Genetic aspects of viability in small wolf populations

- with special emphasis on the Scandinavian wolf population

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Genetic aspects of viability in small wolf populations

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Report from an international expert workshop
at Färna Herrgård,
Sweden 1st – 3rd May 2002

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Abstract

The Scandinavian wolf (*Canis lupus*) population was re-established during the 1980's through natural immigration. The population is based on only three founders, one female and two males. The population has grown from eight animals in 1990 to about 100 animals in 2002. The population is isolated with a gap of approximately 800 km to the nearest source population in eastern Finland. There has been some controversy regarding how large a population of wolves in Scandinavia must be to stay viable also in the long term, and whether it at present is possible to allow any take out of wolves for damage control purposes. Because of its isolated situation, the most pressing problems for the viability of the population regard genetic aspects.

In an attempt to further clarify these issues and learn more about conservation and management of a small wolf population, an international expert workshop discussing genetical aspects of conservation of small wolf populations with emphasis on the recently founded Scandinavian wolf population was initiated and organized by the Scandinavian Wolf Research Project SKANDULV.

An expert panel consisting of six internationally well-reputed scientists was invited, including three geneticists (Fred Allendorf, Philip Hedrick, Curtis Strobeck), one population biologist (Mark Boyce) and two wolf ecologists (David Mech, Ed Bangs). Other invited participants were concerned Scandinavian scientists, conservation management personnel and representatives from NGOs. In all, 29 persons attended the workshop.

The workshop was held at Färna Herrgård in Västmanland 1 – 3 May 2002. During three days, the workshop discussed issues like the general importance of genetics in relation to other problems for small populations, signs and demographic effects of inbreeding, the effectiveness of purging, the need for long-term evolutionary potential for Scandinavian wolves, the theoretical and empirical basis for the so called 50/500 "rule", different ways of calculating ratio between genetically effective population size (N_e) and total population size (N), the usefulness and shortcomings of Minimum Viable Population estimates, and risks and possibilities of performing control operations in the small Scandinavian wolf population.

The most important conclusions of the workshop were:

- The Scandinavian peninsula (Sweden + Norway) is probably too small to hold a long-term (> 100 yrs) 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 (N_e/N) for Scandinavian wolves lies between 0.25 and 0.33.

- Even with a satisfying rate of immigration, the effective population size N_e should not be smaller than 50, i.e. 150 – 200 wolves in total with a N_e/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 200, giving a total population of 600 – 800.
- At the present size of 100 wolves, control operations removing less than five wolves per annum would not seriously jeopardize the viability of the wolf population, unless the target wolves were of special genetic value. If possible, this value therefore should be determined before killing. Larger culls should be preceded by a viability analysis (PVA).

Abstract (Swedish)

Sammanfattning på svenska

Vargen (*Canis lupus*) utrotades på den skandinaviska halvön i slutet av 1960-talet. Under 1980-talet uppstod en ny vargpopulation i mellersta Skandinavien genom naturlig invandring från Finland/Ryssland. Populationen är baserad på endast tre invandrande individer, en hona och två hanar. Populationen har växt från 8 individer 1990 till omkring 100 tio år senare. Den är isolerad från andra vargpopulationer. Avståndet till den finsk-ryska vargstammen, som ligger närmast och varifrån de invandrande är ungefär 800 km. Frågan hur många vargar som krävs för att denna isolerade skandinaviska vargstam ska vara livskraftig även på lång sikt har varit kontroversiell ända sedan den väcktes i mitten på 90-talet, liksom frågan huruvida det är möjligt att ta ut enskilda skadegörande individer utan att allvarligt äventyra stammens fortsatta existens. Genom sitt isolerade läge, har de genetiska frågorna stått i centrum för debatten om denna populations livskraft.

För att ytterligare belysa dessa frågor samt lära mer om bevarande och skötsel av små vargstammar, organiserades på initiativ av det Skandinaviska Vargforskningsprojektet SKANDULV ett internationellt seminarium för att diskutera de genetiska aspekterna vid bevarandearbetet för små populationer med särskild hänblick på den skandinaviska vargstammen. En panel med av några av världens främsta experter inom området inviterades. Denna grupp innefattade tre genetiker (Fred Allendorf, Philip Hedrick, Curtis Strobeck), en populationsbiolog (Mark Boyce) och två vargekologer (David Mech, Ed Bangs). Dessutom inviterades berörda skandinaviska forskare, personal från naturvårdsmyndigheterna i Sverige och Norge samt representanter för några ideella naturvårdsorganisationer. Totalt deltog 29 personer vid seminariet.

Seminariet hölls på Färna Herrgård i Västmanland 1 – 3 maj 2002. Under dessa tre dagar diskuterades ämnen som den generella betydelsen av genetiken i relation till andra problem för små populationer, tecken på och demografiska effekter av inavel, förekomst och effektivitet av rensning av skadliga gener genom selektion (”purging”), behov av långsiktig evolutionär potential för de skandinaviska vargarna, teoretiskt och empiriskt stöd för den s.k. 50/500-regeln, olika sätt att beräkna kvoten mellan total och genetiskt effektiv population (N_e/N), användbarheten hos begreppet Minsta Livskraftiga Population, samt risker med att bedriva begränsad skyddsjakt i den skandinaviska vargstammen.

