# Effects of migration and selective harvest for the genetic status of the Scandinavian wolf population.

A report to the Swedish Environment Protection Agency SEPA (Naturvårdsverket)

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## THE MISSION

The original mission in Swedish (an English summary is given at the end of this section).

Naturvårdsverket uppdrar till Sveriges Lantbruksuniversitet (SLU), Grimsö Forskningsstation att utreda de biologiska förutsättningarna för att rikta licensjakt efter varg mot revir med särskilt låg genetiskt status samt att undersöka effekterna på populationens inavelsnivå av en sådan jakt. Utredningen ska också inkludera en analys av huruvida licensjakten kan utformas så att den genetiska förstärkningen av vargstammen kan påskyndas och ytterligare förstärkas genom att populationen hålls på en lägre nivå under tiden för de inledande åtgärderna för genetisk förstärkning. Om detta anses möjligt ska uppdragsredovisningen innehålla konkreta förslag på hur en populationsreglerande jakt ska utformas för att uppnå sådana effekter, inklusive kriterier för hur mest lämpliga vargrevir för en selektiv jakt ska identifieras. Analysen ska utgå från senaste säsongens inventeringsdata (2011/2012).
Uppdraget ska genomföras efter samråd med andra relevanta forskningsmiljöer. I uppdragsredovisningen ska det på en övergripande nivå framgå om det i delaktiga forskningsmiljöer finns skilda uppfattningar om delar av eller hela redovisningen, och vari dessa i så fall består. Bästa dokumenterade vetenskapliga kunskap ska användas vid analyser och förslag.
Fakturering kan ske från och med att Naturvårdsverket erhållit slutrapporten, faktura ska vara Naturvårdsverket tillhanda senast den 15 december 2012.

### Bakgrund

Det främsta hindret för att den svenska vargstammen ska nå en gynnsam bevarandestatus och att dess långsiktiga förekomst i landet ska säkras är att stammen är isolerad och starkt inavlad. Det krävs därför både kort- och långsiktiga åtgärder som innebär att nya obesläktade vargar introduceras i stammen och reproducerar sig.

Naturvårdsverket fastställde i maj 2012 en nationell förvaltningsplan för varg. I planen beskrivs i kapitlet genetisk förstärkning ett antal åtgärder för att förbättra den svenska vargstammens genetiska status. Dessutom anges följande i kapitlet Populationsreglerande jakt - licensjakt:

"Naturvårdsverket avser att 2012 inleda arbetet med att utveckla former för en mer selektiv licensjakt…. Bland annat kommer möjligheten att rikta jakten mot revir med särskilt låg genetiskt status och effekterna av en sådan jakt att undersökas."

Den senaste rovdjursutredningen gör i delbetänkandet Rovdjurens bevarandestatus bedömningen att den primära bevarandeåtgärden för vargen måste vara att minska inavelsgraden genom invandring, utplantering eller på annat sätt. Vidare anger utredningen att den skandinaviska vargpopulationen i ett andra steg, när inavelsgraden sänkts, bör öka i storlek.

## English summary of the mission

The Swedish Environment Protection Agency commissions to the Swedish University of Agricultural Sciences, through concerned experts at the Grimsö Wildlife Research Station to investigate the possibilities to direct a selective harvest in the Swedish wolf population towards packs with the lowest genetic value for the population, and to calculate the effects on the average inbreeding level in the population by such a selective harvest. The commission also includes an analysis of the possibilities to speed up this improvement of the inbreeding situation, including whether this can be achieved by initially keeping the population at a lower level, while other action are performed to assist this process (i.e. active translocation of unrelated wolves to the population). The mission shall be performed after consultations with other relevant research institutes.

## THE SCOPE OF THE REPORT

In accordance with our comprehension of the mission, we have in this report estimated the changes in genetic status (inbreeding coefficient and/or relatedness coefficient) of the Scandinavian wolf population under different harvest strategies (random harvest vs. selective harvest directed towards wolf packs/pairs with low genetics status) under different immigration rates and at different population sizes. After an additional request from SEPA we have divided the work in two parts, short term effects after the first two years of a selective harvest, and long term effects where we used a time horizon of 100 and 300 years respectively

## METHODS

### Some terminology

This report is about possible positive effects on the genetic situation that can be achieved through selective harvest, directed at territorial wolf packs or pairs with low genetic status. For the effects of the harvest, it does not matter much whether the targeted pairs have bred or not, or whether they will breed following spring. Therefore we will not in this report separate between wolf pairs that have not yet bred, and those that have and live in a pack. For simplicity we therefore also will use the term "pack" both for pairs without pups and pairs that have pups and live in packs. This is also in accordance with North American terminology, where all groups of two or more wolves are called packs.

### Criteria for selecting target animals in selective harves

When selecting animals for breeding in breeding programs, for example in zoo populations (Mats Amundin pers. com.) aimed at improving the genetic status of the stock, or at least not losing more genetic quality than necessary, using some measurement of relatedness is a more powerful tool, than using inbreeding coefficients ((Fred Allendorf pers. comm). The reason is that relatedness predicts inbreeding levels in next generation

For analyzing long term effects of migration and selective harvest, we have used an already constructed population model that we have used before (Forslund 2011). This model is very appropriate for the present task, as it is specifically designed for the Scandinavian wolf population (see below). It however has the disadvantage that it presently lacks the capacity to calculate relatedness or kinship coefficients. As there was no time to develop the model further, the selective harvest simulated with this model was restricted to differentiate between migrants and their offspring versus the rest of the population not related to new migrants (the inbred part of the population).

