, they ran a number of scenarios with different demographic and genetic data as input values, including varying lambda between 1.02 and 1.35. Even in the worst scenario, including inbreeding effects and 3.0 lethal equivalents per individual, they found that a population without immigration and with a management ceiling of 200 individuals was enough to keep extinction risk in 100 years below 5%. To retain at least 95% of the genetic variation for 100 years, they however found that the population without immigration could not be capped lower than 500 wolves.

Nilsson 2004

Nilsson (2004) also used the Vortex program for a PVA of the Scandinavian wolf population. Like Johnsson and Ebenhard he tested different input values, but restricted the analysis to three scenarios (A, B and C), where scenario A had the presumed most likely demographic and genetic input values, while B and C had more pessimistic input values, B regarding demography and C genetics. The number of lethal equivalents ranged between 1.57 and 6.1 in the different scenarios. He included environmental variation and also infrequent larger catastrophes in the simulations, but his model population was closed with no immigration. He investigated both what he called short time perspectives (100 years) and long perspectives (1000 years). An interesting result was that a small, but closed, population that is viable for the first 100 years still may go extinct in a 1000 year perspective, indicating a late threshold effect of inbreeding. In his most optimistic Scenario A, a population where the management ceiling was as low as 400 was enough to keep extinction risk for 1000 years below 5%. In the more pessimistic scenarios, the population ceilings had to be at least 1300 (Scenario B) and 3000 (Scenario C), respectively.

The Färna meeting 2002

In 2002, there was held a 3-day workshop on the genetic problems of the Scandinavian wolf population with six invited international experts on population genetics or wolf ecology, the so called Färna-meeting (Liberg 2006).

The most important conclusions of the workshop were:
- The Scandinavian peninsula (Sweden + Norway) is probably too small to hold a long-term (> 100 years) viable wolf population on its own. Therefore promotion of immigration of wolves from Finland/Russia should have highest priority.
- The present narrow genetic basis of only three wolves makes this recommendation even more important.

- One or two immigrating wolves per wolf generation (approx. 5 years) would guarantee enough genetic variation for long-term viability.
- The ratio between total population and genetically effective population (Ne/N) for Scandinavian wolves range between 0.25 and 0.33.
- Even with a satisfying rate of immigration, the effective population size Ne should not be smaller than 50, i.e. 150 – 200 wolves in total with a Ne/N ratio of 0.25 – 0.33.
- If there, despite all efforts is no further immigration of wolves, the population should retain at least 95% of its present genetic variation for the next 100 years, which would need a minimum effective population of approximately 200, giving a total population of 600 – 800.

Chapron et al. 2012

The first PVA of the Scandinavian wolf population based entirely on data from this population was performed by SKANDULV on a request to from the Swedish government via an assignment from the Swedish Environment Protection Agency SEPA in summer 2012 (Chapron et al. 2012). For the analyses three population models with increasing level of structural complexity were used. The models were specifically designed for the Scandinavian wolf population. The models were purely demographic, not considering the genetics. The reason genetics was not included in the analyses was that the deadline given for the report was extremely short. As stated in the assignment, the analyses aimed at estimating what is the minimum demographically viable population of wolves in Scandinavia under IUCN Red List criterion E (excluding genetic criteria). This criterion proposes that for a population to qualify as not being “Vulnerable” or any more serious threat category, a quantitative analysis should show that the probability of extinction is less than 10% within 100 years (IUCN 2003, 2006).

Similar simulations for all three models were run. Given that genetics is no problem, the results showed that a population of 38 wolves with a demography like the Scandinavian wolf population was large enough to keep the risk of stochastic extinctions below 10%, and with 42 wolves the risk decreased to 5%. There was no detrimental environmental variation or larger catastrophes included in this analysis. Scenarios, with catastrophes of varying intensity and frequency included, demonstrated that a population capped by management at a ceiling as low as 100 individuals could sustain (extinction risk < 10%) single catastrophes which killed up to 90% of the population, if their frequency was not higher than two per century (Figure 19 and 20). With the same management ceiling the population could sustain up to 5 catastrophes per century if they did not kill more than 70% of the population each time. It was also concluded that 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.

Liberg and Sand 2012

In autumn 2012, SKANDULV was asked by SEPA to complement its demographic PVA from the same year with genetic aspects. A report was delivered in October 2012 (Liberg and Sand 2012). No new analyses were made and the report was based on a literature review

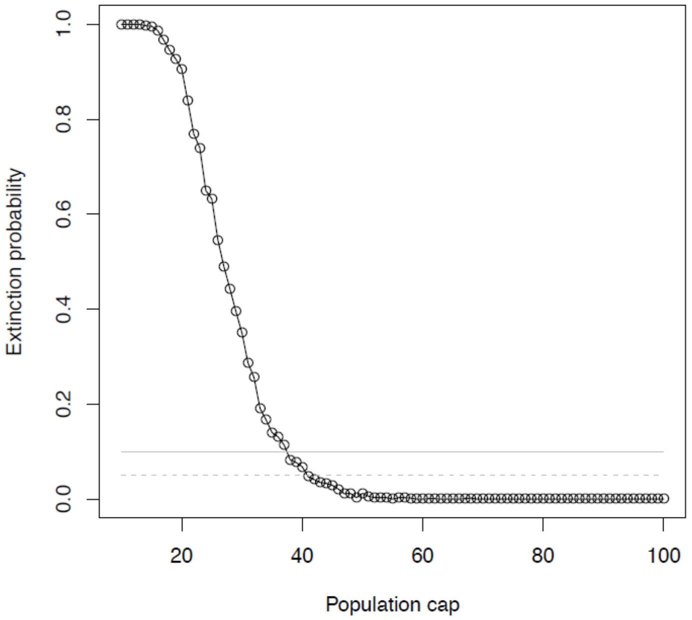


Figure 19. Extinction probability as a function of population cap for a theoretical population with parameters obtained from the Scandinavian wolf population. Horizontal grey lines are 5% (dashed) and 10% (continuous) threshold of extinction risk. From Chapron et al. 2012.

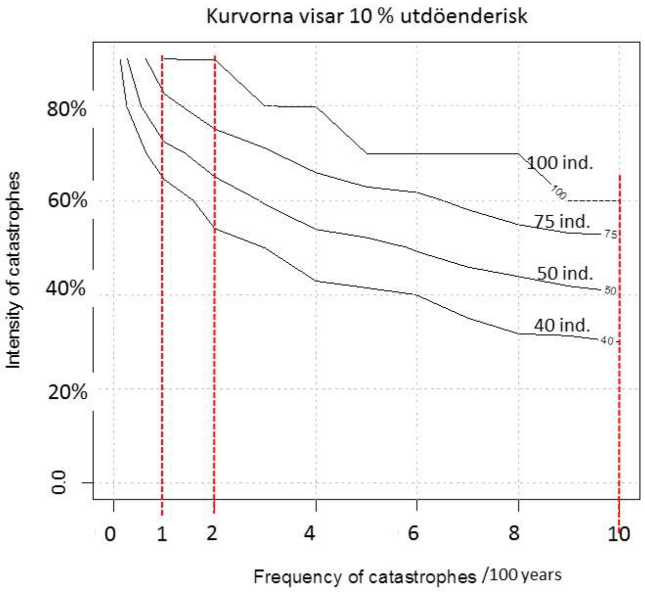


Figure 20. MVP contour curves with extinction risk of 10% as a function of frequency of catastrophes and of intensity (mortality (%) due to the catastrophe) for a theoretical population with parameters obtained from the Scandinavian wolf population. Irregular patterns are stochastic artefacts. The four curves are scenarios with populations capped at 40, 50, 75 and 100 individuals respectively. An example: with a frequency of two catastrophes per 100 years a population capped at 40 individuals can sustain a loss of maximum 55% to keep the extinction risk at maximum 10% while a population capped at 100 individuals can sustain a loss of up to 90 % to keep the extinction risk below 10 % (from Chapron et al. 2012).

and on earlier analyses. In the report it was stressed that assumptions play a much larger role in genetic PVAs than in pure demographic PVA´s, especially concerning the effect that loss of genetic variation can have on extinction risk ("…*the effects of inbreeding depression on individual fitness and population growth can normally be incorporated in standard PVAs, such as those generated by VORTEX, but the potential harmful effects of loss of adaptability on population viability cannot*…" ; Jamieson and Allendorf 2012). Typically, the population size needed to retain a certain amount of genetic variation is larger than the size needed to cope with inbreeding depression (c.f. the so called "50-500 rule"; Franklin 1980). It was however also pointed out that the need for genetic variation to retain the evolutionary potential of the population refers to the global rather than the local population as long as there is some gene flow into the latter (Hoegh-Guldberg et al. 2008, Jamieson and Allendorf 2012). This turns the attention away from focus on population size per se, to the demand for genetic inflow, which also was the approach chosen for the report. Instead of trying to give a certain population size to reach a genetic MVP, the relation between different immigration scenarios and resulting levels of inbreeding and genetic variation was discussed. No definite recommendation on migration flow was given.

In this report a graph was presented to illustrate how much genetic variation is lost from a population that is cut off from a large metapopulation (figure 21). The graph was originally presented by Ryman and Laikre (2009). It is based on theoretical population genetics and is described in Ryman and Leimar (2008). However, its relevance for the Scandinavian wolf population has beeen questioned, and the authors of the report (Olof Liberg and Håkan Sand) have later advised against using it for the purpose of describing retention of genetic variation in the Scandinavian wolf population (Liberg et al. 2013).

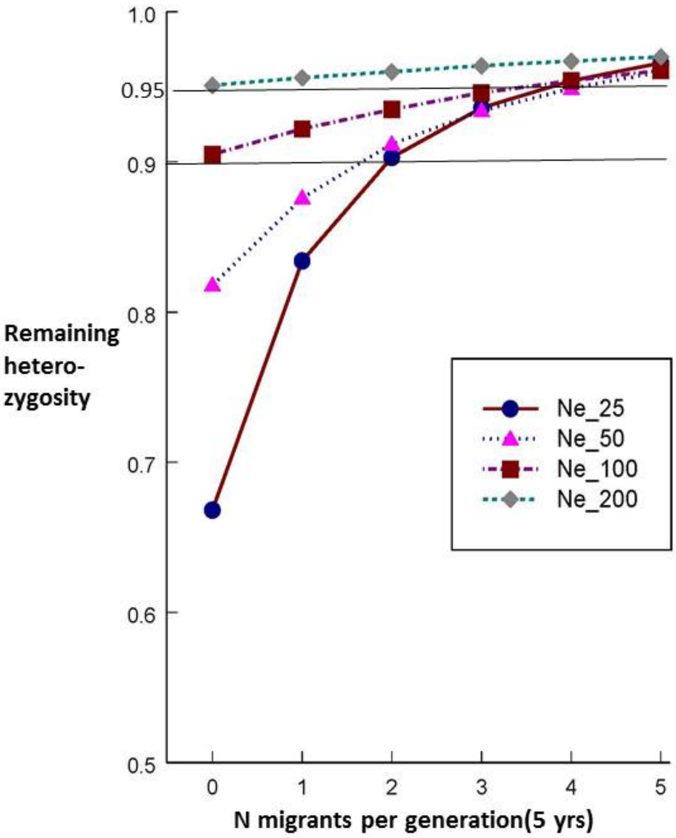


Figure 21. Remaining degree of heterozygosity [H(t=20)/H(t=0)] after 20 generations (≈100 years) at different effective population sizes (Ne) and for different immigration frequencies. Migrants come from an infinitely large population (reproduction of Figure 3a in Liberg & Sand 2012).

Bruford (2015)

As it has become increasingly clear that genetic connection with other populations is the key component for the viability of the Scandinavian wolf population, SEPA asked in November 2013 the English conservation geneticist Michael Bruford to perform a PVA with special emphasis how many effective immigrants per generation will be needed to prevent significant inbreeding or loss of variation (Figure 22, 23, 24). A final report was delivered in July 2015.

Bruford used the Vortex program, where he tested two different models – (1) the *pedigree plus supplementation model* and (2) the *allele frequencies and dispersal model* - to simulate trajectories of the inbreeding coefficient and genetic variation. Both models utilized real data available from Scandinavia and neighboring populations. An important difference between the two models is the way inbreeding is measured. The *pedigree plus supplementation model* estimates the inbreeding coefficient from the degree of co-ancestry between two individuals, as given from the pedigree. The *allele frequencies and dispersal model* utilizes allele

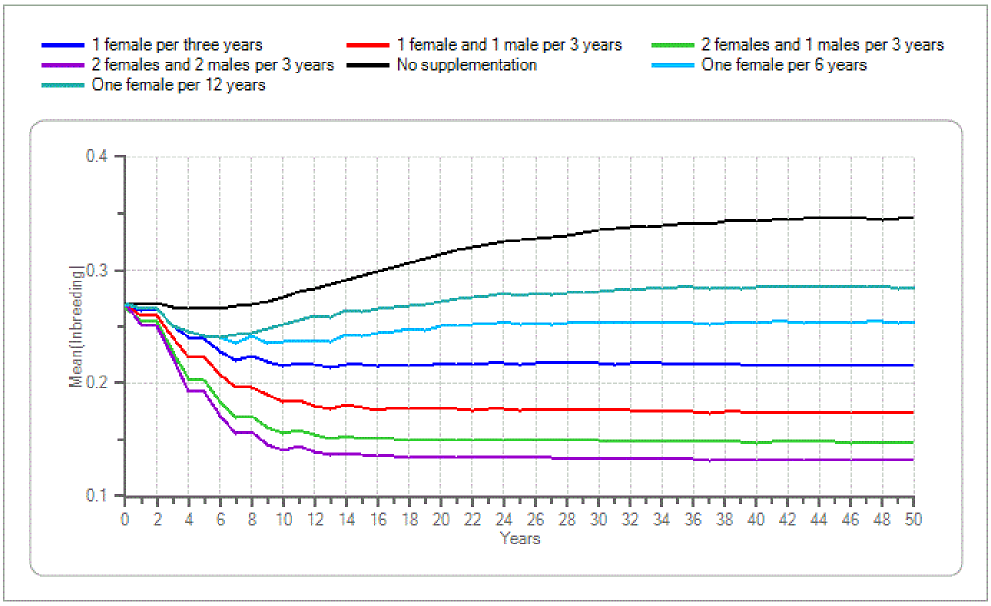


Figure 22. Inbreeding coefficient in the Scandinavian wolf population starting from 2012 pedigree values using a carrying capacity of 700 with population supplementation. Means of 1000 simulations (PS-model) are presented (from Bruford 2015).