De viktigaste slutsatserna från seminariet var:

- Den skandinaviska halvön (Sverige + Norge) är sannolikt för liten för att ensamt hålla en livskraftig vargstam på lång sikt (> 100 år). Därför bör åtgärder för att underlätta och främja invandring från den finsk/ryska vargpopulationen vara av högsta prioritet.
- Den smala genetiska basen, endast tre individer, för den nuvarande skandinaviska vargstammen gör denna rekommendation så desto viktigare.

- En eller två invandrande vargar per generation (ungefär fem år) skulle ge tillräckligt tillskott av genetiska variation för att säkra en långsiktig överlevnad för populationen.
- Kvoten mellan total och genetiskt effektiv populationsstorlek (N_e/N), ligger mellan 0,25 och 0,33.
- Även om en tillfredsställande invandringsfrekvens uppnås, bör den genetiskt effektiva storleken på den skandinaviska vargstammen inte underskrida 50, vilket skulle innebära 150 – 200 vargar vid en N_e/N-kvot på 0,25 – 0,33.
- Om man, trots alla ansträngningar, inte lyckas åstadkomma något ytterligare tillskott av genetisk variation till vargstammen, bör man försöka att bevara åtminstone 95 % av dess nuvarande genetiska variation för de närmaste 100 åren, vilket kräver en genetiskt effektiv population på 200, vilket skulle motsvara en total population på 600 – 800 individer.
- Vid den nuvarande nivån på vargstammen, runt 100 individer, medför skyddsjakt på upp till fem vargar årligen inte något allvarligt hot mot den fortsatta livskraften hos denna, förutsatt att inte någon av dessa individer besitter speciellt högt genetiskt värde. Innan skyddsjakt beslutas bör man försäkra sig om att detta inte är fallet. Om större uttag än fem vargar skulle anses nödvändig, bör detta föregås av en sårbarhetsanalys.

Foreword

This is a report from a closed scientific workshop at Färna Herrgård, Sweden, 1 – 3 May 2002. The aim of the workshop was to discuss genetic aspects of conservation of small wolf populations and come up with specific and practical conclusions that could be of help for the management of the Scandinavian wolf population. Invited to the workshop was an expert panel, consisting of six internationally recognized scientists, covering population genetics, molecular biology, theoretical population biology and wolf ecology. Other invited participants were concerned Scandinavian biologists, officials from government agencies in Norway and Sweden responsible for the management of large carnivores, and representatives from a couple of NGO's. The discussion part of the report has been reviewed and recognized in several steps by all the members of the expert panel , and the conclusions of the report have been agreed upon by the whole panel. The full responsibility for all details in the report however rests solely with the author of the report. The initiative to the workshop was taken by the Scandinavian Wolf Research Project SKANDULV, who also selected the participants and worked out the program of the workshop. The workshop was financed by Direktoratet for Naturforvaltning in Norway (the Norwegian Directorate for Nature Management) and Naturvårdsverket in Sweden (the Swedish Environmental Protection Board).

Background

The environment

The Scandinavian Peninsula consists of Norway and Sweden and covers approximately 770.000 km^2 (fig. 1). For the sake of brevity, in this report the Scandinavian Peninsula sometimes will just be called "Scandinavia", although the correct use of that term also includes Denmark, which is divided from the peninsula by the Sound and holds no wolves. In the northeast the peninsula is connected to the large Eurasian continent by a 400 km wide isthmus. Forest is the dominating vegetation. The peninsula is situated within the boreal forest biome with the southern tip of Sweden entering the transition zone to the nemoral broadleaf deciduous forest biome. Alpine tundra covers higher altitudes of the Scandinavian Mountain Range that comprises the north-south backbone of the peninsula and runs from southern Norway north along the border between the two countries. Forest and tundra covers around 85 % of the peninsula.

The northern and interior parts of the peninsula are sparsely populated by humans, and the majority of the 13 million inhabitants (Norway 4,4 and Sweden 8.9 million) live in the south and along the coasts, where most of the agriculture also is concentrated (fig. 1).

