Selective hunt and its genetic background

Compiled by Dag Lindgren last edit 140220, not well-written, but considering number and relevance of predicted readers, I do not feel motivated to work more to make it better, unless a real and important user explicitly asks for a specific purpose. Most are just not interest to spend time on understanding something.

Doubt has arisen if there is a scientific justification for selective hunt. Most statements are based on misunderstandings on what selective hunt is and what it does. This document makes an effort to explain the genetic background concepts. It is for reading of those who makes statements about selective hunt to Swedish wolf. Comments or statements from those, who have not cared to understand the Basic Genetics should not be trusted. Sand has confirmed that Sand and Liberg have a sufficient understanding. This text is written by Dag Lindgren and I am presently certainly not a good text book author and it is possible the text contains minor mistakes.

There are five chapters with the following approximate themes:

Chapter A explains why low numbers are genetically favourable in a situation like the current Swedish wolf

Chapter B explains that selective hunt is a standard procedure used in many situations including current wolf.

Chapter C is a tutorial I made myself, references to the thesis of some students I have supervised and extracts of from. This offers a deeper background and many references.

Chapter D focus on selective hunt as applied to Swedish wolf

Chapter E justifies simulation as a better method than fundamentalist trust in theory

Chapter A. Scientific background on population size and why low population size appears favourable.

Two major forces affect “inbreeding” in different directions. That is drift and migration. There is (usually) a value of inbreeding, where these two counteracting forces balance each other and inbreeding will remain stable over generations. Usually the balance inbreeding does not depend on the population size. At a stable simplified situation with discrete generation shifts and all individuals behave ideally, the influence the forces has on inbreeding are depending on population size (N), in the same way, but in opposite direction. Inbreeding approaches an equilibrium where the counteracting forces get equally strong. That the equilibrium is not depending on N, population size, is strongly counterintuitive but still an established genetic fact. Den som söker en referens kan titta i genetikboken (Hartl & Clark 2007) eller http://gul.gu.se/public/pp/public_noticeboard_attachment/fetch?messageId=801021&fileId=19648139 .

Under standard conditions (Wrights island model) the equilibrium value is given by: $F = 1/(4Nm+1)$. One may discuss the conditions for the equilibrium in complicated situations. It is valid if

N and m is replaced by effective N and effective m more or less by definition of what effective means in this context.

But what is changing is the speed at which the equilibrium is achieved, in standard conditions the rate of speed is the inverse of the population size, both the change at generation turn over by drift (1/2N) and by migration (m/N) double when population is reduced to half. Thus given that the migration is sufficient to get inbreeding sinks, it sinks faster the smaller the population is. For Swedish wolves immigration reduces the inbreeding in spite of genetic drift. Thus inbreeding will sink the smaller the population is and the more wolves we have the more inbred they will be in some generations. Thus to maximize population growth some years means that inbreeding will be higher in the future.

There are many assumptions for simple applications, which can be claimed not to be literally fulfilled, but still strong reasons to believe the main conclusions are approximately valid over a wide range of conditions including Swedish wolf. To get quantitative results simulation is more reliable, but a check is recommended if the results are reasonable compared to the expectations from formulae.

For short term applications (one or a few single years change considering a few known immigrants) it is important to understand that the time pattern of the influence of the force are different for wolf. If a single migrant starts to reproduce, the "migration" (impact on the frequency of gene copies of the migrant) will continue to grow for almost a decade. Contrary, the drift can be seen as occurring at generation shifts. There are many generation shifts, so on average drift per year can be seen as a variable only influenced by current population size. Migration is probably magnified by "heterosis" and sooner or later by selective harvest even if not during the short-term interval, and can thus raise considerable for a decade.

E.g. no relatedness (or a constant relatedness) between the recipient population and the source population. Increasing relatedness can be expected in most long term applications for Swedish wolf. Such difficulties and deviation cannot reasonable be handled by complicating the formulae.

A semantic observation is that "inbreeding" here is an expectation under some type of random mating regime. Thus the "coefficient of inbreeding" may be very different. The coefficient of inbreeding depends on mating pattern, while the population inbreeding (=group coancestry) does not.