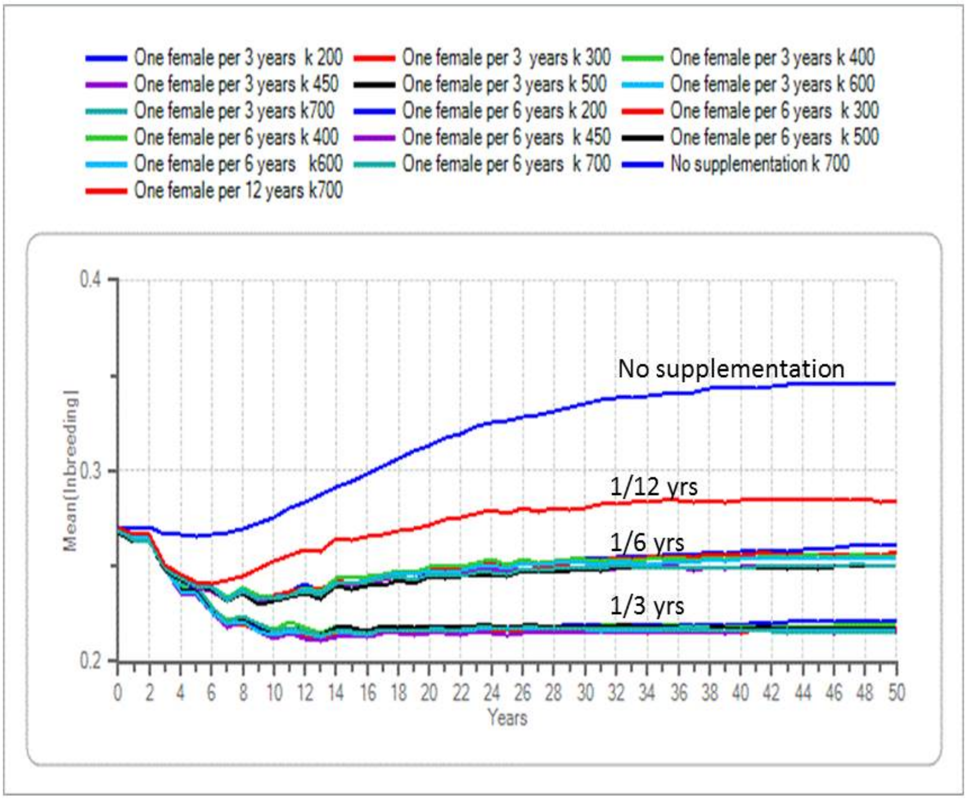


Figure 23. Inbreeding coefficient in the Scandinavian wolf population starting from 2012 pedigree values using carrying capacities of 200-700 with population supplementation ranging from zero to one female per three years. Means of 1000 simulations (PS-model) are presented (from Bruford 2015).

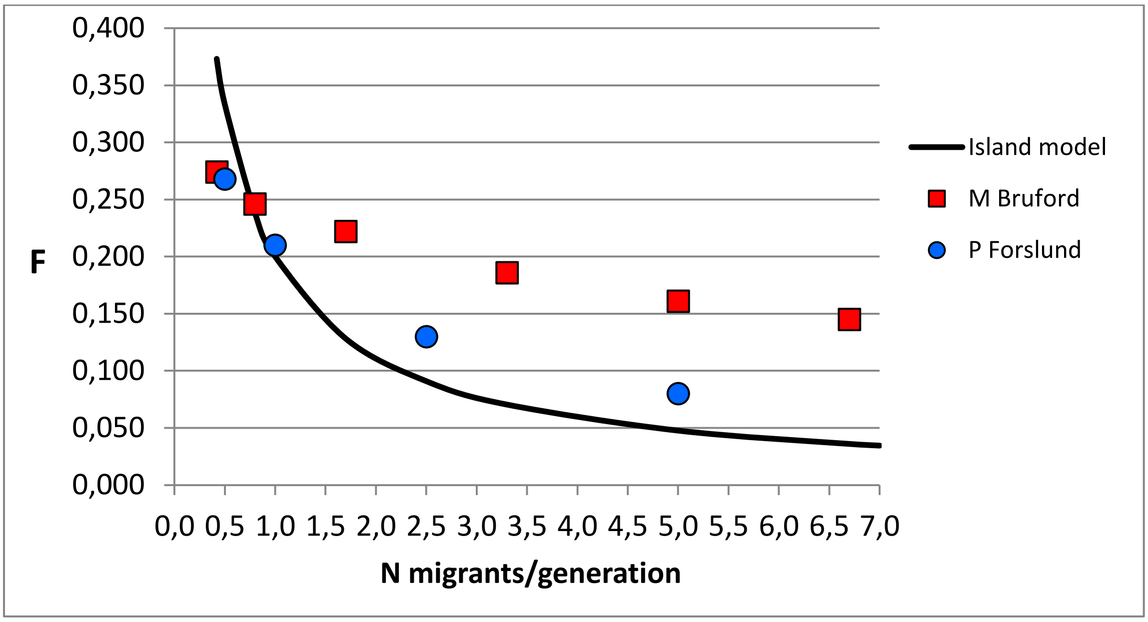


Figure 24. Relationship between immigration rate and equilibrium inbreeding coefficient according to the island model (Wright 1969) final inbreeding level after 50 years in the Bruford pedigree + supplementation model (Bruford 2015) and after 100 years in the Forslund model (Liberg & Sand 2012). Generation time is five years.

frequencies and their departure from Hardy-Weinberg frequencies to calculate F_{is}, an estimator of local (within-population) correlation of allele frequencies or inbreeding.

Both models were openly discussed by the author and the reviewers. The *pedigree plus supplementation model* was considered to better reflect the demography and inbreeding trajectories. However due to limitations in Vortex, the immigrants in this model carried unique alleles, leading to unrealistically high genetic differentiation between the donor and the recipient populations. Still this model produced lower effect of immigration than what is expected from the island model (Wright 1969), and also from Forslund's model (Figure 24). The *allele frequencies and dispersal model* was considered to better represent the genetic similarity between the Scandinavian wolf population and its neighbors in Finland. Thus, this model was supposed to provide a more realistic assessment of the effect of immigration, but had clear limitations in reflecting demography and inbreeding trajectories.

Several different scenarios were modelled, addressing the effect of different levels of immigration with the population size varying between 170 and 700 in Scandinavia, defined in the models as the carrying capacity. The simulations clearly demonstrated that modest levels of immigration (one effective migrant per six years or 0.83 per generation) were sufficient to maintain gene diversity at acceptable levels (95% of its current state), provided a population size of at least 300 wolves. Inbreeding levels were also constrained close to 0.2 with a moderate number of immigrants. As expected, the ability to retain rare alleles improved with increased population size. Neither of the models predicted significant probabilities of extinction in any of the simulation scenarios.

An important conclusion from this report, pointed out several times by the author, is that population size does not matter much for reduction of inbreeding or retention of genetic variation, once there is a continuous supplementation (effective immigration) into the population. The key parameter is the frequency of effective immigration. This is also in accordance with the classical island model (Wright 1969).

Genetic drift and loss of genetic variation are directly connected to the effective population size (Ne), rather than the census size (Nc). Bruford calculated Ne from the loss of gene diversity through time. With no immigration the Ne/Nc ratio varied between 0.32 and 0.39 depending on which carrying capacity (k) was used in the simulation ("219/686 (k = 700; ratio 0.32), 180/499 (k = 500; ratio 0.36) and 115/297 (k = 300; ratio 0.39"). Bruford also presented an alternative method to calculate Ne based on loss of heterozygosity, which gave lower ratios. For k = 300 in the absence of immigration, the ratio is 0.246 and for k = 700 it is 0.224.

Scenarios with immigration included provided much higher ratios. For one immigrant per three years, the *N*e/*N*c ratio varied between 0.66 and 0.86, depending on carrying capacity, and for one migrant per six years the ratio varied between 0.53 and 0.79. However, several of the reviewers pointed out that these ratios are problematic, since they reflect the dependence of the whole meta-population. The complex problem to calculate Ne and thus also the ratio Ne/N in meta-populations where there is connection between the sub-populations has been treated by several papers, and cannot be regarded to be definitely solved (Allendorf et al. 2013, Hössjer et al. 2014).

The report provides some closing remarks on an appropriate FRP-level in the Scandinavian wolf population. Bruford emphasizes that it is the meta-population of which Scandinavia is a part, that should be the unit of assessment for FRP status, and refers to the conventional goal of Ne = 500 (from the 50/500 rule, Franklin 1980) as a minimum for the meta-population. In that sense, the appropriate level for Scandinavia would strongly depend on what fraction of the meta-population that the Scandinavian population represents and how large the total meta-population is.

Earlier suggestions of management goals or FRP values for the Scandinavian wolf population

During the last fifteen years there have been a number of suggestions for how large the Scandinavian or Swedish wolf population ought to be. This has caused a lot of confusion, especially in the broad public, and has been used as an argument to discredit any further suggestions. However, these different figures have all been suggested for different reasons, in different situations, and/or under different assumptions, and some have been temporary goals whereas other has been permanent long term goals. In an effort to increase the understanding and reduce confusion, we here give a brief review where we bring up most of the different suggestions for wolf population levels that have appeared in the wolf debate, and try to explain the context of each one of them. Note that several of these suggestions have not been made by scientists but politicians, with a political agenda.

1999 Large Carnivore State Inquiry (Rovdjursutredningen) SOU 1999:146
The expert group within this inquiry commission concluded that for short term demographic viability at least 500 wolves were needed (Andrén et al. 1999). For **long term** survival minimum **3000 – 5000** (Ne = 500) wolves were needed. With a large genetic connectivity to other populations, and under the condition that the total meta-population had at least this size, it would be enough if the Swedish part of the meta-population made up 30%. With very little, or no connection, 100% must occur in Sweden. A **short term** survival (10 – 50 years) would need **500** (Ne = 50) wolves. It is not said explicitly, but it is obvious that these two levels were based on the so called 50/500 rule (Franklin 1980), and a Ne/N ratio of 0.1. No specific viability analysis of the Scandinavia wolf population was made.

In spite of these high figures from his expert group, the commissioner of this inquiry in his final report suggested a minimum of **200** wolves. The reason given for this reduction was that a population of 500 wolves or more would not be accepted locally, and would cause large damages to life stock and domestic reindeer both in Sweden and in Norway.

2000 Swedish parliament decision
On basis of the suggestion from the 1999 inquiry, the Swedish parliament in 2000 decided a so called **stage goal** (Sw: Etappmål) for the wolf population of **20 reproductions in Sweden**, including border territories, corresponding to approximately 200 wolves. When this goal was achieved, a new evaluation should be made before a new stage goal, or definite goal should be decided.

2007 State Inquiry about the Large Carnivores (Utredningen om de stora rovdjuren) SOU 2007:89
In the directives for this mission, suggestions for new population goals were not included. This mission suggested that when the Swedish wolf population had reached the stage goal of **20 reproductions**, decided by the parliament in 2000, the population should be limited to this level for three years, to keep damages low, reduce the illegal hunting and increase local

acceptance by demonstrating that the authorities are able to control the population. Thereafter a new evaluation of population goal should be made.

2009 *Swedish parliament decision*

The **temporary goal of 20 annual reproductions** should be prolonged until the effects of this population size had been evaluated, and until its conservation status, including actions to improve its genetic status, has been evaluated. It was decided that maximum 20 new wolf individuals from other populations should be brought in and included in the breeding population in Scandinavia (i.e. being effective immigrants). During this period the population should be controlled through harvest, and **should not exceed 210 wolves**.

2011 The Large Carnivore State Inquiry (Rovdjursutredningen) SOU 2012:22

This was the third national inquiry about the large carnivore management and conservation in Sweden within 12 years. An international expert panel appointed by this Inquiry stressed that the most important concern regarding the wolf population was to reduce the inbreeding level, and that the only way of doing that was through connectivity between the Scandinavian wolf population and the larger meta-population in Finland/Russian Karelia and Kola. Again the experts referred to the 50/500 rule, and claimed that for long term survival the meta-population needed to have a minimum Ne of 500, meaning a true population of 3000 – 5000 wolves. They based their suggestion for an FRP for Sweden on the philosophy that all the countries sharing the meta-population should take responsibility for a part of the meta-population that was proportional to their respective proportion of the total habitat for the meta-population. Based on total land area, a fair share of this meta-population for Scandinavia (Sweden + Norway) would be approximately **700 wolves**, but a better analysis should be based on available suitable habitat.