However, the analysis of short term effects opened a possibility to base the selection of targeted packs for harvest on relatedness. As the analyses only included two consecutive harvests, they could be done manually, which also made it possible to base the simulated harvests on average relatedness, calculated for each pack. The disadvantage was that simulations could be iterated only a limited number of times, as the process was very time consuming.

## Short term genetic effects by selective harvest:

The calculations were performed in Excel, based on demographic and pedigree data from SKANDULV. Inbreeding coefficients (F), and so called "numerator relationship" (R) have been calculated with the program CFC 1.0 (Co-ancestry, inbreeding F, Contribution). The numerator relationship gives a value for kinship or co-ancestry between individuals. It can vary between 0 and 2, and to make it more comparable to inbreeding coefficient F, we divided it by 2 (R/2), which we here will call "relatedness". The relatedness between two individuals measured with R/2 will be identical with the inbreeding coefficient of the offspring from these two individuals if they breed together. Established wolf packs, presumed active in autumn 2012 according to the latest monitoring report (Wabakken et al 2012) and unpublished data, were ranked according to the average relatedness of their offspring (R/2), not only to offspring of the other presently active packs, but also to offspring to all families that had bred at least once in 2008 or later. Effects of selective harvest were measured for two different levels of harvests, taking out the five and ten packs with the highest average relatedness (R/2).

For measuring effects of a harvest in the coming winter 2012/13 we just ranked all active packs according to their average relatedness, and removed the packs (5 or 10) with the highest relatedness coefficient. The average relatedness and inbreeding coefficients with (before harvest) and without (after harvest) these 5 or 10 packs were then estimated. We were also asked also to measure the effects after two harvests. This was done through a manual simulation process. The central part of this process was to "create" new packs that would replace those that had been taken out in harvest 1, and also replace packs that were lost for other reasons. We used SKANDULV data on annual turnover of packs (both breeding and non-breeding) to calculate how many packs we could expect to be lost till next year, and used a random procedure to pick those out among existing packs. Then all lost packs were replaced by new packs that we simulated by a random selection among a "candidate pool". The candidate pool consisted of all pups born between 2008 and 2011 according to the monitoring reports, but where all pups known to already be in a pack or having died were removed. Also new partners to simulated wolves that had lost their partners were selected in this way. In this simulated population for winter 2013/14, we then again ranked the packs according to their relatedness and removed the packs (5 or 10) with the highest relatedness coefficient. As this was a rather time consuming procedure, only five simulations were run. We then again harvested the five and ten packs with the highest scores for relatedness in this simulated population, and recorded the resulting average coefficients for relatedness and inbreeding. We also present the range of results from the five simulations.

Packs with territories entirely within Norway were not considered possible to harvest even if they ranked high on the relatedness list. Excluded from the ranking list were a few territories where we lack complete information about their relatedness.

## Long term genetic effects by selective harvest

The long term effects of selective harvest have been analyzed by Pär Forslund with an individual based population model constructed in Matlab by Forslund in cooperation with other SKANDULV-researches, and described in earlier reports ((Naturvårdsverket rapport [Dnr 429-8585-08 Nv]; Liberg et al. 2009, Naturvårdsverket rapport Dnr 235-3697-10, Forslund 2011). The model is specifically designed for the Scandinavian wolf population. It integrates demography and genetics by simulating kinship between individuals. Input data are empirical data from the SKANDULV-project, i.e. recorded probabilities for changes between life history stages (e.g. from pup to dispersal stage and further to territory establishment, and eventually to reproductive stage etc.) including data on reproduction and stage specific survival (Sand et al 2010, Liberg et al 2012). Genetic data includes those effects of inbreeding on litter size that have been recorded in the present wolf population (Liberg et al. 2005).. Migration from other populations can be included, as well as various management actions, like different types of harvest. Migrants are regarded as effective , i.e. they have the same probability to survive and breed as native animals. The model simulates population growth with demographic stochasticity and development of the inbreeding level. Also migration rates were given with stochastic variation. Even though much of the "genetic improvement" in fact might be arranged by setting out pups to wild dens for adoption, in the simulations we have treated migrants as adult wolves, coming in to the population with the same probability to survive and breed as adult native wolves. This is because there is great uncertainty about the success of the adoption process. Relatedness coefficients are presently not calculated in the model. Genetically selective harvest therefore was simulated by excluding migrants and their offspring (F1´s) from the harvest. Apart from immigrants and F1's the harvest was random. Scenarios have been simulated for 100 and 300 years respectively, and each simulation has been iterated 500 times. The start population for all simulations was 300 animals. In those scenarios with a lower population ceiling, the population was harvested down to this level already the first year. When the targeted population level was higher than the start population, there was no harvest until the population reached the target level.

## RESULTS

### Short term effects

Here we present results from a selective harvest directed at the wolf packs with the highest relatedness coefficients. The effects concern only two years ahead from present time. No new immigration to the population during these two years is included in the analysis. We also briefly present a calculation of maximum number of packs that can be harvested the present winter to have at least the same number of packs next winter.