Known objections: I have run two wolf blogs which together received 400 comments and there this is one of the central themes. The only rather knowledgeable objections raised origins from Per B… He objects in the following way (in green) with my comments (in red) ";…Vad jag vänder mig mot är osakligheten i debatten. Oavsett vad Dag anser så är det ganska basalt att inaveln sjunker snabbare i en liten stam (givet invandring), …. Vad Dag inte påpekar är att det leder till en rad andra problem. Till exempel kommer den genetiska variationen/diversiteten ovillkorligen bli lägre,
"Genetisk variation/diversitet" mätt med "average heterozygosity" är nästan samma sak som inavel (ändring av populationsinavel), inte något som reagerar annorlunda på populationsstorlek än "inavel"
inavelsgraden kommer öka väldigt mycket snabbare i avsaknad av invandring,
I avsaknad av invandring ja. Men eftersom det faktiskt förekommer invandring är detta irrelevant. Specifikt I den svenska vargstammen kommer Tiveden vargarnas migration successivt reducera

“group coancestry” =”inavel” de närmaste sju åren.
och givet den grad av invandring som Dag, SJF och regeringen tycker vara tillräcklig (en ”effektiv” varg per generation),
Det enda som nämns om invandring (och därigenom också indirekt “inavel”) i EU-direktivet är att migrationen skall vara större än en effektiv migrant per generation. Det har mycket god teoretisk grund att välja detta värde som skiljelinje mellan divergerande respektiva sammhållna populationer. Det är gravt missvisande att beskriva det som en idé som härrör “Dag, SJF och regeringen”. Men jag föreslår att man skriver in minst fyra effektiva invandrare per decennium (två per generation) som ett *förvaltningsmål* i förvaltningsplanen för varg, sista tiden har det invandrat mer än så.
så kommer vi med tiden hamna på en betydligt högre genomsnittlig inavelgrad i en liten population än vad vi skulle gjort i en större
Inavelsgraden som man så småningom hamnar på är oberoende av populationsstorleken, även om detta är svårt att förstå. Inte heller om en komplicerad modell väljs finns det någon logik i att resultatet skulle bli motsatt mot den enklare modellen.

Conclusion: there does not seem to be any serious objections.

Chapter B explains that selective hunt is a standard procedure used in many situations including current wolf.

Selective hunt generally aims at minimizing group coancestry under the constraints enforced by the particular situation on a case to case basis.

Management aiming to minimize coancestry under constraints is a common praxis widely used. And the measure group coancestry is still wider used.

For the suggested licence hunts 2013 and 2014 a practical constraint was that only wolves or wolf packs with identified territories were exposed to the hunt, otherwise the wolf identities would be too uncertain.

Exclusively selective hunts have been performed in Sweden. At the licence hunts 2010 and 2011 “genetically valuable” wolfs were protected. Laikre et al. 2013 pointed out that more sophisticated methods to minimize group coancestry (=average kinship) would result in lower group coancestry, and the development of a more sophisticated tool by Liberg and Sand (2011) should be seen as a response to what Laikre and others pointed out.

Even derogation for protection purposes is selective, the chance that a “genetically valuable” wolf will be killed is intentionally reduced. Even this type of hunt is a variant of genetic selective hunt. My guess is that even this type of hunt has improved the genetic status of the wolf, but no actual calculations has been presented and the actions against the “Junselevargen” has a heavy negative weight.

Selection goals and algorithms aiming at minimizing group coancestry among other breeding goals are very common in breeding domesticated crops and animals.

Group coancestry considerations is a standard procedure in Swedish forest tree breeding which I know best. The group coancestry in each compartment of the breeding population is calculated in annual descriptions about the state (progress report) of each breeding subpopulation (about 50).

Relevant references to some of these activities can be found in Chapter C.

Chapter C. Basic genetics for the purpose of selective hunt (minimizing Group coancestry), tutorial, PhDs and extracts

It is basic to have a measure of diversity. Many usually use “group coancestry”. Jag tror jag myntat “gruppsläktskap” för en Svensk översättning. This is near average heterozygosity. But group coancestry is like coefficient of inbreeding relative to a reference point. The same or very similar concepts are used both in zoological gardens and animal breeding. Animal people have often difficult to understand the role of selfcoancestry (“selfing”). Sometimes coefficient of relatedness is used, which in my opinion causes problems without solving any and nowadays the trend is to only use group coancestry (or its equivalents). Sometimes this is called “inbreeding” and I sometime use that terminology myself to make it clear what it is about, but people who are not very good in genetics often misunderstand and interpret it literally which does not matter very much until it comes to real hunting algorithms. Group coancestry can be seen as latent inbreeding and almost equivalent. I made a short “tutorial” some decades ago and it is still on the web http://daglindgren.upsc.se/Breed_Home_Page/Tutorials/Tutorial_Menu.htm . A major problem is that the opinions in letters given to court usually are based on this misunderstanding as well as some others.