In the final report by this inquiry, the commissioner suggested that the mean inbreeding coefficient should be reduced down to 0.1 within a 20 year period by 5-10 effective immigrants per wolf generation during this period. If this immigration did not happen naturally, it should be done through artificial introductions. The ambition for the Scandinavian wolf population should be 500 wolves. The justification for this figure was that it meant a doubling of the present wolf population at that time, and that this should secure also in the long term the reduction of the inbreeding level achieved through the suggested introduction of new wolves, even if the natural migration flow would cease in the future. Based on this Scandinavian ambition, a suggested provisional reference value for the Swedish wolf population should be **450 wolves.** It was recommended that this value should be re-evaluated before next FCS report to the European commission in 2019. This was the first suggestion of a FRP-value for Swedish wolves.

2012 Swedish Environment Protection Agency (SEPA)

Based on figure 3a (in this report reproduced as figure 21) in the the SKANDULV genetic complement to the 2012 demographic PVA (Liberg and Sand 2012), mentioned earlier in this report, SEPA suggested that a Scandinavia wolf population of 417 wolves would fulfil the requirements for FRP, provided that a migration flow to Scandinavia of 3.5 effective immigrants per generation could be achieved. The figure concerned illustrates the relation between population size, immigration rate, and retention of genetic variation after 100 years according to the so called “island model” in population genetics theory (Wright 1969, Sved and Latter 1977). With a Ne value for the wolf population of 100 and 3.5 migrants per generation, the 95% level of genetic variation will be reached. SEPA used a Ne/N ratio of 0.24 which transforms a Ne value of 100 to a total population of 417. Given that 30-40 wolves will be accepted in Norway, SEPA suggested on basis of these data a FRP for the Swedish wolf population of **380 wolves**.

2012 The Swedish minister for the environment

Based on the same figure 3a in the the SKANDULV genetic complement to the 2012 demographic PVA as was used in SEPA´s suggestion, the Swedish minister for the environment made a different suggestion, assuming a somewhat more optimistic scenario for future migration flow to Scandinavia. According to this figure, if the migration flow increased from 3.5 per generation to 4, the Ne value of the population could be reduced from 100 to 50 and still retain 95% variation in 100 years. With a Ne/N ratio of 0.25 (suggested by Liberg and Sand 2012) this means a true population of 200. The minister then presumed that Norway should take responsibility for 30 wolves, leaving **170 wolves** for Sweden, which the minister then suggested as a FRP value.

As previously underlined in this report, the authors of the concerned SKANDULV genetic complement (Liberg and Sand 2012), containing the graph that both SEPA and the minister based their suggestions on, have later recommended that this graph should not be used in this way. This is because the way the “island model” is used in the calculation of the graph does not apply to the retention of the present genetic variation in the Scandinavian wolf population.

2013 Laikre et al. (2013) in Conservation Biology

In this paper Laikre et al. (2013) suggested that a large wolf meta-population in the minimum range of *Ne* = 500-1000 should be re-established throughout Scandinavia, Finland, and the Russian Karelia-Kola region and that Sweden should take a leading role in the international efforts in this respect. To reach Favourable Conservation Status the Swedish wolf population should make up a substantial part of this meta-population with a gene flow so that the Swedish segment of the total meta-population is not isolated. The average inbreeding level should be <0.1, the population should maintains its own genetic variation, including measured in terms of founder alleles, and the Swedish wolves should also be able to contributes to the total population. At a minimum the Swedish part of the meta-population should be large enough to not be classified as threatened according to International Union for Conservation of Nature (IUCN) Red List criteria (IUCN 2003). According to Laikre et al. (2009) applying existing red-list criteria, such a goal translates into at least 1000 sexually mature individuals. Considering the age composition of the Scandinavian wolf population during the monitoring period in the winter (SKANDULV unpublished data) this would translate into a total population of minimum **1600 wolves.**

2013 Letter from 10 scientists to SEPA and the Ministry of Environment

Concerned about the increasing polarization in the Swedish society regarding its wolf management, and worried that this situation might be aggravated by an unrealistic suggestion for FRP-value for the wolf population in the imminent Article 17 report to EU, ten Scandinavian wildlife biologists and geneticists wrote a letter to SEPA, with copy to the Ministry of the Environment. In this letter they suggested a FRP for the Scandinavian wolf population of 300, with **270 wolves** in Sweden and 30 in Norway, provided that the population has a "satisfactory" connection with the eastern population. They based this suggestion on their interpretation of the Habitats and Species Directive of the European Union. Specifically they discussed the eight operational points in the *Guidelines for Population Level Management Plans for Large Carnivores*, 2008, prepared by the Large Carnivore Initiative for Europe (Linnell et al. 2008), and found that the Scandinavian wolf population at that time satisfied all these points.

2013 Swedish parliament decision

In autumn 2013 the Swedish Parliament accepted a Government proposition that the FRP value for the Swedish wolf population should be within the interval **170 – 270 wolves**. In this decision it was also stated that SEPA should find the final value for FRP within this interval in its reporting of the Conservation Status for the Swedish wolf population to EU according to the Article 17 in the Habitat Directive. In its motivation for this level of FRP for wolf, the government referred to the formulation in the Habitat Directive and its Guidelines that the FRP value should be at least as high and preferably higher than the MVP value. For MVP value in this case, the government selected the SKANDULV demographic PVA from 2012, which concluded that a demographic (but not genetic) MVP for wolf in Scandinavia, including a reasonable risk for rare catastrophes, was 100.

2013 SEPA's Article-17 report of Dec. 2013

In *SEPA's Article-17 report of Dec. 2013* to the European commission it was suggested that the FRP value for the Swedish wolf population should be **270**, the highest value within the interval of 170-270, given by the parliament decision in 2013.

Interpretation of the criteria for Favourable Reference Population in the Habitat and Species Directive of the European Union regarding the Scandinavian and Swedish wolf population.

This section written by OL, CW, ØF, PW and HS

In this analysis of criteria for Favourable Reference Population we will primarily search for guidance in three documents:

1. "COUNCIL DIRECTIVE 92/43/EEC of the European Union on the conservation of natural habitats and of wild fauna and flora", hereafter called "the Habitats Directive"
2. "Assessment and reporting under Article 17 of the Habitats Directive. Explanatory Notes & Guidelines for the period 2007-2012 (Evans and Arvela 2011)", hereafter called "Article 17 Guidelines"
3. "Guidelines for Population Level Management Plans for Large Carnivores. Contract nr. 070501/2005/424162/MAR/B2", prepared by Large Carnivore Initiative for Europe (Linnell et al. 2008) and hereafter called "the LCIE Guidelines"

Sentences and paragraphs that we have found especially relevant for this report are highlighted with italicized text. Other documents that will be referred to in this analysis will be presented as they occur.

The wolf is listed in Annex II and IV of the Habitats Directive. Achievement of a "Favourable Conservation Status" (FCS) for species and habitats listed in these annexes is the primary goal for the conservation work of the Union. FCS is defined in article 1(i) of the Habitats Directive as follows:

"*Conservation status of a species means the sum of the influences acting on the species concerned that may affect the long term distribution and abundance of its populations within the territory referred to in article 2. The conservation status will be taken as "favourable" when:*

- population dynamics data on the species concerned indicate that it is maintaining itself on a long term basis as a viable component of its natural habitat, and

- the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and

- there is, and will probably continue to be, a sufficiently large habitat to maintain its population on a long-term basis."

In the Article 17 Guidelines the concept of "*Reference Values*" (RV) is introduced. For judging the conservation status of species, two types of Reference Values are relevant: *Favourable Reference Range* (FRR) and *Favourable Reference Population* (FRP). Both have to be achieved to declare a species to have a Favourable Conservation Status. These two concepts are explained as follows:

Favourable Reference Range = The "*range within which all significant ecological variations of the habitat / species are included for a given biogeographical region and which is sufficiently large to allow the long term survival of the species; favourable reference values must be at least the range when the Directive came into force, if the range was insufficient to support favourable status the reference for favourable range should take into account of that and should be larger (in such a case information on historic distribution may be found useful when defining the favourable reference range); best expert judgement may be used to define it in the absence of other data*"

and

Favourable Reference Population = The "*population in a given biogeographical 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*"

As our assignment for this report only concerns criteria for Favourable Reference Population, we will in the following disregard the concept Favourable Reference Range except when we judge that range and habitat requirements are important for determining appropriate criteria for Favourable Reference Population.

As can be seen, the definitions for FCS and FRP in the Habitats Directive are not very specific. Terms like "long term basis"," viable component of its natural habitat" or "foreseeable future", are not defined, nor is an exact percentage probability associated with "probably continue" given. As pointed out in the LCIE Guidelines this is hardly surprising as the Directive text, like any legal text, is not based on scientific definitions, but is meant to refer to a statement of general principle – in this case that the EU intends to conserve its species and habitats for the future. Furthermore, it would have been problematic to be too specific in a statement common for all the species of plants and animals occupying the European continent, from bryophytes to large mammals. This on the other hand opens for a certain degree of flexibility in the single case which may have been intentional when the text was written.

The Article 17 Guidelines elaborate a little more on the requirements for FCS and FRP. They state that "*Favourable Reference Populations should be based on the ecology and genetics of the species..*" and that the "*..population should be sufficiently large to accommodate natural fluctuations and allow a healthy population structure* ". Later in the document the difference between fluctuations and trends are discussed: "*Trends are decisive for the assessment of conservations status since usually only stable or increasing trends can result in a favourable* *conservation status. Trend is a directed change of a parameter over time. Fluctuation (or oscillation) is not a directed change of a parameter, and therefore fluctuation is not a trend*."

The most informative statements in Article 17 Guidelines regarding definition of FRP are the statement of the potential connection between the formal concept of a minimum viable population (MVP) and Favourable Reference Population. It is suggested that when "*..viability assessments are available they can be used to help set a FRP". After that comes the most specific criterion of FRP in this document: "*The estimates of Minimum Viable Population (MPV) will, by definition, be lower than FRP*". In the 2006 version of Article 17 Guidelines, this statement was a little more developed: "*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 favourable conservation status*." The LCIE Guidelines comment this: "*In other words, this means that 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 Habitats Directive to maintain populations at levels significantly larger than those needed to prevent extinction*."

Another very specific criterion for both FRP and FRR in Article 17 Guidelines is that "*...favourable reference value must be at least the size of the population when the Habitat Directive came into force*". For Sweden that is 1995, when Sweden had approximately 50 wolves. This requirement however only gives a bottom-line for FRP and FRR.

Not much is written on genetic requirements for FRP in the Article 17 Guidelines. Apart from the general statement that FRP should be based on the ecology and genetics of the species, it is simply stated that "*..it may be relevant to consider the genetic structure of a species*", and after that just a reference to Laikre et al. (2009): "*The importance of genetics in the evaluation of conservation status is discussed in more detail in Laikre et al. (2009)*". The operational genetic recommendation in Laikre et al. (2009) is that a minimum for attaining FRP is that Ne > 500. It is however also recognized that "*for some species in some countries, it is hardly conceivable that the country could host an effective population size of 500 of the species. Population genetics theory can provide guidance for such. The population within a member state can maintain its genetic variation, and hence its long-term viability, if it is a part of a larger population or system of populations that in total has a large enough effective size. There is also a well-founded quantitative guideline for how much exchange of individuals is required in such cases: each subpopulation should receive at least one genetically effective migrant per generation to prevent eroding the genetic variance within subpopulations. This general guideline may be modified in cases where there is detailed genetic information motivating such a change (cf. Mills & Allendorf 1996; Wang 2004), but in the absence of such information the rule of thumb of one migrant per generation is a useful guideline*".

It can therefore be interpreted that Article 17 Guidelines through their reference to Laikre et al. (2009) give a recommendation for a quantitative criteria of FRP: either a population with Ne > 500, or connection with such a population by minimum one migrant per generation.

There is no recommendation for a minimum size of the single sub-populations once they are connected to the meta-population, but it is obvious that Laikre et al. (2009) wanted to see a flow of migrants in both directions, i.e. each sub-population should both receive and produce migrants.

The LCIE Guidelines point out two factors that make large carnivore conservation and management different from most other organisms. First, due to their placement on top of the food chain combined with large body size, they demand large home ranges and occur in low densities, which means that viable populations of large carnivores demand enormous areas, often measured in tens or even hundreds of thousands of square kilometers (the average size of a wolf territory in Scandinavia is approximately 1000 km^2 (Mattisson et al. 2013). In the densely human populated Europe, there are few, if any, wilderness areas of this size, which in reality forces large carnivores to share habitat with humans. And this leads us to the second factor special for large carnivore conservation, potential conflicts with humans. The LCIE Guidelines puts it this way: "*Conservation of large carnivore requires their integration with human activities in human-dominated landscapes*. This means coexistence between large carnivores and humans, which is not always easy to achieve. It almost always requires active management (such as reintroduction, translocation, hunting, lethal control) of large carnivore populations and coordinated planning with conflicting land- uses and activities (farming, hunting….etc.). The LCIE Guidelines thus considered that this "*..requires that a very pragmatic approach be taken to large carnivore management*" and continues by interpreting that *"..it is possible to make certain compromises concerning the measures adopted to achieve conservation of large carnivores in order to take human interests into accounts, although the main goal of the Habitats Directive is clearly to conserve biodiversity*".

The LCIE Guidelines list eight operational criteria for large carnivore populations to attain Favourable Conservation Status FCS. Five of them (1, 4, 5, 7 and 8) concern Favourable Reference Population FRP. The explaining or interpreting text in normal font, following the introductory statement in italic font, is the text of LCIE, not of the authors of this report.

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

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

(3) "*There is, and will probably continue to be, a sufficiently large habitat to maintain its*

population on a long-term basis" (Article 1 (i)). We (LICE) interpret this to imply that the quality and continuity of habitat should be sufficient, and have a stable or increasing trend. And,

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

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

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

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

(8) *"Member States shall undertake surveillance of the conservation status of the natural habitats and species referred to in Article 2 with particular regard to priority natural habitat types and priority species"* (Article 11) and "*Member States shall establish a system to monitor the incidental capture and killing of the animal species listed in Annex IV (a)"* (Article 12.4). These statements combine to indicate that the population should be subject to a robust monitoring program.