### Short term effects of selective harvest on the wolf packs with the highest relatedness coefficients

Two years of selective harvest, where in each harvest bout ten packs with the highest relatedness are taken out, will reduce the average inbreeding coefficient among potential offspring to active packs from 0.260 (autumn 2012) to 0.229 immediately after the second harvest in winter 2014 (Table 1). This corresponds to a 12 % reduction of the inbreeding level. Approximately 55 % of this effect comes from the protection of migrants and their first generation offspring (F1´s), and 45 % from the selection of the most inbred packs among the rest of the population. Lower total harvests will result in correspondingly less reduction of inbreeding levels, while the effect with a higher harvest presumably will be higher.

### Possible harvest of packs

Presently Sweden includes packs that hold territories on the border between Sweden and Norway in its national wolf count. In the wolf monitoring report from 2011/2012 there were 55 packs recorded in Sweden including border territories. The average annual rate of increase (lambda) for number of packs for the last ten years has been 0.15. With this increase rate, the expected number of packs the present winter 2012/13 is 63. With the same increase rate, a maximum of 9 packs could be taken out without reducing number of packs for the winter 2013/14.

*Table 1. Short term effects of selective harvest on the territories with the highest relatedness (R/2). Population means are given for relatedness R/2 and inbreeding coefficients F for offspring to wolf packs active in autumn 2012 (start), to remaining packs directly after a harvest 1 in winter 2013, and to remaining packs after a simulated harvest 2 the winter 2014. The means are not weighted for different number of offspring in the different families.*

| | **5 packs harvested** | | | **10 packs harvested** | |
|---|---|---|---|---|---|
| | **R/2** | **F** | | **R/2** | **F** |
| **Start 2012** | **0,254** | **0,260** | | **0,254** | **0,260** |
| **After harvest year 1** | **0,251** | **0,255** | | **0,246** | **0,248** |
| **After harvest year 2** | **0,247** | **0,246** | | **0,237** | **0,229** |
| Range after harvest 2 | 0,245-0,250 | 0,240-249 | | 0,230-0,241 | 0,224-0,235 |