I have advocated that annual reports of wolf should comprise group coancestry and one report of the development over time actually do use a variant http://vargweb.wordpress.com/2012/10/19/genomsnittligt-slaktskap-2/

I am old (71) and retired since some years and it is no duty to SLU who paid me as professor and the duty to serve as the formally highest qualified competence in genetics as far as questions connecting to forests are concerned. I am not quite healthy and do not like very much and is not perfectly fit for this text book approach. I will not spend time on getting a nice writings with formal qualities and many references. I have not access to the text books and literature I used above and it is difficult to use library service and I have no account for e.g. library expenses so I just use what I can find on the web (including the hard disk). Part of my background is a PhD dealing with inbreeding. Much of my Science was to balance gain and “diversity” (see some of the thesis I supervised in another attachment to give background). The main theme in my scientific work has been to supply the forestry with as good regeneration material as possible both by own work but also by mentoring collaborators. This was much more important for me than publishing in fancy general journals and to get recognized by other geneticists. The concepts and relevant literature is found in the introduction of the thesis of some students I have supervised, which I list. Most of these theses are identified by working URL. In the thesis where is theoretical background information which give useful references

Andersson, E.W. 1999. *Gain and Diversity in Multi-Generation Breeding Programs.* Acta Universitatis Agriculturae Sueciae. Silvestria **95** 42pp+4 chapters.

Rosvall, O. 1999. *Enhancing Gain from Long-Term Forest Tree Breeding while Conserving Genetic Diversity.* Acta Universitatis Agriculturae Sueciae. Silvestria **109** 65pp+4 chapters.

Bila, A.D. 2000. *Fertility variation and its effects on gene diversity in forest tree populations*. Acta Universitatis Agriculturae Sueciae. Silvestria **166** 32pp+4 chapters.

Kang, K.S. 2001. *Genetic gain and gene diversity of seed orchard crops*. Acta Universitatis Agriculturae Sueciae. Silvestria **187** 75pp+ 11 chapters. Contents.

Olsson, T. 2001. *Parameters, relationship and selections in pines.* Acta Universitatis Agriculturae Sueciae. Silvestria. **192** 27pp+4 chapters

Ruotsalainen, S. 2002. *Managing breeding stock in the initiation of a long-term tree breeding program.* Finnish Forest Research Institute, Research Papers **875**., 95 + 61

I glue from Rosvall 1999

Genetic diversity

Genetic variability can be understood in several ways, for example:

(i) the allelic richness that can be identified by biochemical methods and expressed for individuals or populations (e.g., proportion of polymorphic loci, number and frequency of alleles in these loci, proportion of heterozygous loci) (Berg and Hamrick 1997);
(ii) quantitative variation in metric characters, assessed by a statistical analysis of variance; and
(iii) effective population size based on relatedness within and among individuals and populations.

Allelic diversity and genetic variance

The **genetic diversity** of the gene pool in terms of gene frequencies determines the quantitative **genic variance,** assuming perfect Hardy-Weinberg (H-W) and gametic phase or linkage equilibrium, which should be distinguished from how the individuals of the population carry this pool, determining the **genotypic** (**or genetic**) **variance** (Bulmer 1976; Falconer and Mackay 1996).

The genetic information is re-combined at generation shifts and renewed by mutations. Under natural conditions, changes in the gene pool generally occur slowly over an evolutionary time scale, and the pool ordinarily contains a huge allelic variability if assessed by the number of alleles (Ledig 1986; Williams et al. 1995). Also, lethal and deleterious mutant alleles, which constitute the “genetic load”, are carried in individuals if the complementary allele in the homologous pair is functional.

These genes contribute to inbreeding depression when they appear in homozygous genotypes (Ritland 1996).