Proposed criteria for FRP for Scandinavian/Swedish wolves

Section written by OL, CW, ØF, PW and HS

Discussion on principles

When we have interpreted the Habitat Directive and associated documents in our efforts to suggest criteria for FRP for the Swedish wolf populations, we have felt forced to compromise between two principles, the precaution principle that calls for large safety margins, and the principle to integrate wolf conservation with human interests, as expressed and exemplified by the LCIE guidelines (see above). The latter implies an effort to minimize conflicts and maximize acceptance, for the wolf in the local areas where it is intended to live, and for the official wolf policy of the country.

We are aware that suggesting a high FRP for the Scandinavian wolf population, referring to the precaution principle, probably would be applauded by most of the conservation community. However, we are not convinced that it would serve the conservation of the wolf in Sweden and Scandinavia well. In fact, we see some serious problems with choosing a high FRP-value. The most acute threat to the Scandinavian wolf population presently is not genetic impoverishment or demographic stochasticity, but poaching (Liberg et al. 2012b). It is possible that suggesting a high level for the wolf population would trigger an increase in poaching, and in the worst case lead to a situation where the authorities would lose control over the wolf management, and that criminality rather than legal policy would set the limit for the population. It is not known whether this is what has happened in Finland, but the decline of the Finnish wolf population with more than 50 % in just two years, most likely caused by poaching (Kojola et al 2014), is an illustration of how rapid population status may change.

Conflict

The increase in populations of large carnivores and their co-occurrence with humans may often result in controversies and promote conflicts (Skogen and Krange 2003), Treves and Karanth 2003, Bisi et al. 2010). Across Europe, people's attitudes toward wolves became less favorable the longer people coexisted with them (Dressel et al. 2015). An analysis of Swedish survey results from 2004 and 2009 showed that while bear and wolf populations are still growing, positive attitudes toward their presence are decreasing as people gain direct personal experience with these predators (Eriksson et al. 2015). These results imply that attitudes towards wolves are likely to become more negative as populations continue to grow. At the individual level, negative attitudes toward carnivores may result in illegal killings, which already threaten some of the European wolf and bear populations (Kaczensky et al. 2011, Liberg et al. 2012, Gangås et al. 2013). Recent research has emphasized the need for sustainable carnivore management programs that integrate social, cultural, political, ecological, and biological components (Treves and Karanth 2003, Bruskotter and Shelby 2010, Decker et al. 2012). This view is also stressed in the text of both the LCIE guideline document and in the Habitat directive Article 2, point 3: "*Measures taken pursuant to this Directive shall take account of economic, social and cultural requirements and regional and local characteristics*". Indeed, the viability of large carnivore populations is affected both by a favorable ecological and genetic status as well as local acceptance. Acceptance is considered to be key to achieving sustainable long-term conservation of large carnivores (LCIE).

The LCIE guidelines also acknowledge the uncertainty of the future and the need for flexibility through the use of the adaptive management process: "*Another reason to not place too much security in minimum numbers lies in the difficulty of accounting for, in all PVAs, the direction and rate of changes of environmental conditions and demographic parameters throughout the entire period for which predictions are made (Soulé 2002)……It is therefore crucial to monitor several parameters that reflect population size and population status to permit the adjustment of goals through an adaptive management approach."*

An adaptive management approach has recently become increasingly important in conservation and management of wildlife populations (Shea et al. 2002, Rout et al. 2009) and has been recognized as an important tool which should be used not only to manage a system, but also to learn about the system (Holling 1978, Walters 1986). Because adaptive management is based on a learning process, it improves long-run management and conservation outcomes. The challenge in using the adaptive management approach lies in finding the correct balance between gaining knowledge to improve management in the future and achieving the best short-term outcome based on current knowledge (Allan and Stankey 2009).

We recommend such an approach for the future management of the Swedish wolf population. A rigorous and extensive monitoring system and regular and systematic collection of important and relevant data on both demography and genetics for the Scandinavian wolf population, is and has been the norm for many years. With this annually updated information both demographic and genetic problems can be detected well before their effects have been realized into decreasing growth rates or reduced population size.

Suggestion of FRP-values

Concerning long-tern viability, there seems to be a rather broad consensus in the general conservation literature (see e.g. Jamieson and Allendorf 2012, Laikre et al. 2009) and the reports specifically dealing with the Scandinavian wolf population (e.g. SOU 2012, Bruford 2015*)* that to be viable in the long term, a population either has to be large enough to prevent inbreeding and loss of genetic variation or to be connected to a large population in a meta-population system. Considering the large space requirements of large carnivores, the LCIE Guidelines even put a larger emphasis on connectivity among populations than on the size of each single population. "*Given the enormous space requirements and low densities of large carnivores the most important practical consideration in maintaining genetic viability is to ensure as much connectivity as possible between populations (Liberg et al. 2006; Miller and Waits 2003)".*

There is some disagreement of how large the meta-population has to be, but an absolute minimum seems to be Ne 500 (Jamieson and Allendorf 2012, Laikre et al. 2009), to which we will adhere, although we are aware that there are suggestions of minimum Ne 1000, or even more (Franklin and Frankham 1998, Lynch and Lande 1998). Based on this we have found three factors to be of importance when setting a FRP-value for the Scandinavian wolf population. 1) The size of the meta-population to which the Scandinavian is or is supposed to be connected to, 2) the migration frequency between Scandinavia and the larger meta-population (i.e. the magnitude of the connection), and 3) the size of the Scandinavian wolf population itself.

1) *Size of the meta-population*

Both in the 2011 Large Carnivore State Inquiry and in the Bruford report, it is assumed that the meta-population to which the Scandinavian could belong covers Finland and Russian oblasts of Karelia and Murmansk (including the Kola Peninsula). Based on the study by Aspi et al. (2009) it was assumed that this population is semi-isolated from the large wolf population further east and south-east. It is currently not known how large this Finnish-Karelian-Murmansk population is, but with approximately 200 wolves in Finland (I. Kojola pers. com.) and 300 in Karelia (Danilov and Tirronen 2014), it is not likely to be more than 1000, resulting in an approximate Ne value of 300. Together with the Scandinavian Ne value of 100 (Bruford 2015) this results in a meta-population value of 400 which is lower than the minimum 500 required. However, it can be questioned that this population is isolated. In Aspi et al. (2009) the connection between Karelia and Archangelsk further east was found to be 4.7 migrants per generation. Even if not all assumptions of these calculations were satisfied, these figures still indicate some exchange of individuals between these populations. That the Finnish wolf population has more exchange with wolf populations further east is also supported by the results in a study by Stronen et al. (2013). They analyzed variability in 67,000 SNP´s from 177 samples and found no differentiation within a large panmictic wolf population in northeastern Europe, including samples from Finland, the Leningrad oblast immediately south of Karelia and the Baltic countries (Figure 25). It included no samples from Karelia and Archangelsk, but in a study by Pilot et al. (2006) it was shown that Archangelsk samples did not indicate a separation from Baltic or Leningrad wolf populations (Figure 25).

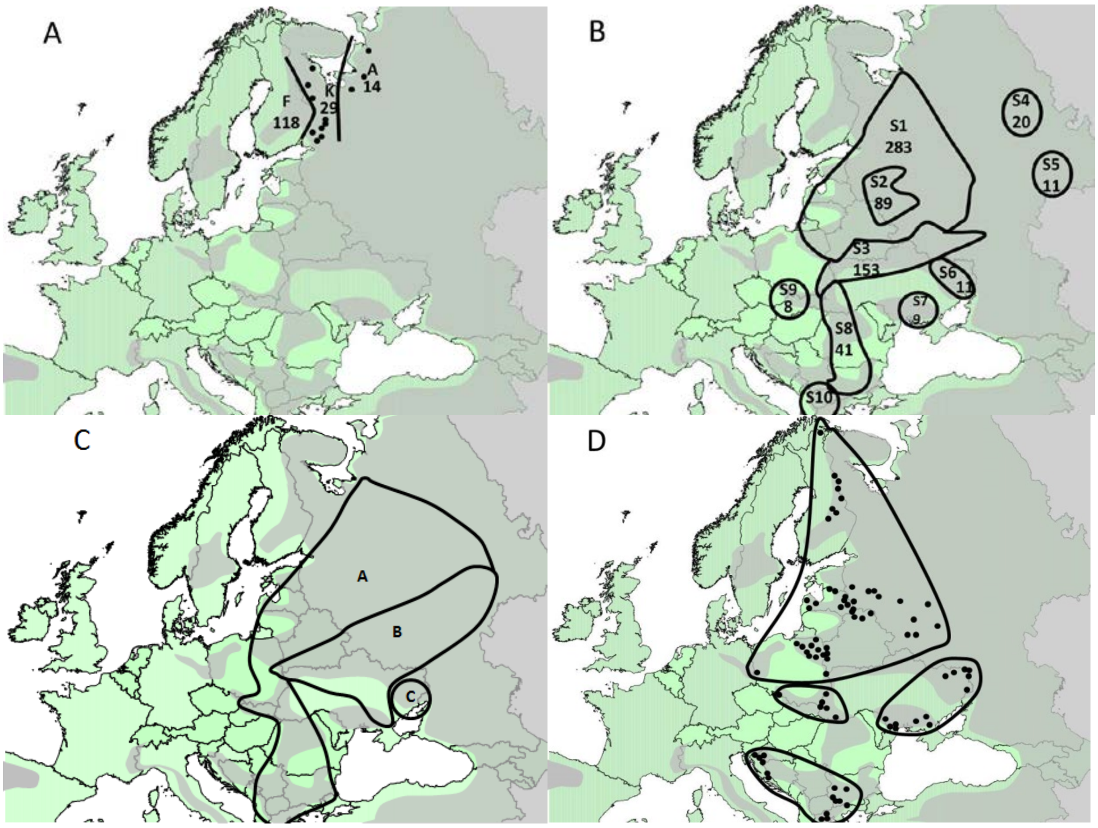


Figure 25. Results from four different analyses of genetic structure of the wolf population in north-eastern, eastern and central Europe using various genetic techniques. Wolf occurrence is denoted by light gray shading. A: Aspi et al. (2009) found limited genetic exchange between the wolves in Finland (F), Russian Karelia (K) and Russian Archangelsk (A), based on analysis of 14 microsatellite loci in 161 samples. Number of samples from each of the three sub-populations and the approximate sampling sites in Karelia and Archangelsk are shown. B: Pilot et al. (2006) identified 10 different subpopulations (S1 – S10) based on percentage frequencies of 21 mtDNA haplotypes in 643 samples. The number of samples from each sub-population is shown. C: Pilot et al (2006) identified three subpopulations based on frequencies of 14 microsatellites in 643 samples (same as in B). D: Stronen et al. (2013) identified four subpopulations based on analysis of 67.000 SNP´s from 177 samples. The approximate sampling sites are shown. From Stronen et al. (2013).

The results in both Stronen et al. (2013) and Pilot et al. (2006) were based on the effects of genetic drift. Genetic drift works quite slowly in medium to large-sized populations, which means that the connection demonstrated by these analyses does not necessarily show the present but rather the historic situation. Recent changes towards a more structured population would not turn up until after rather long time. However, as there are no physical barriers and there is no reason to assume recently created large gaps in the distribution of wolves over this vast area, the most likely state is that the population still is panmictic. This assumption is supported by the description of this region in the LCIE Guidelines: "*In cases where a very large area of distribution contains areas where the species is exposed to very different management or ecological conditions we have chosen to split it into two or more populations in an effort to identify units which have relatively homogenous demography. This was* *especially necessary when it came to eastern countries bordering onto Russia. For Eurasian lynx, bears and wolves Russia represents a massive population, stretching from the Baltic Sea to the Pacific Ocean. In order to limit our scope we have only considered the provinces (“oblasts”) from Moscow (35 degrees east) and westwards. In addition to this east-west truncation we have made a north-south truncation, grouping the oblasts of Murmansk and Karelia with Finland and Norway into a population and separating these from the oblasts bordering the Baltic States, Belarus and Ukraine into another. Although there is a set of natural geographic features marking this border (Lakes Onega and Ladoga and the White Sea) the carnivore populations extend continuously across the region, and our separation is intended to be pragmatic rather than biological.”*

We therefore conclude, given that connectivity exists, that Scandinavia is part of a much larger meta-population than just Finland and Karelia, with a Ne value far exceeding 500.

Can wolf populations in non-EU countries be considered?
Another importance question is whether the Habitats Directive allows that populations outside the territory of the European Union can be considered when FRP is defined for a Member State. We cannot find anything with bearing on this aspect in the main document of the Directive, but in the Article 17 Guidelines the question of transboundary populations is briefly treated: “*There may also be cases where it is biologically relevant to consider populations in a neighboring non-EU country. This should be clearly described under field 2.8.3 Transboundary assessment*”. The LCIE Guidelines also treat the question of connection to wolf populations outside of EU in chapter 7 (Developing population level management plans), page 32:*“Most of the main large carnivore populations in Europe contain countries that are not EU members. These countries need to be involved in the process through novel diplomatic approaches as their cooperation can only be requested rather than required. For countries that are signatories to the Bern Convention it should be possible to encourage participation if this convention could also adopt these guidelines. Recommendation No.115 (2005) on the conservation and management of transboundary populations of large carnivores from the Bern Convention secretariat already goes a long way towards encouraging this process. For key countries that are not signatories of the Bern Convention it may be necessary to find other incentives to encourage their voluntary participation. The Bonn Convention may be one suitable platform to exploit, as is the Convention on Biological Diversity.*

We interpret this to mean that non-EU populations can be considered as long as this is clearly stated in the Article 17 report.