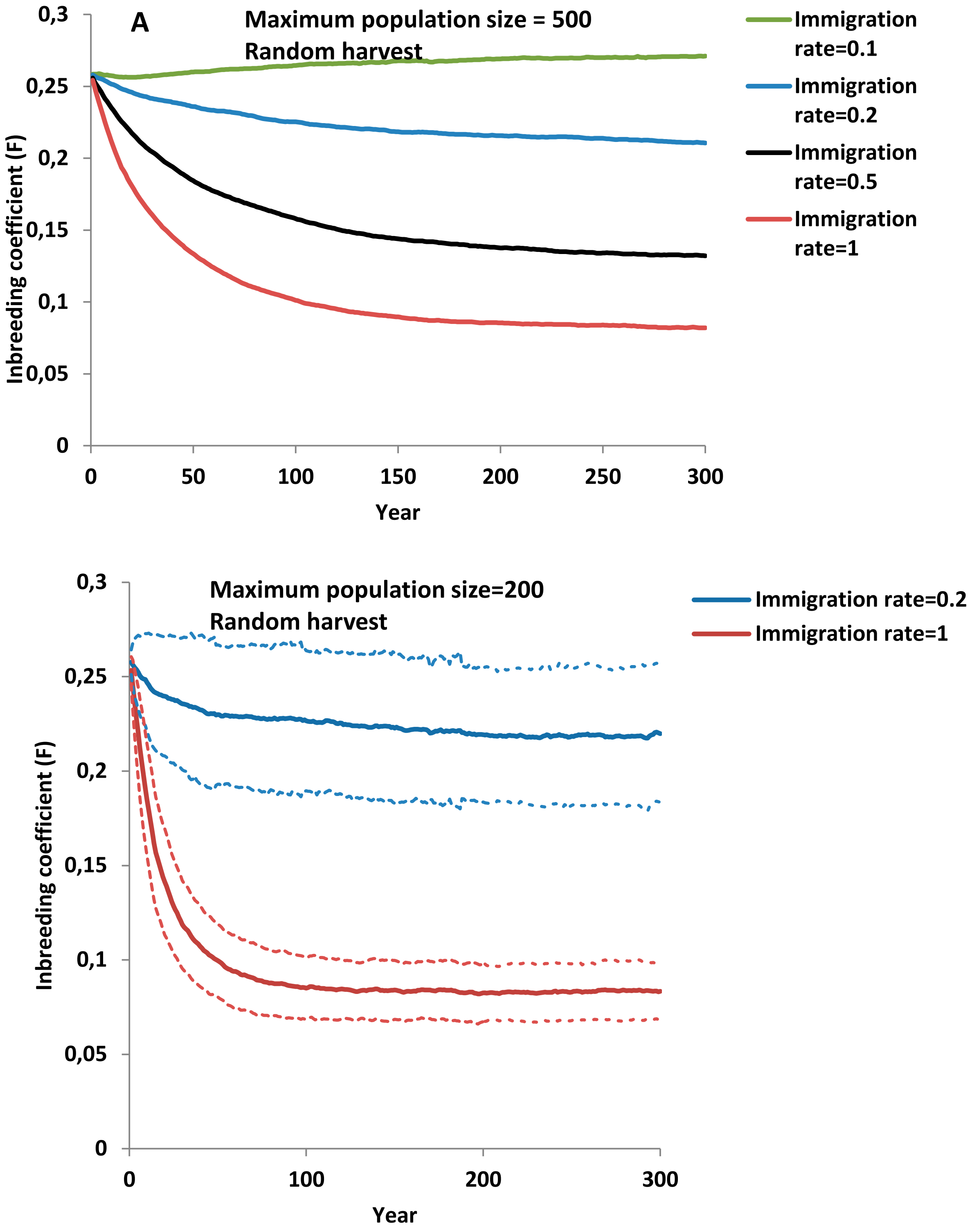

*Figure 1. Mean inbreeding coefficient (F) over time, estimated from simulations, for different immigration rates (number of effective migrants per year). Figure 1A is for a maximum population size of 500, and figure 1B is for 200. Standard deviations (broken lines) for the resulting inbreeding coefficient are given in figure 1B. Harvest strategy is random harvest.*

## Long term effects

In the analysis of long term genetic effects , we investigated effects on the genetic status by three factors, (1) migration rate of effective migrants, (2) population size, which might be manipulated through regulating harvest; and (3) harvest strategy.

Two harvest strategies were investigated: (1) random harvest which was non-selective, and (2) selective harvest, where migrants and their first generation offspring (F1´s ) were excluded and the rest of the population was harvested randomly. First we look on effects on the equilibrium inbreeding level, and then on the time taken to reach certain inbreeding levels.

### Equilibrium levels of inbreeding coefficient F.

Figure 1A illustrates that with a continuous influx of migrants, after a certain time an equilibrium value of the inbreeding coefficient will be reached. The more migrants, the lower the equilibrium inbreeding level will be. To reach below F = 0,1 approximately 1 migrant per year will be needed. One important aspect of this relation between migration rate and inbreeding level is that it is independent of population size. The curves for immigration rate 0.2 reaches an asymptote at the same level in both Figures 1A and 1B, although the population sizes are different (500 and 200 respectively), and the same applies to the curves for immigration rate 1.0. This independence of population size for the equilibrium of F is in accordance with Wrights (1951) “island model”, expressed in the equation $F = 1/1+ 4M$ where $F$ is inbreeding coefficient and $M$ is migration rate expressed as number of migrants arriving per generation.

This independence of population size for equilibrium F is also illustrated in figure 2, where different population sizes but the same migration rate have been plotted in the same graph. It also illustrates that the time needed to reach the equilibrium is correlated to population size. The process is faster in small populations. The simulations were run for only 100 years, in this graph, which was not enough time for populations of 300 and larger to approache their equilibrium levels

Figure 2 illustrates another interesting thing. If the population is regulated with harvest, and migrants and F1´s are protected (Figure 2B), the equilibrium of F will be substantially lowered, compared with a situation with the same migration but random harvest (Figure 2A). The probable reason for this is that the selective harvest strategy will cause a relatively lower mortality of migrants and F1´s compared with other wolves in the population, and thereby in fact increase the “effective” migration influx, even if the actual number of migrants is the same .

Figure 3 is a different way of illustrating the negative correlation between migration rate and equilibrium level of F. The figure is based on simulations with a population size of 500, but the equilibrium level is in fact independent of population size, as pointed out before. With 0.2 migrants per year the equilibrium level of F will be 0.22, and with a rate of 1 per year the level will get down to 0.08, irrespective of population size (Table 2). This is under a random harvest strategy. With protection of migrants and F1´s the equilibrium levels will be lower (approximately 0.04), as illustrated in figure 2B.