While long-term maintenance of genetic variance in a population under selection is more dependent on the alleles present in the population than on heterozygosity (Robertson 1960), the number of alleles at a locus (**allelic diversity**) has a low impact on heterozygosity and thus current genetic variance (Allendorf 1986). Alleles that are initially rare must increase in frequencies by chance and selection, before they will influence genetic variance.

For a commercial forest stand to cope with temporal and spatial variation in the environment and to resist biotic stresses, it is the heterozygosity within individuals, i.e. loss of heterozygosity due to inbreeding, as well as the genotypic variation from tree to tree that is of prime importance (Lindgren and Gregorius 1976; Ledig 1986; Lesica and Allendorf 1992). Roberds and Bishir (1997) discuss models for risk analysis to guide plantation diversity in clonal forestry, where genetic uniformity can be brought to its extreme. However, if planted stands are not harvested or naturally regenerated, the quality of their gene pools will influence the following generation, both on the site and in the population as a whole (Ryman and Laikre 1991).

Management of genetic diversity

Sampling of alleles and population size

Since the transmission of alleles between generations is a sampling phenomenon, population size is fundamental to several aspects of genetic diversity and its maintenance in small populations (Robertson 1960; Nicholas 1980; Franklin 1980; Lande and Barrowclough 1987; Kang 1991). First, the size and quality of the sample from the natural forest population determines the initial allelic diversity of a BP (Gregorius 1980; Nienstaedt and Kang 1987; Danell 1993b). Second, the structure and effective size of the BP determines the sampling from generation to generation. The smaller the population, the larger is the random genetic drift in gene frequencies, which eventually will result in the total loss or fixation of alleles, and the larger is the measurement error variance due to the sampling of a limited number of individuals for testing (Aggrey et al. 1995). Third, the size of the BP, together with the mutation frequency, determines the total number of new mutations that are potentially available for selection. In the long term, mutations will contribute to genetic diversity and variance also in a managed population (Hill 1982; Lynch 1988).

The non-random selection of BP founders can itself increase genetic variance through heterosis and release from linkage (Falconer and Mackay 1996). Increase in variance may also occur from the reduction in population size when there is dominance and epistasis, by changes in gene frequencies and departure from H-W and linkage equilibria, analogous to the changes in variance after a bottleneck (Wang et al. 1998).

Conservation of alleles

The conservation of the gene pool of a BP is influenced by how the natural processes within the population (random genetic drift, as well as directional forces on gene frequencies: mutation, natural

selection and migration) are affected by management: (i) how the population is structured; (ii) the methods of breeding (mating and selection); and (iii) introduction of new genes. These actions also influence how the alleles are arranged into genotypes and, thus, the genotypic and phenotypic variance among trees, i.e., the quantitative variance.

In a random mating BP of constant size, without substructure and with unrelated founders, genes are best conserved by balanced within-family selection, and balanced mating, giving equal gene contributions from each founder (Ballou and Lacy 1995; Lindgren et al. 1996). When the loss of diversity is minimised in this way, random genetic drift sets the limit for gene retention. Conservation is even greater in a sub-structured population as drift can change gene frequencies in different directions among the sub-groups (Robertson 1960; Lande and Barrowclough 1987; MacKeand and Bridgewater 1998). The extreme case of this phenomenon is regular inbreeding, e.g., repeated selfing (Lindgren 1976; Falconer and Mackay 1996). Consequently, any form of imbalance in parental contributions will accelerate the loss of genetic diversity. If desirable, a balance can sometimes be re-established from an unbalanced situation by genetic management of the population to minimise average coancestry (i.e., average mean kinship) (Ballou and Lacy 1995).

The loss of diversity by drift in a small population results in a loss of allelic variants and lower heterozygosity, while inbreeding due to non-random mating only changes the level of heterozygosity. Genetic drift and inbreeding affect both target traits and neutral alleles, while selection will only affect target and linked genes. Directional or disruptive selection will ultimately fix one allele and thereby deplete genetic variation. For traits where heterozygosity has an advantage, due to whatever cause (inbreeding depression, overdominance), natural and artificial balancing selection slows down the loss of allelic variation due to drift over what neutral models predict (Lesica and Allendorf 1992). In addition, selection and assortative mating cause gametic phase disequilibrium, without changing the gene frequencies of the loci affecting the character and for linked loci (Bulmer 1976; Jorjani et al.1997b,c).