2) *Migration frequency or how much exchange is needed?*

According to population genetics theory (Wright 1931), and also pointed out e.g. in the Färna meeting (Liberg 2006), and demonstrated by the simulations in the Bruford (2015) report, the key issue for retention of genetic variation and stabilizing inbreeding is the immigration frequency (the unit for measuring migration in population genetics is effective migrants per generation, Me), not population size. Emerging from this fact was the so called one migrant per generation (OMG) rule (Mills and Allendorf 1996, Wang 2004), which states that in an infinitely large meta-population, a flow of one effective (i.e. reproducing) migrant per generation (Me 1) between subpopulations will retain 80% of the total genetic variation in each sub-population, and the rest is maintained among the sub-populations, and inbreeding levels will stabilize at 0.2. These levels are no magic thresholds, but just gradual values on a continuous scale. But remarkably, the effect of drift on the frequency of single alleles changes abruptly just below this value (Wang 2004). At Me < 0.5 the probability for single alleles to become fixed or lost from the population through drift increases dramatically, while at Me > 0.5 the allele frequency tends to approach that of the population mean (Figure 26). One migrant per generation is the minimum frequency of migration proposed by the LCIE guidelines for attaining FCS, and is also the minimum recommended in Laikre et al. (2009) as well as in many other reports and publications, e.g. the Färna meeting (Liberg 2006). Bruford (2015) simulations demonstrated that >95 % of heterozygosity would be retained after 100 years, provided one effective immigrant per generation, regardless of population size above 300 (Table 5 and 6).

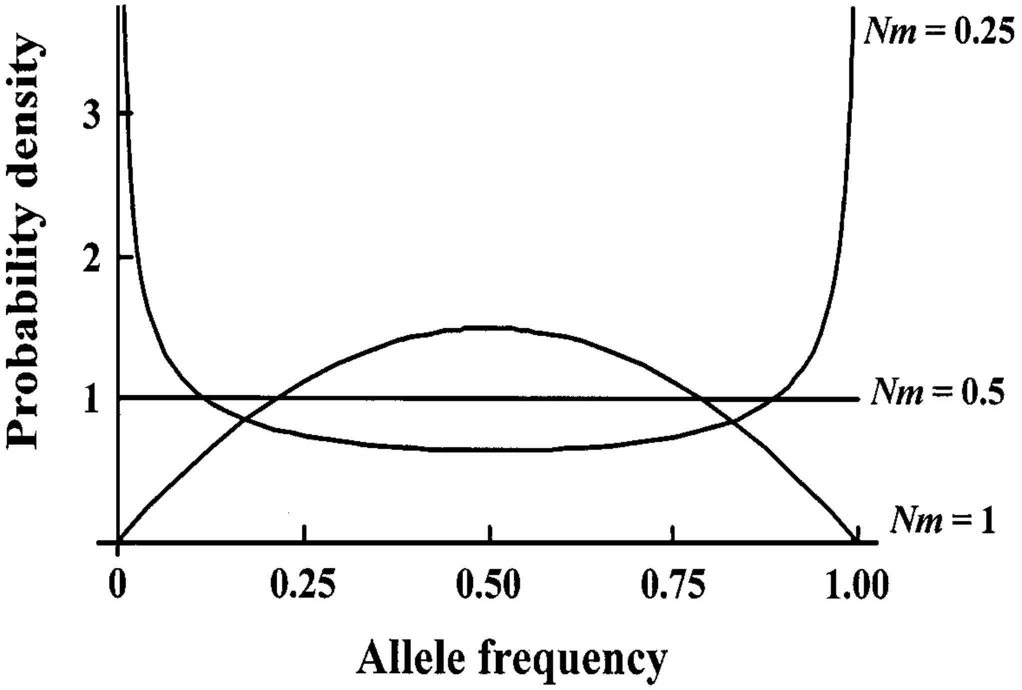


Figure 26. Distribution of gene frequencies among subpopulations in the island model for various values of Me = Nm, assuming an average gene frequency across subpopulations of 0.5. The figure is taken from Wang 2004, but is drawn based on Eq. 9.2.5 in Crow and Kimura (1970).

Table 5. Key model outcomes (pedigree + supplementation model) for the Scandinavian wolf population after 50 years with different carrying capacity and effective immigration scenarios (from Bruford 2015). The mean starting value for inbreeding coefficient was 0.267 and for gene diversity (MLH) it was 0.725.

Scenario	Stochastic r (growth rate)	SD (r)	Mean Population size	SD Population size	Gene diversity	SD (GD)	Percentage of initial Gene Diversity retained	Inbreeding coefficient
One female/ 3 years k200	0.139	0.23	192.86	23.14	0.769	0.04	106.2	0.223
One female/ 3 years k450	0.141	0.232	435.94	51.66	0.78	0.038	107.7	0.22
One female/ 3 years k700	0.142	0.23	679.06	85.92	0.782	0.037	108.0	0.221
One pair/ 3 years k200	0.171	0.241	196.01	19.31	0.818	0.032	112.9	0.184
One pair/ 3 years k450	0.176	0.235	438.02	49.65	0.823	0.031	113.7	0.186
One pair/ 3 years k700	0.175	0.233	684.94	71.11	0.823	0.033	113.7	0.186
Two females and two males/ 3 years k200	0.214	0.245	195.63	20.54	0.863	0.023	119.2	0.143
Two females and two males/ 3 years k450	0.215	0.238	491.36	46.32	0.867	0.023	119.8	0.145
Two females and two males/ 3 years k700	0.216	0.236	689.84	55.48	0.865	0.024	119.5	0.147

Table 6. Key model outcomes after 50 years using the allele frequencies + dispersal model years with different carrying capacity and effective immigration scenarios (from Bruford 2015). The mean starting value for inbreeding coefficient was 0.267 and for gene diversity (MLH) it was 0.725.

Scenario	Stochastic growth rate r	SD (r)	Mean final Population size	SD Population size	Gene diversity	SD (GD)	Percent GD retained from starting value	Inbreeding coefficient
Six immigrants/ 3 years k700	0.367	0.23	691.4	53.51	0.728	0.016	101.0	0.271
Three immigrants/ 3 years k700	0.363	0.245	683.7	73.92	0.718	0.014	99.4	0.280
Six immigrants/ 3 years k500	0.363	0.239	496.7	19.76	0.729	0.016	101.0	0.267
Three immigrants/ 3 years k500	0.363	0.235	496.8	33.13	0.716	0.015	99.1	0.280
Six immigrants/ 3 years k300	0.360	0.222	299.6	13.04	0.728	0.015	101.0	0.268
Three immigrants/ 3 years k300	0.350	0.24	292.1	38.05	0.715	0.021	99.0	0.279

Importance of connectivity for inbreeding levels

Based on the above given information we suggest applying a minimum migration frequency of one effective migrant per generation for attaining FRP for the Scandinavian wolf population (Mills and Allendorf 1996, Wang 2004). This is also the migration frequency listed as point 7 in the criteria list for FCS of the LCIE guidelines. However, this suggested level of migration frequency is based on the assumption that the meta-population from which these migrants shall come has a Ne larger than 500. As this is not un-disputably determined, we suggest that two additional conditions to this criterion should be met. The FRP status is only valid as long as the mean inbreeding level F continues to decline until it is below 0.2, after which it should be kept below this level. The second condition is that multi-locus heterozygosity increases or stays stable. These two conditions are part of the adaptive management of the Scandinavian wolf population, and should be considered over each 6-year reporting period to the European Commission, as stated in Article 17 in the Habitats Directive. In addition, a close monitoring of the demography and of the genetic health of the population should be performed continually, including measuring of demographic parameters and frequencies of congenital malformations. At any sign of increasing inbreeding depression over a six-year period, the operational criteria for FRP should be reconsidered.

It seems that for most populations, a level of F below 0.2 should be acceptable ("*As a rough guide an inbreeding coefficient of 0.25 seems acceptable for many species…. To be conservative an inbreeding coefficient of 0.2 appears appropriate considering the random processes, such as inbreeding, drift and environmental stress, associated with inbreeding depression and extinction*"; Wang 2004). Another reason why the level for mean inbreeding can be set at 0.2 (other experts have suggested 0.1) is that there are now 32 years of experience and data from the inbred Scandinavian population, with 25 years above this level, without any strong effects on the population growth rate.

According to the Bruford's (2015) simulations, the average inbreeding level would stabilize at 0.22 with one immigrant per 3 years (1.6 per generation), regardless of population size. As acknowledged by the author, the simulations were based on neutral expectations with random mating within the population. However, a recent study has shown that immigrants are more successful breeders than are more inbred wolves (Åkesson et al. in review). In addition, a selective hunting regime, where immigrants and their offspring in most cases are not legally hunted, would provide an additional selective advantage for the immigrants and their offspring, further reducing the average inbreeding level. Also, the expected equilibrium level of inbreeding in the "island model" with one migrant per generation is 0.2. From this it seems likely that one effective immigrant per generation would be sufficient to stabilize inbreeding levels at an acceptable level of 0.2 or even below this level (Figure 24).

Direction of dispersal

There is nowhere in the Habitat Directive or associated documents stated that the migration flow has to be in both directions, i.e. that the Scandinavian population not only shall receive migrants, but also contribute to the meta-population with migrants in the opposite direction. However, we agree with Laikre et al. (2013) that this is desirable. Since 2005, when the population had reached approximately 150 wolves, we have recorded two cases of wolves born in Scandinavia that have migrated to Finland/Russia (Wabakken et al. 2007, SKANDULV unpubl.). As approximately 5 - 10% of the population is radio-collared annually, we can assume that the true number of migrants from Scandinavia to the eastern population has been much larger, possible as many as 30 during the last ten years. Although there is no information on how many effective migrants there has been, we know that the first of the two known migrants established in a pair in northern Finland before she was legally shot in a control operation. As far as known, the second recorded migrant is still alive in northern Karelia just inside the Russian border 225 km east of Uleåborg (Oulu).

3) *Minum level of the Scandinavian wolf population to be at FRP*

The only quantitative criterion given for FRP in the Habitats Directive, or associated documents, is that "*estimates of Minimum Viable Population (MPV) will, by definition, be lower than FRP*" as it is expressed in the Article 17 Guidelines. The LCIE guidelines are a little more specific: "*According to our proposal this (*the FRP value; our comment*) will be set at levels greater than those regarded as being viable using the IUCN red list criteria E or D*". According to criterion D a population is viable if it contains minimum 1000 mature individuals, and according to criterion E if a PVA shows that the probability of extinction is less than 10% in 100 years. Criterion E was applied in the demographic PVA produced by SKANDULV in 2012 (Chapron et al. 2012), which showed that the Scandinavian wolf population was demographically viable for 100 years if it was larger than 100 individuals. This analysis included a frequency of up to two catastrophes per 100 years with a mortality of 90%. It did not explicitly include genetic risks, but it was based on demographic data from the inbred Scandinavian population and thus can be regarded as having included a certain amount of genetic risk. In Bruford's PVA (2015) parameters on genetic variation and lethal equivalents were included. Bruford showed that a population size of 300 in Scandinavia would retain 95% of the gene diversity after 100 years provided an effective immigration rate of one reproducing migrant per generation. All simulations showed insignificant probabilities of extinction.

Suggestion of FRP

In this report we have repeatedly stressed that the key parameter for retention of genetic variation and limiting inbreeding is not population size, but effective migration. As we already have included meta-population size and connectivity in the criteria for FRP, it could be argued that the genetic aspect of FRP is satisfied, and a FRP clearly larger than the demographic MVP of 100 would be enough to satisfy the condition by the Article 17 Guidelines that FRP should be larger than MVP. However, already at the Färna meeting it was expressed that even with a satisfying connection to a larger population, the Scandinavian wolf population should have a minimum of Ne 50 (taken from the 50/500 rule; Franklin 1980). This was justified by a need to protect the population from short-term genetic problems, for example caused by a temporary break in the migration flow. More recent papers also argue that Ne=50 is an appropriate level for short-term genetic viability (Jameson & Allendorf 2012, Rosenfeld 2014).

Using the same Ne/N ratio of 0.3 as Chapron in this report, Ne 50 corresponds to a true population of approximately 170 individuals. We argue that a population which is double the size of MVP would satisfy the Article 17 Guidelines definition "*….estimates of Minimum Viable Population (MPV) will, by definition, be lower than FRP*". A doubling a MVP of 170 individuals will give a FRP of 340. Using 340 as FRP is also supported from Bruford (2015) simulations. With the pedigree + supplementation model he demonstrated that a population as low as 200 retained more than 106 % of its genetic diversity (GD) for 100 years, with an immigration rate of one wolf every third year. With his more conservative model (allelle frequency + dispersal) he showed that a population of 300 retained at least 96.5 % of its genetic diversity in 100 years. He did not simulate lower population sizes with this model, but the decrease in GD retention with a decrease of carrying capacity from 700 to 300 was negligible (from 97.1 to 96.5), indicating that even with a further decrease of the population to say 200, it would still have retained more than 95 % of its genetic diversity. Equally important, extinction probabilities in 100 years were insignificant in all simulation scenarios, regardless of population size. Accordingly, a FRP level of 340 should be well above the genetic viability level presented by Bruford (2015), provided an effective migration rate of one wolf per generation.