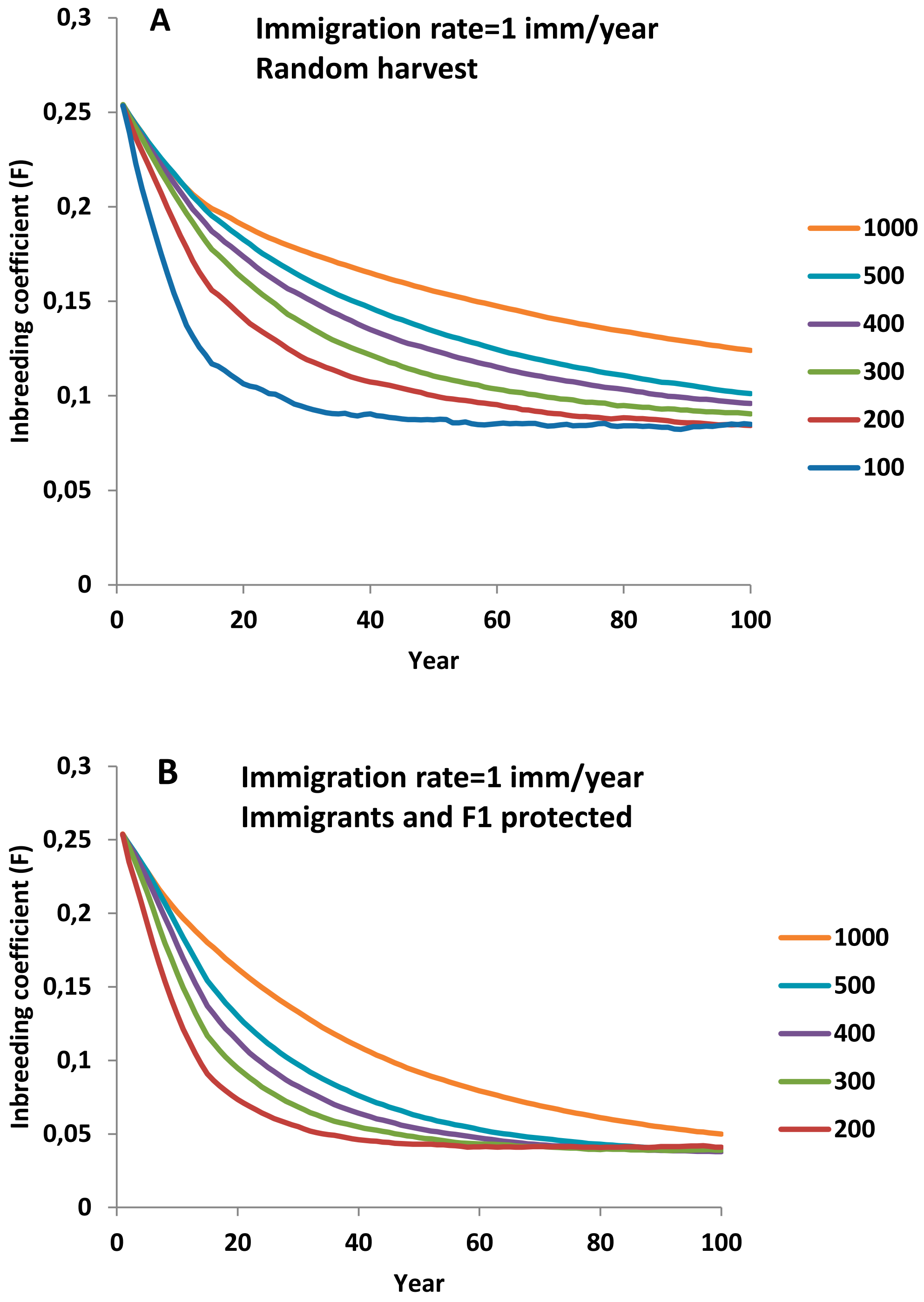

*Figure 2. Mean inbreeding coefficients (F) over time, as estimated from simulations, for different maximum population sizes, different immigration rates, and different harvest strategies. In figure 1B results for maximum population size=100 are missing because there were too few wolves to harvest to limit the population to 100 individuals since immigrants and F1 were protected.*

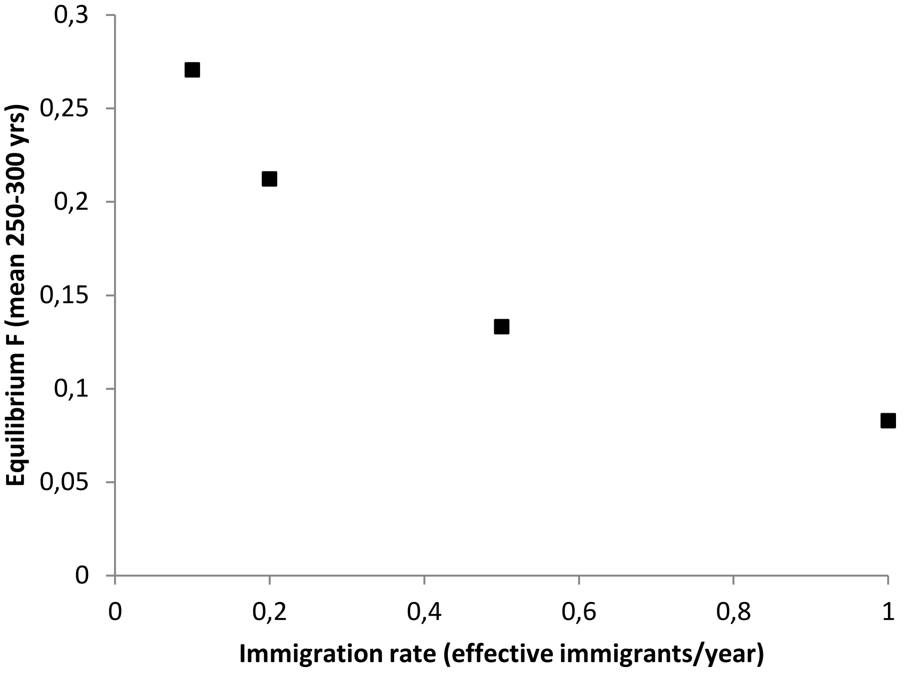

*Figure 3. Approximate equilibrium levels of inbreeding coefficient as estimated as the mean of the inbreeding coefficient (F) at 250-300 years from simulations (see Figure 1A). Standard deviations of the mean are too small to visualize in the graph. Maximum population size is 500, harvest strategy is random harvest.*

*Table 2. Approximate equilibrium levels of inbreeding coefficient as estimated as the mean of the inbreeding coefficient (F) at 250-300 years from simulations with maximum population sizes of 200 and 500 individuals, respectively.*

| Maximum population size | | Immigration rates | | |
|---|---|---|---|---|
| | 0.1 | 0.2 | 0.5 | 1 |
| 200 | * | 0.219 | * | 0.084 |
| 500 | 0.270 | 0.212 | 0.133 | 0.083 |