Measuring loss of genetic diversity

Group coancestry and inbreeding

Given an initial pool of unrelated founder genes, the potential changes and losses of genetic diversity can be assessed by the increase in relatedness, i.e., the increase in genetic similarity due to genes being identical by descent. **Group coancestry** (Θ) is the probability that two genes taken at random from the gene pool, with replacement, are identical by descent (Cockerham 1967). Similarly, **pair-wise coancestry** (θ_{ij}) (coefficient of kinship) is the probability that genes sampled from each of two individuals i and j are identical by descent. The inbreeding coefficient (F_i) is the probability that the two homologous genes within an individual i are identical by descent. **Self coancestry**, i.e., the coancestry of an individual with itself is $0.5(1+F_i)$ ($i=j$) (Falconer and Mackay 1996; Lindgren and Mullin 1998). Thus, Θ of a population with N individuals is the average of all self- and pair-wise coancestries, including reciprocals,

$$\Theta = \frac{N0.5(1+F)+N(N-1)\bar{\theta}}{N^2} \qquad [1]$$

where $\bar{\theta}$ is the average of all pair-wise coancestries; and *F* is the average inbreeding. As Θ includes the repeated sampling of the same gene, Θ depends on population size by 1/2N, which is well-known from other formulations of the effect of genetic drift (Falconer and Mackay 1996).

The loss of genetic diversity within an individual, due to inbreeding and drift, results in decreased heterozygosity, which is measured by the inbreeding coefficient (*F*). Selection against inbreeding depression may change the average *F* of the population, while other possible changes in individual heterozygosity by selection, including changes in gene frequencies, are not seen in *F*. Pair-wise coancestry between two mates becomes inbreeding of their progeny, and group coancestry in one generation becomes the expected average inbreeding in the next, following random mating.

Kang 2001:

Gene diversity and group coancestry

The accumulated loss of gene diversity is the group coancestry (Lindgren and Kang, 1997). The gene diversity can be estimated relative to the reference population (**II** and **VII**). The reference population is defined as having an infinite number of unrelated individuals, and thus a group coancestry of 0 and gene diversity of 1. No genes of individuals in the reference population are identical by descent. The inbreeding in the reference population is also considered to be 0 (**III**; Yeh, 2000).

Loss of gene diversity may occur in two stages: (1) when seed orchards are established with a limited number of parents; and (2) when there is unequal contribution of gametes by the orchard parents (Harju, 1995). On the other hand, pollen contamination increases the gene diversity of orchard crop (Lindgren and Mullin, 1998).

The term group coancestry was introduced by Cockerham (1967), who defined the group coancestry coefficient as referring to the probability of identity of a random pair of genes sampled, with replacement, among the 2*N* genes of the *N* individuals in a population. By definition, therefore, group coancestry is the average coancestry of all pairs of population members including individuals with themselves (self-coancestry). Group coancestry is equivalent to "average coancestry" or "average kinship", as used in some studies (e.g., Askew and Burrows, 1983; Fries, 1994; Lacy, 1995), but other studies (or even in the same studies) also use the terms "average coancestry" or "mean kinship" referring to averages of other sets of values. As the term is used with different meanings by various investigators, without being intuitively clear as to which values are to be averaged, the term easily causes misunderstandings. Lindgren et al. (1996) coined "status number" calculated from the group coancestry, which gives clear intuition on the concept of effective number

Chapter D Selective hunt applied to the Swedish wolf

The probably most important aim of genetic management of populations with few founders, like the Swedish wolf, is to maximize the increase in diversity till a reasonable level is reached. The most important is reproductive migrants. This should be complemented by actions to spread the genes of the immigrants and to balance their contributions to maximize diversity. The frequency of the new genes with a low share in the population should increase and the frequency of the genes from the initial founders which cause inbreeding by their high proportion should be decreased to increase

diversity. To manage diversity quantitatively a measure must be used. This is here called group coancestry (see attachment) and it is commonly used and applied and is the equivalent of inbreeding on the population level. But the terminology varies (average kinship, average coancestry). Gene diversity is defined as 1-group coancestry. Selective hunt aims at minimizing group coancestry. But algorithms for application must also be manageable and therefore the aim of minimizing diversity is somewhat compromised with simplicity of application and other aims and unavoidable errors of different types. Wolf hunts 2010 and 2011 were selective hunts excluding territories with migrants and their offspring as well as grandkids as long they remained in the kids (parents) territories. The more complex situations now emerging as a more general way of applying selective hunt a more general tool was developed. Selective hunt is a standard method generally used under different names and conditions.