We argue that this figure should apply to the Scandinavian population. Norwegian official policy is to allow 3 reproductions of wolves completely inside Norway, corresponding to approximately 30 wolf individuals, and there is an agreement between Sweden and Norway to share border territories on an equal basis. It is therefore reasonable to assume that Norway will take the responsibility for having at least 40 wolves (3 family groups in Norway and half of the border territories), and is why we suggest a FRP for the Swedish wolf population to be 300. This number will include 50% of the wolves living on the border between Sweden/Norway and all wolves within Sweden. Although this figure to a certain extent may be regarded as an arbitrary choice, all levels between a scientifically defined MVP and the global Ne 500 (or possibly 1000) are arbitrary. Our expert judgement is that a population of 340 wolves, connected through a minimum of one migrant per generation, to a large meta-population with Ne > 500 will have long term viability according to the criteria in the Habitats Directive.

FRP and the operational criterial in LCIE guidelines
In conclusion, a FRP of 300 satisfies well all the five criteria from the LCIE guidelines that according to our judgement affect the assessment of the FRP level. We will comment on these in more detail below:

Point 1 contains an interesting passage*: "… maintaining itself on a long term basis as a viable component of its natural habitat"*. The LCIE guidelines have interpreted this to mean that the population shall also have an ecological role over large areas. For a large carnivore, this means that it should have an impact on its prey populations, interact with other carnivores in a natural way and have indirect effects typical for large carnivores, for example on scavengers. We argue that this criterion is satisfied for wolf in Scandinavia. Figure 10 show that even if the breeding range is limited to central Scandinavia, wolves appear regularly and in high frequency anywhere on the peninsula, including the reindeer husbandry area. They have impact on their prey populations, especially moose and roe deer (Sand et al 2005; 2008, 2012), over a large part of the peninsula, they interact with other large carnivores like lynx and brown bear (Ordiz et al. In press, Wikenros et al. 2011), and they affect the scavenger guild by altering the availability of carrion over the year (van Dijk et al. 2008, Wikenros et al. 2013).

However, there is a limit to how much of its natural role a large carnivore can play in human dominated landscapes today. In densely populated regions, like most of Europe today, human activities control densities of large mammal species through hunter harvest and habitat changes (forestry and agriculture etc.). This contrasts with large wilderness areas in historic time and the few large protected areas where humans still have little impact on the ecology. The wild top predators in Europe will rarely reach the level where they play an essential ecological role (Linnell et al. 2005). On the Scandinavian Peninsula, human density is lower than in most of Europe, but even here humans currently have the role of the ultimate apex predator affecting all three levels (wolves-moose-forest) through intensive managements. Human harvest has replaced wolf predation as one of the major mortality factors in the moose population and has likely resulted in a loss of anti-predator behaviour in moose as exemplified by high hunting success rates by re-colonizing wolves (Sand et al. 2006a, Wikenros et al. 2009, Gervasi et al. 2013) and the absence of a change in moose habitat use in relation to the risk of wolf predation (Nicholson et al. 2014).

Point 4 states that the population size and range are equal to or greater than when the Directive came into force. A FRP of 340 will with great margin satisfy this requirement. Sweden entered the Union in 1995, a time when the Swedish wolf population was less than 50 animals

Point 5, which contains the central criterion (larger than MVP) has been treated in detail above.

Point 7 (connection by at least one genetically effective migrant per generation) is also treated above.

Point 8 requires a robust monitoring system. We argue that the monitoring system for wolves in Scandinavia probably is one of the best in the world, with its combination of intensive snow tracking by a large group of specially trained trackers, DNA-analyses of several hundred samples annually, and radio telemetry.

The need for adaptive management

The adaptive management approach based on the type of data that can be collected continually, given enough resources, will result in a situation where management promptly can respond to any early sign that the development is not favorable, and act accordingly. Important parts of this adaptive management is continued annual high-qualitative monitoring of the population size, of its demography and health, of its genetic status (with help of continually updating the pedigree), of the flow of effective migrants, and of the status of the meta-population. It is especially important that the Swedish conservation authorities establish a close contact with their counter parts in Finland and Russia, and acquires tools to early detect any signs of a drop of wolf numbers in the meta-population.

Finally, we would like to stress the view proposed by a passage in the LCIE document that links modern conservation efforts to more traditional strategies "*If overall objectives and policy frames are set at a central European level, and population-specific management plans are developed, it should be possible to allow a great deal of flexibility at the level of the subpopulation or management unit to implement this in a manner compatible with local traditions, conditions, and conflicts. In other words, as long as the goals are decided on a large scale, there should be some flexibility to modify the means that are used at a more local scale.*"

Clarification of the concept of Favourable Conservation Status (FCS)

This section written by GC only

The following text is adapted from Epstein, López-Bao & Chapron. 2015. A legal-ecological understanding of Favourable Conservation Status for species in Europe. *Conservation Letters*. 10.1111/conl.12200 to which the reader is referred for a more substantial treatment of the concept of FCS.

The Habitats Directive seeks to achieve its biodiversity goals by requiring EU Member States to take measures to reach or maintain the favourable conservation status (FCS) of natural habitats and species. In Article 1(i) of the Directive, the conservation status of a species is defined as "*the sum of the influences acting on the species concerned that may affect the long term distribution and abundance of its populations within the Member States' European territory",* and further that *"conservation status will be taken as "favourable" when: population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats, and the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis*".
In this section, we clarify and interpret several aspects of FCS for species, which have not yet been conclusively settled by analyzing and weighting a variety of sources. The most relevant aspects of the Directive for the Swedish wolf cases are *1)* whether FCS should be measured at the species, population or national level, *2)* what it means for a species to be a "*viable component of its natural habitat*", *3)* how long is a "*long-term basis*", *4)* what it means for a species to "*maintain itself*" and *5)* whether FCS should be measured from extinction or carrying capacity. The methods of legal scholarship – followed in this section – are somewhat different from ecological research as the data examined here consists of various legal sources. Importantly, the Directive itself and the decisions of the European Court of Justice (ECJ) are the only legally binding sources, and where a decision of the ECJ seems to contradict the Directive, the ECJ's interpretation trumps.

At what level should FCS be measured?

Based on the text of Article 1(e) of the Directive, a population at FCS is required at least at the EU, rather than the global, level: "*conservation status of a species means the sum of the influences acting on the species . . . within . . . the European territory of the Member States to which the [EU] Treaty applies.*" Member States each have a responsibility to take measures to protect those species within their European territory The Commission requires reporting of a species conservation status for each biogeographical region within each Member State (Evans & Arvela 2011). The essential question of whether FCS should be achieved at the European, population, or Member State level has been analyzed by scholars both within the natural and legal sciences. Mehtäla & Vuorisalo (2007) propose viewing FCS as a hierarchical concept occurring at each of these levels. Guidance from the Commission has been inconsistent. As Trouwborst (2014) points out, the Commission has suggested that question of scale is species-dependent and may require population based analysis for some species, such as large carnivores (European Commission 2007), but has nevertheless focused only on national assessment in some situations such as the Finish wolf case. The Large Carnivore Initiative for Europe (LCIE) guidelines support the idea that when populations are transboundary, with FCS recommended to be achieved at the population level (Linnell *et al.* 2008). However, the jurisprudence of the European Court of Justice (ECJ) indicates that FCS may also be required to be achieved at the national level (Trouwborst 2014). In the 2007 Finnish wolf case (ECJ 2007), the ECJ considered only the wolves in Finland in stating that the population was not at FCS, and not those in neighboring Russia, Sweden, or Norway. Importantly, the 2009 hamster *(Cricetus cricetus)* case (ECJ 2011) indicates that the ECJ would favor a narrow interpretation of what constitutes a population: the court considered there were multiple populations of hamsters within Alsace (France), rather than treating the French hamsters as one small part of a very large population that extends till Hungary (Weinhold 2008). Similarly, while emphasizing a population approach, Trouwborst (2014) recommends that Member States thus pursue FCS at both the national and population level.

What does it mean for a species to be a "viable component of its natural habitat?"

A standard method for ecologists of assessing viability is to determine minimum viable population (MVP) (Thomas 1990; Boyce 1992; Traill *et al.* 2007; Frankham *et al.* 2014; Reed & Mccoy 2014). This is the approach recommended by guidelines produced by the LCIE (Linnell *et al.* 2008), which suggest that one of several factors for determining FCS could be a MVP based on the IUCN Red List criterion E, which defines a MVP as a population with less than 10% chance of extinction within 100 years estimated from a model that "makes full use of all relevant available data" (IUCN 2001). These guidelines also discuss that FCS may require greater numbers than MVP, although it is not clear where the threshold should be. The commission's own guidelines introduced the concept of Favourable Reference Population (FRP) to define the population size at which FCS is considered reached, but through a more qualitative approach by including the consideration of ecological data such as historic distribution and abundances, potential range, biogeographical and ecological conditions, gene flow or genetic variation and add that a population should be sufficiently large to accommodate natural fluctuations and allow a healthy population structure (Evans & Arvela 2011). The 2006 Article 17 Reporting Guidelines (European Commission 2006) were the first to suggest that MVP could be linked to FCS. However, they claimed only that MVP could be "*of use*" in determining FRP and "*by definition different*". The 2011 Article 17 Reporting Guidelines again indicated that MVP is one possible means for determining FRP, adding that MVP is necessarily lower than the number required for FCS (Evans & Arvela 2011). The 2011 guidelines cited favourably a scientific article that recommended MVP be used with a criteria of extinction risk <1% over 40 generations (Trail *et al.* 2010). It should also be noted than none of the Article 17 Reporting Guidelines mention IUCN criterion E, which tolerates a much higher extinction risk (1 out of 10 populations becoming extinct over 100 years). The LCIE guidelines' recommendation to use criterion E is wholly unjustified and should be rejected; there is no reason why IUCN's criterion E should be used in determining whether a species is a "*viable component of its natural habitat*". Indeed a textual analysis of the Habitats Directive indicates that MVP in general may not be sufficient to determine FCS. The relevant clause of the Directive does not emphasize that the species is just demographically viable as an isolated entity, but instead the role the species plays in the ecosystem of which it is a part, even though having a viable role naturally requires being first a viable entity. That a species must remain a "*component*" of its habitat implies ecological functionality in addition to demographic viability. The LCIE chose narrowly to focus on demographic viability. The language of the Directive indicates rather that ecological viability, which considers interactions among species and between a species and its habitat is the more appropriate interpretation for this particular clause.

What is a "long-term basis"?

The Habitats Directive primarily implements the Bern Convention, which in its preamble recognizes the need to preserve wild flora and fauna for future generations. But the stronger interpretive guidance stems from the preamble of the Convention on Biological Diversity (CBD), which specifically talks about the importance of biological diversity for evolution, and of preserving biological diversity for future generations. The importance of the CBD for the interpretation of the Habitats Directive is underscored by the EU biodiversity strategy to 2020, which implements the Strategic Plan for Biodiversity and Aichi Biodiversity Targets adopted under the CBD (European Parliament 2012). The EU biodiversity strategy to 2020 expresses a goal of improving the conservation status of all species and habitats through the improved implementation and enforcement of the Habitats Directive. It is not explicitly stated for how long a population must remain a viable component of its natural habitat, but in light of the goals stated in the preambles of the Habitats Directive, the Bern Convention, and the Convention on Biological Diversity, populations should remain viable indefinitely.

This implies that to be considered at FCS, a population must maintain evolutionary potential or genetic viability (Laikre *et al.* 2009). The need for genetic viability, in addition to ecological viability, seems to be implicitly supported by the 2011 Article 17 Guidelines, which recommend Traill *et al.* (2010) to those considering using a PVA for setting FCS. Traill *et al.* (2010) concluded that long-term survival (and continued ability to evolve) of a species must aim for a metapopulation of thousands of individuals. Laikre *et al.* (2009) also argue that the long-term viability of a population requires genetic viability, requiring in turn at least a genetically effective population size of Ne=500 individuals. An analysis of MVP modelled on this understanding of genetically viability was accepted by the Court of Justice in the hamster case (ECJ 2011). This case referred to an estimation of 1,500 hamsters over 600 ha as MVP, numbers derived from a study using this formulation (Kayser 2005). Recent research shows however that larger numbers may be necessary, as a recent exhaustive review of the role of genetic factors in population viability found that to avoid eroding evolutionary potential, Ne=1,000 would instead be warranted (Frankham *et al.* 2014). While each Member State must reach and maintain FCS, however, it may not be possible for each Member State to have over Ne=500 or 1,000 individuals of every listed species in the different Annexes of the Directive. Instead, Laikre *et al.* (2009) argue that species populations within states can maintain the necessary genetic variation to remain viable if they are part of a larger population or network of connected populations that has the requisite numbers and with connectivity between patches of at least 1 genetically effective immigrant each generation to maintain sufficient genetic diversity. These numbers of genetically effective immigrants necessary are likely to be higher if the concerned population already suffers from a restricted genetic diversity.

What does it mean for a species to "maintain itself"?

It is important to note that an equivalent of the word "*itself*" does not occur in the majority of the other official language versions of the Habitats Directive. All language versions of EU legislation are equally valid (ECJ 1998). The French version, for example, requires that the species "*continue et est susceptible de continuer…à constituer*", which more literally means that the species must "*continue and be likely to continue to constitute*". Where there are differences in the language versions of a law, the court must find a uniform interpretation by interpreting the contested passage "*by reference to the purpose and general scheme of the rules of which it forms a part*" (ECJ 1977). Further clarifications can therefore be provided by looking at what, if any, level of human management is deemed consistent with the purpose of the Habitats Directive. The Directive acknowledges that much of Europe's habitat cannot be truly said to be natural: the definition of natural habitat in Article 1(b) includes both the "*entirely natural*" and "*semi-natural*". In fact, human activity, such as certain agriculture or livestock practices, may be required to maintain habitats of community interest (Bignal & McCracken 2000; López-Bao *et al.* 2013) and necessary to reach FCS for certain species as the Directive's preamble states that maintaining biodiversity may "*in certain cases require the maintenance, or indeed the encouragement, of human activities*". For example, in the Alsace hamster case (ECJ 2011), hamster conservation status was unfavourable due in part to changing agricultural practices—hamsters require the cultivation of particular types of cereals and hay, but changes in the agricultural market had led to these crops being replaced. The ECJ ruled that it was necessary for the management plan for the hamster to include the cultivation of crops needed to support the continued existence and recovery of the hamster. The court considered that while the hamster is not at FCS, the attainment and maintenance of its FCS would necessarily require agricultural activity. It does not however logically follow that FCS of a species could be considered to be maintained if its continued existence was wholly dependent on human intervention as this is also not in line with the purpose of the text. For example, a metapopulation dependent on regular artificial translocations should not be considered to have reached FCS, as such dependence would likely not be consistent with the Directive's goal. While it is not literally required that a species maintain "*itself*", the fact that several language versions have expressed the clause in question using the reflective "*itself*" support the interpretation that the intention was that the amount of human assistance required should be limited.