*Not estimated

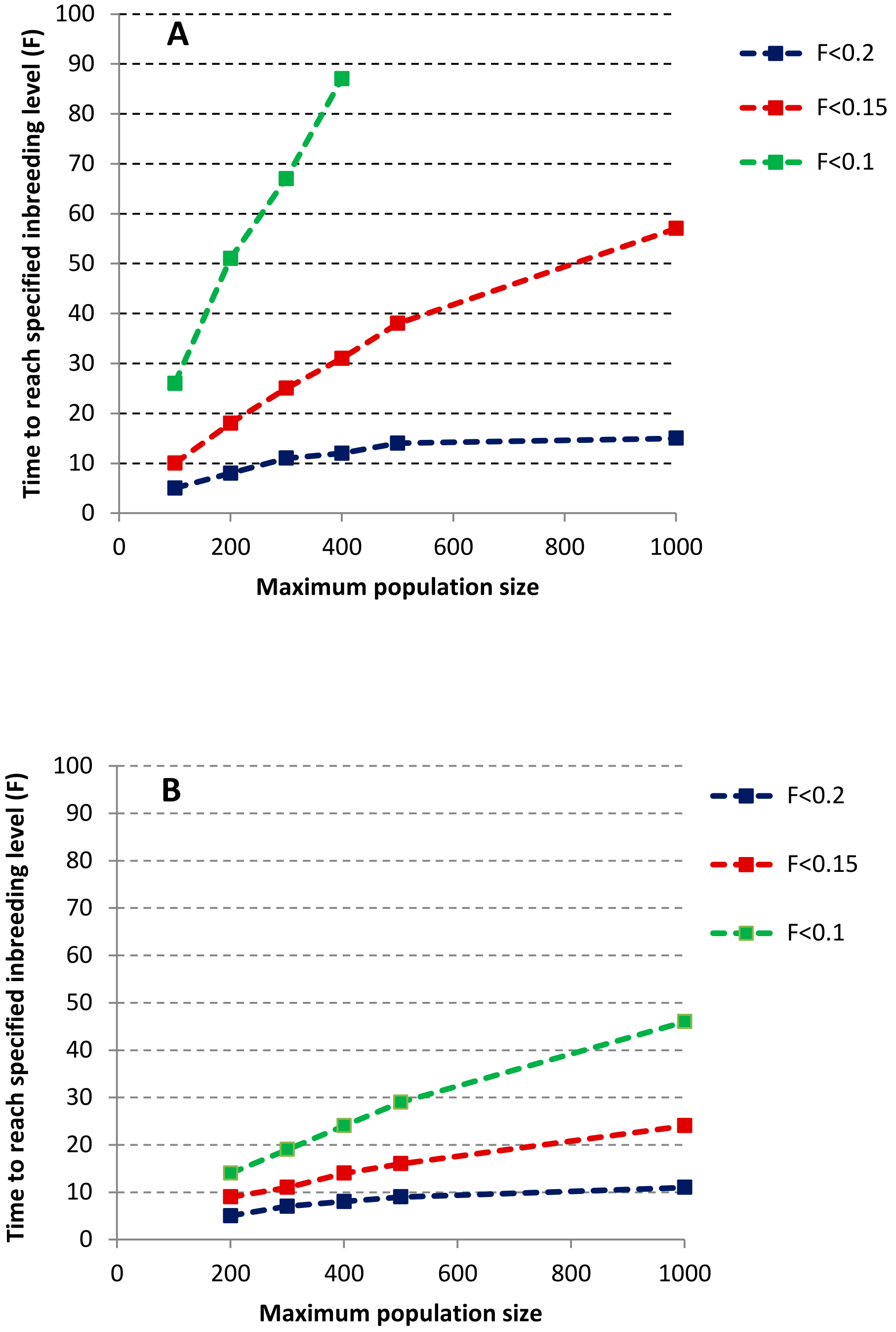

*Figure 4. Number of years until a specific inbreeding level (F) is reached in relation to maximum population size. Immigration rate is 1 effective immigrant/year. Relationships are shown for random harvest (4A) and protection of immigrants and F1 progeny (4B). In figure 4A, no values are shown for maximum population sizes > 400 and F<0.1 because F never reached F<0.1. In figure 4B, there are no values for maximum population size=100 for F<0.1 because there were too few wolves to harvest to limit the population to 100 individuals since immigrants and F1 were protected (although not in all simulations).*