The aim of the procedures applied by Liberg and Sand (2012) is to maximize gene diversity and minimize group coancestry some generations ahead thus minimize future inbreeding, but with simplifications which are necessary to apply it to practice. Their study is a simulation, thus testing what happens if a procedure for selecting wolves to cull. A simulation proves that the procedure works, it cannot be argued that the procedure is not expected to work for one reason or another. This is the commonly used scientific method to test if a method which is predicted to work on theoretically ground also works. It gives also quantitative predictions of the applications. There is a risk the simulation itself misunderstands what it should do so some rough checks with theoretical predictions is recommendable. I predicted the results based on considerations in an EXCEL work sheet, and try to present the logic in popular form in Lindgren D 2011. Licensjakt minskar inaveln. Svensk jakt 2011(8): 34-35. http://www.jagareforbundet.se/svenskjakt/Nyheter/Debatt/Debatt-Svensk-Jakt/Licensjakt-minskar-inavel/ The predictions I made was mainly confirmed by Liberg and Sand (2012). When the real geography does not fit with the map, why should it be concluded that the geography is wrong and the map right?

Chapter E Simulering är en standardmetod för att bedöma de kvantitativa effekterna av åtgärder.

Inför ett urval med selektiv jakt, så har man applicerat jaktstrategier på en virtuell vargpopulation och sett vad utfallet blir. Det spelar ingen roll om man förstår den teoretiska bakgrunden, simuleringen visar ändå ”verkligheten”.

Det finns inget alternativ sätt än simulering att få mer detaljerade förutsägelser om utfall av en åtgärd eller troliga händelserutvecklingar under olika förutsättningar. ”Formler” och ”allmänkunskap” förmår inte beakta den variation som finns i en verklig situation. Det må gälla biltrafik och röda ljus, vargar, universums uppkomst, vädret i övermorgon eller härdsmältor i kärnreaktorers reaktion. Mer exakta kvantitativa förutsägelser av effekten av olika åtgärders inverkan i en komplicerad verklighet mer eller mindre fordrar simulering.

Däremot kan det vara rekommendabelt att kolla resultaten mot teoretisk förväntan enligt teori för att öka säkerheten att simulatorn verkligen fungerat som förväntat och inte ”spårat ur” (tekniskt inte gör vad som förväntas). Acceptabel överenstämmelsen med teoretisk förväntan i vargjakt fallet ger inte underlag att befara att simulatorn inte fungerat eller matats på fel sätt, men antyder att

detaljförbättringar i funktionen är möjliga. Man kunde också testat att man använt simulatorn för att köra tester. En anekdot från mitt eget liv. Jag testade i samråd med utvecklaren vad som hände med urvalseffekten om man satte heritabiliteten (ärvbarheten) till noll, då genetiskt urval enligt teorin inte skall ge någon effekt. Men simulatorn hade tydligen inte läst grundkursen i genetik, för att urvalet förutspåddes få effekt. Det tog ett dygn för oss att komma på att simulatorns simulering av en genetiker var helt korrekt. När det simulerade materialet fick observationer under noll på heritabiliteten så betedde sig simulatorn precis som en förnuftig genetiker och satte värdet till noll, medan om värdet av slumskäl hamnade över noll så accepterade den förnuftiga simulerade genetikern det observerade värdet.

Det finns standardsimulatorer, men de är knappast möjliga att använda för detta problem. Hemsnickrade simulatorer kan göras väl anpassade till vad de skall simulera. Därför måste generellt simulatorprogram användas, som inte är allmänt tillgängliga, men väl anpassade för det speciella ändamålet, såsom vargförvaltning. De kunnigaste simulatoranvändarna använder oftast hemsnickrade simulatorer eller simulatorer där de står i direktkontakt med en som utveklar simulatorn och inte standardsimulatorer. Den som önskar testa reproducerbarheten kan säkert få simulatorprogrammet via författarna.