Should FCS be measured from extinction or carrying capacity?

The commission guidance documents consistently emphasize that FCS must be assessed as "*distance from some favourable state*" rather than distance from extinction (Evans & Arvela 2011). Therefore, conceptually, measurement from carrying capacity appears to be a better fit. That is, if conservation status is evaluated based on the distance from favourability, but the FRP value is based on distance from extinction, the conservation status is indirectly being measured from extinction. It is more logically consistent to base the FCS from the most favourable state which is carrying capacity. The European Commission notes positively the use of carrying capacity to determine the FRP values and describes in detail how this has been done in Poland for wolves (Evans & Arvela 2011; based on the suitable habitat for the species, Jędrzejewski *et al.* 2008).

Operationalizing Favourable Conservation Status

This section written by GC only

The commission guidance makes it clear that political context should be given no role in setting what is FCS. Evans & Arvela (2011) explicitly write that "*Favourable Reference Values should be based purely on scientific grounds*". While biodiversity conservation is a political choice, this choice already lies in the Habitats Directive itself as well as the others international legislations (Bern Convention, Convention on Biological Diversity) that Swedish politicians have signed. These legislations translate a broad societal goal to restore and keep a flourishing biodiversity into legal instruments. Therefore I should restrict myself to providing the scientific and legal interpretation of legal instruments, unencumbered by any past statements quantifying FCS.

My approach is to interpret the Habitats Directive in line with the European Court of Justice (ECJ) numerous clarifications that the provisions of the Directive to contribute towards ensuring biodiversity through the conservation of natural habitats and of wild fauna and flora "*must be interpreted strictly*" (see e.g. C-6/04, Commission v. UK; C-342/05, Commission v. Finland). One could argue that such a strict interpretation would contravene Article 2(3) of the Directive, which states "*Measures taken pursuant to this Directive shall take account of economic, social and cultural requirements and regional and local characteristics*". However, Article 2(3) mentions only measures and not the goal of the Directive, and the ECJ has considered in Case C-371/98 that Article 2(3) was not a reason to derogate from the provision of Article 3(1) and its goal to reach FCS. The court suggested a rather limited scope of the provision, ruling that a member state "*cannot of its own accord, whether because of economic, social or cultural requirements or because of regional or local characteristics, delete sites which at national level have an ecological interest*". This interpretation is re-stated in the Guidance document on strict protection, which adds "*Since Article 2(3) requires the protection of natural habitats and species to be balanced agains one may ask if this provision comprises an independent derogati requirements of the Directive. For Directive 79/409/EEC* [the Birds Directive], *the Court has clearly confirmed that it does not. Mutatis mutandis, it follows that Article 2(3) of Directive 92/43/EEC does not provide an independent derogation from the obligations requirements of the Directive*"

In light of previous decisions by the ECJ, the Commission has also made clear that introducing flexibility in the Directive provisions for the Swedish wolf case was inappropriate in particular by stating that "*by allowing a licensed hunt in 2010, 2011, 2013, 2014 and 2015, Sweden has established a systemic practice which infringes the Habitats Directive* ".

Under the Habitats Directive, Member States have an individual obligation to promote FCS of those populations within or partially within their borders, as well as in each of their biogeographical regions, thus contributing to FCS of the species at the European level. The language of the Directive suggests demographic viability, evolutionary or genetic viability and ecological viability. It is important to understand that reaching FCS is different from facing a low risk of extinction that most conservation scientists are familiar with; and FCS instead indicates a recovered and abundant population. Below, I quantitatively interpret these obligations based on the best available science.

No risk of extinction

The language of the Directive suggests that populations within or partially within borders of Member States should have an infinitesimal extinction probability on the long-term. Most of the PVAs for Swedish wolves have examined extinction risk over short-term periods (e.g. 100 years in Chapron et al. 2012) and are therefore irrelevant to conclude on FCS values (see also Chapron 2014). Chapron et al. 2012 is not a PVA fulfilling the requirement of IUCN criteria E since it did not "*use all the relevant data*" and ignored genetic aspects. An additional condition for reaching an infinitesimal extinction risk is that the population should not be facing any major threat. This reasoning is also in line with Sweden's own suggested approach to the European Commission (see Figure 2 p. 21 in Evans & Arvela 2011) where the existence of threats is given a particular importance in setting reference values.

One threat that has been consistently pointed out by scientists, Swedish authorities and the European Commission is the high inbreeding level in the population and associated inbreeding depression. There is a substantial peer-reviewed scientific literature describing inbreeding as a major concern (Bensch et al. 2006, Liberg et al. 2005, Räikkönen et al. 2006, Räikkönen et al. 2013). In particular, Liberg et al. 2005 found that the number of surviving pups per litter during their first winter after birth was strongly and negatively correlated with the inbreeding coefficients of pups. In 2009, the Swedish parliament decided the wolf population's genetic status must be improved, primarily by making it easier for naturally migrating wolves to move from the reindeer husbandry area to the wolf population located in central Sweden. In 2011, the Swedish government announced that the wolf genetic status was to be strengthened through introduction of new wolves during the coming years. Urgently decreasing inbreeding was also the ground for the decision of the Swedish Environmental Protection Agency (NV-01007-13) to carry a selective wolf hunt. The European Commission wrote on multiple occasions that the genetic status of the Swedish wolf population was not satisfying and needed to be improved (e.g. letter from European Commissioner Potočnik to Minister of the Environment Carlgrén dated 7th Dec. 2010; Motivated Opinion dated 17th June 2011; letter from European Commissioner Potočnik to Minister of the Environment Ek dated 25th Jan. 2013; Additional Reasoned Opinion dated 19th June 2015) and an international scientific report for the European Commission stated that "*inbreeding depression and low genetic variability are important factors to consider in the conservation of the Scandinavian wolves*" (Kaczenski et al. 2013) with a consequent report identifying the genetic reinforcement of inbred populations as a most urgent action for large carnivores (Boitani et al. 2015). Prior suggestions made by other scientists (Jansson et al. 2015a, Laikre et al. 2013) and a previous independent investigation commissioned by the Swedish government (Liljelund, 2011), have recommended that inbreeding coefficient approaches 0.1 before the population can be considered at FCS. Based on the one effective migrant per generation rule, I recommend that inbreeding coefficient becomes less than 0.2.

An additional threat to the Swedish wolf population is poaching which a peer-reviewed scientific paper estimated to account for half the total mortality of wolves, with two thirds of poaching not being reported (Liberg et al. 2011). It has been suggested that poaching could be reduced by capping the population at lower size or allowing license hunting. This approach creates a wicked situation where reaching FCS is contingent on supposedly controlling a threat by reducing the population to a size not satisfying the criteria for FCS. In that regard, it is important to note that the European Commission has explicitly stated that "*social acceptance is not among the grounds specified in Article 16 of the Directive, to exempt from the strict protection of species listed in Annex IV*". In addition, whether capping population will reduce the threat of poaching appears speculative in light of an increasing body of evidence suggesting the opposite. A mailed questionnaire survey by the Montana Fish Wildlife and Parks (Lewis et al. 2012) only found that Montana's wolf-hunt improved perceptions of the administrative agency and its management actions, which is different than tolerance for wolves. Peer-reviewed scientific papers (Browne-Nuñez et al. 2015; Hogberg et al. 2015; Treves et al. 2013) reporting longitudinal studies in Wisconsin, USA 2001–2013, showed that acceptance for wolves decreased and inclination to poach increased after management was made more flexible and wolf-killing was liberalized (Treves et al. 2013). The least tolerant interest groups showed that once culling was liberalized, participants in focus groups said that was not enough and hunting was needed to reduce the wolf population (Browne-Nuñez et al. 2015). The latest study also in Wisconsin from 2009–2013 showed acceptance continued to decline after wolf-hunting was legalized, among males familiar with hunting who lived in wolf range (Hogberg et al. 2015). This seems to suggest that government action to allow killing of wolves sparks intolerance and further demands for killing more wolves not greater acceptance of the smaller wolf population. I therefore conclude that reducing population size to decrease poaching is incompatible with reaching FCS.

Evolutionary potential through *Ne*=500

The language of the Directive suggests it is also necessary that the species has evolutionary or genetic viability by reaching at least a genetically effective population of *Ne*=500. Several estimates of *Ne* for the Scandinavian wolf population have been provided using different methods. Estimating *Ne* is notoriously difficult: whether genetic samples are well representative of the population, which method or estimator is used, which time period is considered and what is the population dynamic during that time period are all important factors affecting *Ne* estimates or *Ne/N* ratio. For example, Jansson et al. 2012 estimated *Ne/N* for the Finnish population and found that it could vary from 0.16 to 1.47, according to the method used or the years considered within the time period 1995-2009. Cherry-picking particular estimates of *Ne/N* is not appropriate, especially considering the complexity added of meta-population level estimates. In that regard, *Ne/N* estimates derived from simulation models may be more relevant, especially when the models are designed for this purpose. In a report to the Swedish Environmental Protection Agency, Forslund (2008) developed a wolf-specific individual-based model and reported a ratio *Ne/N* = 0.24. Bruford (2015) reported higher values for *Ne/N* (0.53–0.86), however a substantial review of the report by geneticists (Jansson et al. 2015b) raised serious concerns about the method used where the *Ne* reflected rate of inbreeding of the metapopulation whereas the *N* reflected local census size. Importantly, when computed for isolated populations in this report, the ratio *Ne/ N* became lower (0.39 for *K* = 300 and 0.32 for K = 700, t = 50 years in both cases, *K* being population cap), in line with a previous report returning *Ne/ N* = 0.35 of Andrén (2005; Vortex simulations). In summary, based on today's state of knowledge, precautionary estimates of the *Ne/N* ratio would suggest a value close to 0.3 in the Scandinavian wolf population implying that *Ne* = 500 would be reached when the population size contains *N* = 1700 wolves. This population size is within the range of sizes for other wolf populations usually considered to be at FCS in Europe (i.e. Romania, Spain, see Chapron et al 2014). Preventing the ratio *Ne/N* from dropping to lower level may also be contingent on a lack of excessive hunting especially if breeding wolves are killed (Jansson et al. 2012, Jansson et al. 2015a).

Can Sweden include foreign wolves to reach FCS?

A major point of contention is whether Sweden can include animals outside the national Swedish or European Union territory when assessing whether Swedish wolves have FCS (Figure 27). The reasoning behind this possibility is that the population size implied by *Ne*=500 (1700 wolves) would be too large for Sweden, although no biological study supports this statement and Sweden actually hosts 2800 brown bears and 1000 lynx. In the French hamster case (Commission v France, Case C-383/09), the ECJ followed a very narrow definition of what a population is when it considered the long-term viability of individual populations in Alsace ("*there were no populations of the species in Alsace which reached its minimum viable population threshold, which is estimated at 1 500 individuals*") and not of the overall French population. Neither did the court take into consideration that French hamsters were the extreme Western patch of a much larger (meta)population ranging as far as Hungary where hamsters are abundant and in Annex V. In the case Finnish case (C-342/05), the government of Finland called attention to the pups born annually in the immediate vicinity of Finland on the Russian side of the border (Letter of observations from Finland to the European Commission dated 05th July 2001), however the ECJ did not keep that argument in its rulings. The ECJ appears to indicate that FCS must be reached at the national population level. The Article-17-guidelines (2011; p. 38) mention cases where "*species may have a population which is shared between two or more Member States*" and the LCIE guidelines clearly focus on population-level management of large carnivores (Linnell et al. 2008). Nevertheless, there is no biological basis to assume there is a functioning Fennoscandian wolf population, as no wolf pack has a territory overlapping Sweden and Finland (contrary to Pyrenean brown bears which the Article-17-guidelines cite as an illustrative example) and breeding Swedish and Finnish wolf packs are distant by roughly at least 1000 km. The Article-17-guidelines further "*encourage Member States to undertake a common assessment and to agree on data and assessments, but each Member State would report the results*". However, it is important to note that this encouragement to standardize monitoring and share data does not suggest that each Member State would face weaker obligations for the conservation status of a population under the Directive as soon as it is shared with other countries. The Article-17-guidelines add that "*joint assessments between two or more Member States should be done primarily in cases where there is a certain level of cooperation and common understanding of the management needs and approaches for that species*". There is no joint management approach of wolves between Sweden and Finland and the countries have not succeeded in improving connectivity between their respective populations. The same conclusion can also be made regarding Russian and Member States of the European Union. The Finnish wolf management plan actually indicates that the Russian-Karelian wolf population has been halved during the past decades to 300-350 wolves, and wolf numbers South of the Gulf of Finland have fallen even more rapidly in recent years. In addition, the Federation of Russia is not bound to the Habitats Directive, has not signed the Bern Convention and does not have a wolf management plan indicating population targets as well as harvest levels. While there is some connectivity across the Finnish-Russian border fence, the actual international context with Russia growing hostility towards Finland precludes from relying on the assumption that the border fence will not be sealed in the near future. A strict interpretation of both rulings by the ECJ and guidelines by the Commission would suggest 1700 wolves are required for the species to have FCS in Sweden. If this number would be larger than the species carrying capacity of the wolf in its natural habitats, then FCS would be reached at carrying capacity (~1200 wolves as a preliminary estimate, see below), while the appropriate level of immigration to reach *Ne*=500 would still need to be secured. Under this reasoning, Sweden would first need to do all what it can in to improve the conservation status of the wolf on its national territory, before relying on wolves outside its national territory.