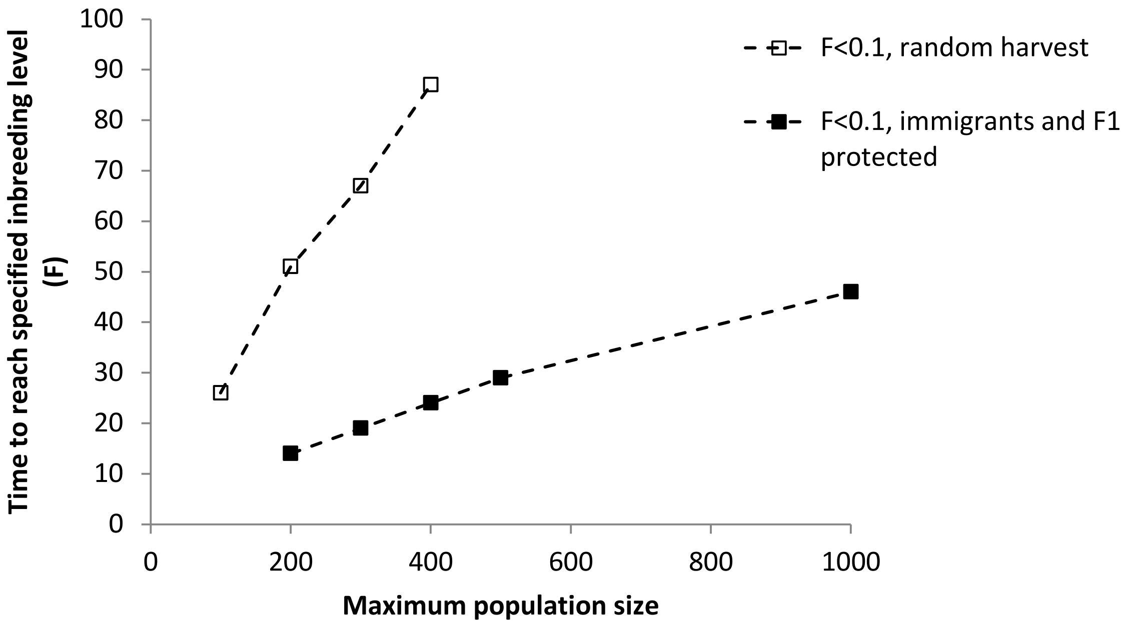

*Figure 5. Same as in figure 4, but compares the two harvest strategies for the threshold value F<0.1.*

Time to reach a certain level of inbreeding

The average inbreeding level today in the Scandinavian wolf population is approximately F = 0,26. With immigration this level can be reduced. Time required to reach a certain lower level is negatively correlated with population size, as illustrated in figure 4A. With the same immigration rate it will take longer time the larger the population is. The process can be further speeded up by a selective harvest strategy as shown in figure 4B and 5. If some extra migrants are added ("boosting") during a few years in the beginning of the period, the process will be even more speeded up (compare Figure 6 with Figure 2).

Table 3 summarizes the effects of population size, harvest strategy and boosting on the time needed to reduce the inbreeding to a certain level, in this case a level of F < 0,1. Only two population sizes are presented here, and the longest time to obtain this lower level among the scenarios presented is for a and a population ceiling of 400 random harvest. No other population sizes are presented in this table, but with larger populations it would take even longer (Figure 4 and 5). The fastest route to the threshold level of F= 0,1 is attained with the lower population of 200, a harvest strategy that spares migrants and F1´s and with an initial boost of six immigrants. When these conditions are met, the level can be reached in just 10 years. This is an almost 90 % reduction of the 87 years it would have taken with maximum

400 animals, random harvest and no boosting. With larger populations it would have taken even longer time. Selective harvest had the strongest effect, around 70 %, while reduction of the population had an approximately 45 % effect, and boosting a 10 – 30 % effect.