Following the explicit request of the Swedish EPA during the reporting meeting on August 24th 2015, I also discuss the case where the ECJ would consider that FCS is defined at a meta-population level. Importantly, the connectivity between Sweden and Finland has so far remained exceptionally low with only 3 wolves effectively and naturally immigrating into the Swedish population after it established, which amounts to less than 1 effective and natural migrant every 10 years. If connectivity had been at the required level of 1 effective migrant per generation (5 years), twice as many immigrants would have bred in the Swedish population. Assuming Swedish wolves would be allowed to regularly roam through Northern Sweden as to form a functioning meta-population with Finnish wolves with 1 effective migrant per generation, the approach promoted by the LCIE may apply. What still remains unclear is how Sweden and Finland would decide on the allocation of these 1700 wolves. The wolf in northern Finland is in Annex V of the Habitats Directive and the Finnish population remains relatively small (220-245 wolves in January 2015). Different approaches are possible, e.g. allocating an equal amount of wolves (850) between the two countries, allocating wolves according to the proportion of suitable habitat in the two respective countries, or according to a political agreement. In any case, wolves would still need to reach a population size deemed compatible with the fulfillment of their ecological role (see next).

Ecological viability across Sweden

The language of the Directive suggests ecological viability in addition to demographic viability for species through its wording "*a viable component of its natural habitats*". This wording is not exclusive to English and is also found in e.g. the Swedish version of the Directive "*en livskraftig del av sin livsmiljö*". The stronger interpretive guidance stems from Article 2 of the Convention on Biological Diversity which states that " *"Biological diversity" means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems."* The LCIE guidelines (Linnell 2008) also acknowledged that ecological viability is implied in the intentions of the Habitats Directive. The science of ecological viability remains however limited (Chesson & Kuang 2008) and in theory, a single wolf could be considered as being ecologically functioning as it would still kill prey. However, with the language of the Directive signaling that FCS is better measured from an optimal state such as carrying capacity than from extinction, ecological viability can be formalized as the species occupying a majority (>50%) of its natural habitats at an abundance of half its carrying capacity in its habitats. This approach is consistent (albeit less ambitious) with Poland's approach to estimate FCS for wolves by using a habitat suitability model and calculating the potential number of wolves at carrying capacity (Evans & Arvela 2011). One proposed estimate of the carrying capacity for wolves in Sweden is 1200 animals or 200 territories (Sand et al. 2014), which would suggest FCS is reached with 600 animals or 100 territories. However, this estimate excludes the reindeer herding area and should be considered as preliminary before more accurate estimates are proposed. It is nevertheless clear that wolves are not ecologically viable in their natural habitats in Sweden as they are de facto not allowed to settle or breed in the Northern part of the country, as illustrated by the so-called 'Junsele female' case and the fact that an offspring of the immigrant so-called 'Tiveden pair' was shot in the reindeer herding area.

Practical recommendations

In light of the analysis above, I conclude that the Swedish wolf population does not have FCS. The inbreeding coefficient remains too high, the population remains too small and the connectivity in Northern Sweden with neighboring Finland is typically broken by human threats (there is no operational plan on how to naturally reach a minimum of 1 migrant / generation). In order to reach FCS, two important points require a particular attention. The first one is to allow wolves (especially immigrants) to roam and establish in Northern Sweden so that inbreeding coefficient drops below 0.2 and natural connectivity reaches at least 1 migrant / generation. It is important to make the difference between a trend and a result: the fact that inbreeding coefficient may be declining (a trend) does not equal this coefficient passing below 0.2 (a result). Therefore, wolves in Sweden can never be said to have achieved FCS as long as their inbreeding coefficient remain > 0.2 and substantial number of immigrant wolves is required to reduce the inbreeding coefficient. This implies that even if a connectivity of 1 migrant / generation would be achieved today, the wolf population would still not qualify for FCS. This connectivity should also be achieved naturally and without artificial translocations. The Directive defines FCS when the population "*is maintaining itself*", and the hamster case (Commission v France, Case C-383/09) only suggests that depending on already existing human actions (such as farming) may be compatible with FCS and does not suggest human actions that would normally not occur such as translocations. Decreasing inbreeding by hunting the most inbred wolves is also a very risky strategy (Chapron et al. 2013) and against the precautionary principle written in EU law. Swedish courts have actually ruled that the 2013 genetically selective hunt was not in line with the Habitats Directive. Similarly, it is unclear how a related idea to 'thin' the Swedish wolf population (under the assumption that local density is now too high for immigrants and their offspring to settle) would decrease inbreeding and not violate the Directive. The practice to de facto avoid wolves settling in Northern Sweden appears to be infringing the Directive on multiple grounds. First, it precludes the population from reaching FCS, second it amounts in reality to a transfer of wolves in Northern Sweden from Annex IV to Annex V (note: wolves in Northern Finland are in Annex V but Sweden does not have this derogation or a mandate to move wolves between annexes) and finally, because protective hunts make use of helicopters, they violate Article 15(b) which prohibits the killing from the modes of transport referred to in Annex VI (aircraft and moving motor vehicles). The second point is to let the population grow to half its carrying capacity (~600 wolves as a preliminary estimate) or, if connectivity is not improved, to its carrying capacity or 1700 wolves (whichever is the smallest). It is in any case critical to allow wolves in Northern Sweden by letting pairs settle and by designating areas of special interest (as mandated in Article 3(1) of the Directive for species in Annex II) where the species can breed.

Synthetic approach to establish FCS for wolves in Sweden

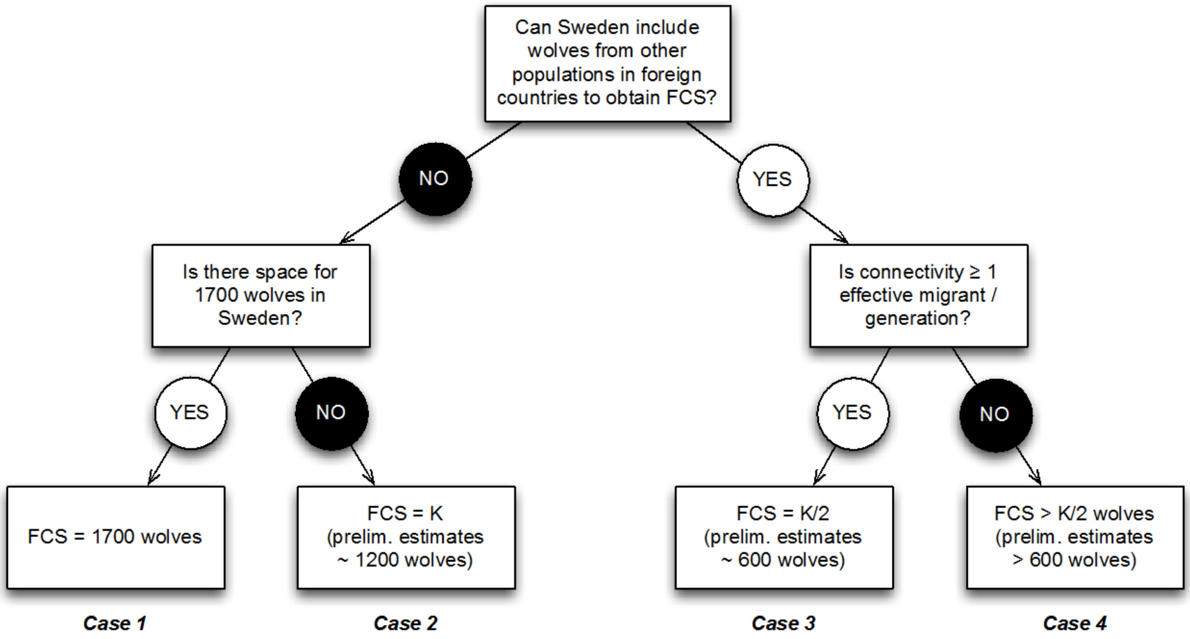


Figure 27: Rules to establish FCS values for wolves in Sweden according to interpretation of the Habitats Directive and ecological parameters. In all cases inbreeding coefficient must pass below 0.2.

1. Sweden cannot include wolves from outside its national territory to reach FCS and there is space for more than 1700 wolves in Sweden: FCS is achieved at 1700 wolves and the country reaches *Ne*=500 by itself.
2. Sweden cannot include wolves from outside its national territory to reach FCS and there is no possibility to have 1700 wolves in Sweden (required for *Ne*=500): FCS is achieved at carrying capacity *K* (preliminarily estimated at 1200 wolves) and the appropriate level of immigration to reach *Ne*=500 should be secured.
3. Sweden can include wolves from outside its territory to reach FCS and the connectivity is more than 1 effective migrant per generation: FCS is achieved at half carrying capacity *K*/2 (preliminarily estimated at 600 wolves) to ensure the species ecological role.
4. Sweden can include wolves from outside its territory to reach FCS but the connectivity is less than 1 effective migrant generation: FCS is achieved at a value larger than half carrying capacity *K*/2 (preliminarily estimated at 600 wolves) and large enough to have *Ne*=500 given the realized connectivity.

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Appendix 1. Monitoring of wolves in Scandinavia.

The County Administrative Boards in Sweden are responsible for performing annual monitoring of wolves. In each county a varying number (5-15) of field workers are employed, on full or part time, to perform the field work (Liberg et al 2012). In Norway, Hedmark University College has the responsibility for monitoring stationary wolves whereas vagrant wolves are monitored by the Norwegian Nature Inspectorate (SNO). The Wildlife Damage Centre (Swedish University of Agricultural Sciences) and Rovdata (Norwegian institute for nature research) are responsible of evaluating monitoring results and make a joint annual report.

The monitoring of wolves in Scandinavia is based through snow-tracking and DNA-analyses of scats and urine. Information from GPS-collars, other research data and dead wolves are used when available. The main method is tracking of wolves on snow (Wabakken et al. 2001). The field workers are actively searching for tracks all through the winter, but are also getting information about fresh tracks from the public. Tracks found, especially groups consisting of two or more wolves, are followed, usually backwards, to avoid disturbance of the animals, for as long distances as possible, depending on time available and competition with other work tasks, but at minimum 3 km. During tracking, number of animals in the group tracked is determined, territorial scent markings and oestrus bleedings are recorded, and found scats/urine are retrieved for DNA-analysis. The second method is DNA-analysis. DNA is extracted from blood or other tissue from live wolves during capture and from retrieved dead wolves, but the majority of DNA-samples are sampled from feces found during tracking (Liberg et al 2005). The DNA-analyses are valuable for verifying reproductions, for identifying newly established pairs, for differentiating between neighboring territories and for identify new immigrants from the Finnish/Russian population. Tracking effort and number of DNA-samples analyzed per year varies. For example, during the winter 2013/2014 a minimum of 2083 km of wolf tracks was followed and 498 DNA-samples were analyzed (Svensson et al. 2014).

For the winters of 1998/1999 through 2013/2014 Scandinavian wolves have been classified as: family groups, territorial pairs, other stationary wolves, or vagrants (Wabakken et al. 1999, 2014, Liberg et al. 2012), during the period October 1 to February 28. Family groups are defined as a minimum of three wolves, of which at least one should be territorial by scent marking, travelling together and sharing a territory. Territorial pairs should include two wolves with different sex where both are territorial by scent marking and share a territory. Other stationary wolves usually include single wolves that have recently settled, or remnants of split family groups. In Norway, also vagrant wolves (not stationary) were recorded, whereas this segment of the population in Sweden was calculated according to an assumed proportion of the population. Also the number of reproductions has been estimated each year during the period May 1 to February 28 based on visual or vocal observations, scats from pups, rendezvous sites during late summer/early autumn, or confirmed using DNA of pups.

The Swedish Environmental Protection Agency and the Norwegian Environment Agency decided in 2012 that monitoring of wolves (and other large carnivores) should be better coordinated and conducted using the same type of methods in both countries exclusively. This resulted in new criteria (Naturvårdsverket and Rovdata 2014) of wolf monitoring in Sweden and Norway. Starting from the winter of 2014/2015, the primary units of the annual population monitoring in Sweden are family groups and territorial pairs during the period October 1 to March 31. Within the Swedish reindeer husbandry area all individual wolves should be registered per Sami village. In Norway, monitoring of all wolves in the field should be continued (the Norwegian Environment Agency, personal communication). As a consequence, determination of the number of territories with pups of the year (monitored since 1978, Wabakken et al. 2001a) is no longer a target neither for the Swedish monitoring nor for the total Scandinavian monitoring, but will be recorded when the criteria for reproduction are fulfilled without any extra effort for the field personnel. The number of reproductions will instead be estimated from the observed number of family groups during the winter monitoring period. The routines for monitoring wolves are regulated by official instructions issued by the responsible central authorities, (Rovdata in Norway and the Swedish Environment Protection Agency).

From every winter since 1998, joint Swedish-Norwegian annual reports have presented the status of the wolf population. Also data from the wolf monitoring in Finland has been included with the exception of the monitoring report including the winter of 2014/2015 (Anon 2015).