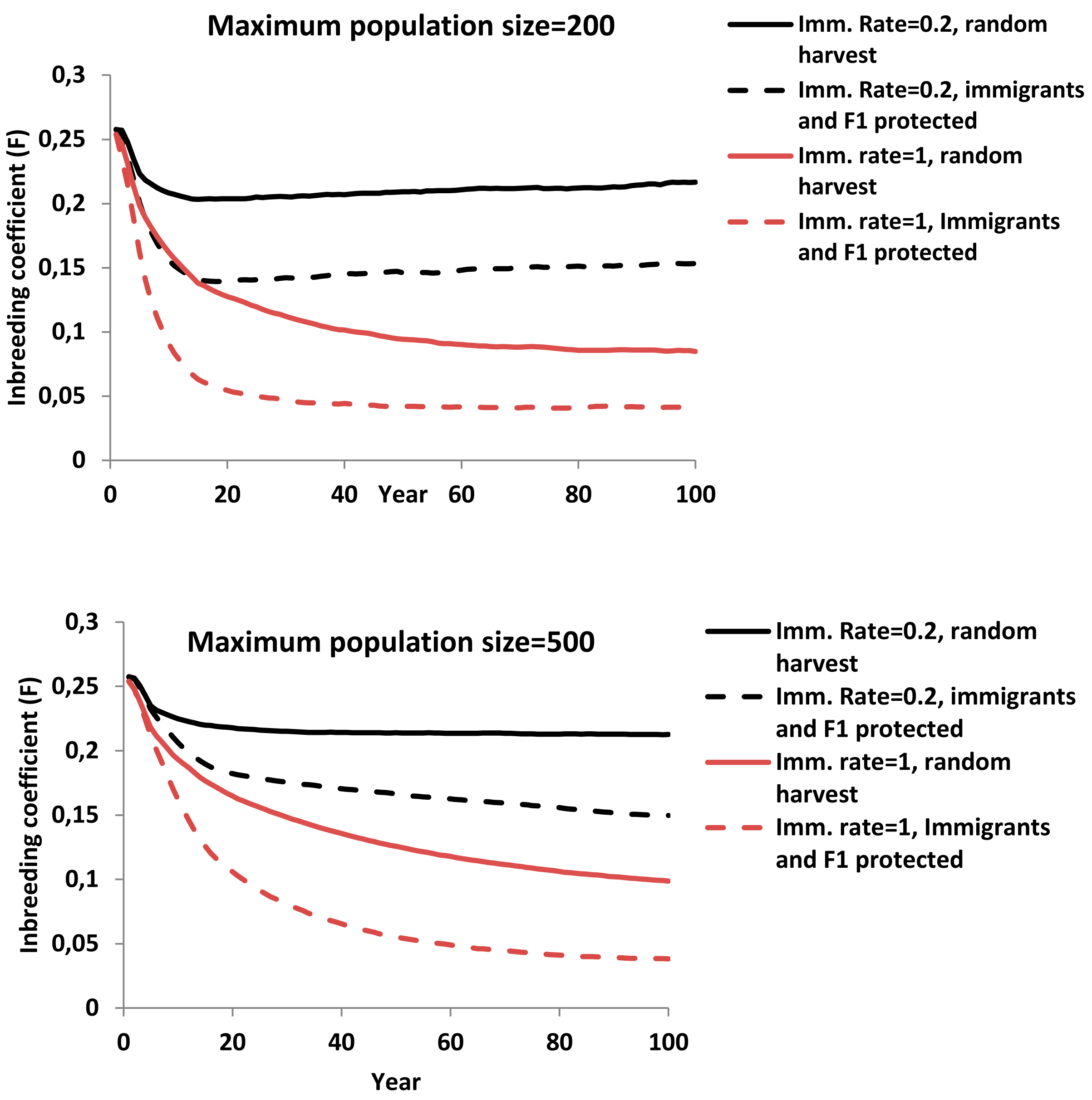

*Figure 7. Same as figure 2, but with six extra effective immigrants added during the years 3-5 to simulate aided immigration. The sex of the extra added individuals was randomized from an expected sex ration of 1:1.*

*Table 3. Time to reach the threshold value of F<0.1 for different harvest strategies, supplement actions, and different maximum population sizes. Immigration rate=1 effective immigrant/year*

| Harvest strategy and supplement | Time to reach F<0.1 | | |
|---|---|---|---|
| | Max pop size = 200 | Max pop size = 400 | Max pop size = 1000 |
| Random harvest, no supplement | 51 | 87 | >100 |
| Protection of immigrants and F1, no supplement | 14 | 24 | 46 |
| Random harvest with supplement of 6 individuals | 42 | 80 | EJ SIMULERAT! |
| Protection of immigrants and F1 with supplement of 6 individuals | 10 | 18 | EJ SIMULERAT! |

## CONCLUSIONS

1. Only harvesting the wolf population can never improve its genetic status in the long term, immigration is central for the reduction of inbreeding and loss of genetic variation.
2. Provided there is a constant influx of unrelated migrants to the population, reduction of inbreeding levels and time required to obtain these lower levels can be achieved with a well-designed selective harvest strategy.
3. Short turn temporary gains can be obtained, even with no further immigration. After two years of selective harvest of 5 and 10 packs directed at the wolves with the highest kinship coefficients, the change in inbreeding level was -0.015 and -0.031 respectively.
4. Assuming that the source population is very large a given steady migration rate will result in F reaching an equilibrium level.
5. The equilibrium inbreeding level corresponding to a certain migration rate will be further reduced if the population is harvested with migrants and F1´s protected. With an immigration rate of 1 per year the level will be reduced from 0.08 with random harvest to approximately 0.04 if migrants and F1´s are protected.

6. The equilibrium of F at a certain immigration rate is independent of population size, but there is a positive correlation between population size and the time it takes to reach the equilibrium, or any arbitrarily set level, of F, i.e. it will take longer time with larger populations.
7. A selective harvest that excludes migrants and F1´s will also reduce the time taken to reach down to a lower inbreeding equilibrium.
8. The time to reach down to a lower equilibrium of F will be further reduced if an initial boost of extra migrants is provided. This effect however is not as strong as the effect of population size and a selective harvest.
9. In a series of simulations with two population sizes (200 and 400), two harvest strategies (random and protection of migrants and F1´s) and boosting or non-boosting (6 extra migrants in years 3-5), the time to reach a threshold value of $F < 0,1$ with a migration rate of 1 migrant per year, was only 10 years in the best scenario (population of 200, selective harvest and boost) and 87 years in the worst scenario (population of 400, random harvest and no boost), i.e.an almost 90 % gain in time achieved with active management measures. With larger population sizes this latency time period will be even longer.

## FINAL REMARK

These model results are potentially of great importance for decisions of management actions. However, they have been produced under strong time pressure. We therefore recommend that before they are used for such purposes, especially for long term decisions, they should be confirmed with an extended analysis. Further, if these results are used for management strategies of the wolf population after such an extended analysis, we advocate an adaptive management approach where model predictions and management actions based on the predictions are followed up by continuous and detailed monitoring of the population. Results from the monitoring should then be contrasted to the expectations from the model, and further actions adapted to these new data. This underlines the importance of continued careful and detailed monitoring of the demography and genetics of the Scandinavian wolf population. The lower level the population is held at, the more important is this point.

## ACKNOWLEDGEMENT

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