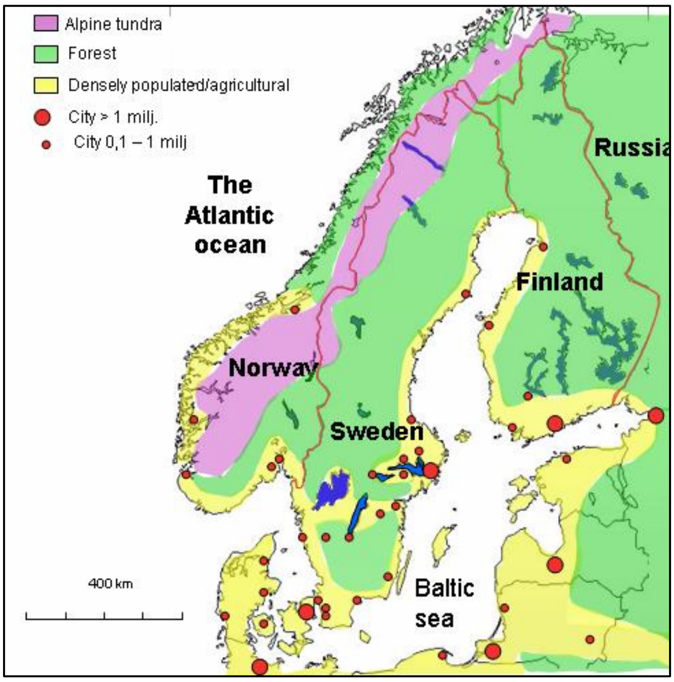

Figure 1. The Scandinavian peninsula and adjoining parts of north-western Europe.

Potential wild prey for wolves is abundant. Moose (*Alces alces*) occur all over the peninsula and numbers more than 300.000 head. Roe deer (*Capreolus capreolus*) total more than one million head, and are also widespread except in the interior of the northern parts. There are also substantial populations of wild reindeer (*Rangifer* *tarandus*) and red deer (*Cervus elaphus*) in southern and western Norway and smaller fragmented populations of red deer, fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) in southern Sweden.

Domestic reindeer husbandry occupies the northern third of the peninsula and involves approximately 400.000 year round free ranging domestic reindeer. During summer/autumn, around 2 million free ranging domestic sheep graze over large parts of Norway, with the highest densities in the mountain range and in western Norway. The much smaller sheep stock in Sweden is mostly confined to fenced paddocks. Large numbers of cattle and horses also graze in the open during summer in both countries.

In addition to wolves, other large mammalian predators in Scandinavia include the brown bear (*Ursus arctos*) that occurs mainly in the north and west of Sweden with a population of around 2000 animals, European lynx (*Lynx lynx*) that occurs over most of the peninsula except in southern Sweden and western Norway and numbers around 2000 animals, and wolverine (*Gulo gulo*) which has a fragmented distribution over mainly alpine habitats with a total population of approximately 400 animals.

The wolf population

By the year 1800, wolves occurred all over the peninsula and the population was continuous with the large Finnish-Russian population. During the 19th century wolves were pressed back from the south, and around 1920, they only occurred in the extreme north. They were declared a protected species in Sweden by 1966, and in Norway 1971. At this time there were fewer than ten wolves left on the peninsula, and no breeding was recorded after 1964. In the beginning of the 1970's the wolf generally was regarded as extinct in Scandinavia, although there were unconfirmed rumours of wolf occurrences in central Scandinavia along the Norwegian-Swedish border. By that time the wolf also was gone from most of Finland, which

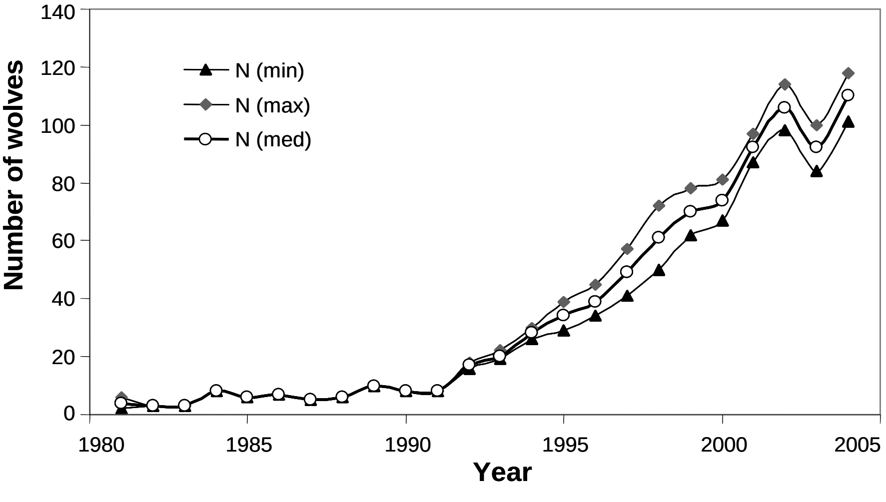

Figure 2. Annual estimates of the Scandinavian wolf population 1981 – 2004.

means that the nearest source population occurred in Russian Karelia along the eastern border of Finland. During the 1970's wolves expanded somewhat in eastern Finland, and by 1977 several wolves were recorded in northern Sweden, presumably immigrants from Finland/Russia. One record of breeding by wolves occurred in 1978 in this area, but the pack was scattered and some members killed during the following winter with the fate of potential survivors unknown.

However, in 1978 and 1979 there also came reports of tracks and sightings of two or three wolves in central Scandinavia. Successful breeding in this area was recorded in 1983, the first in this part of Scandinavia in almost one hundred years. This breeding was followed by several in the same territory, and 1991 was the first year with simultaneous breeding in two different packs.

Between 1991 and 2001 the Scandinavian wolf population was growing with an average rate of approximately 25 % per year (fig. 2, REF 27). By the end of winter 2004, there were 92 – 109 wolves in Scandinavia, including 11 packs and 11 territorial pairs (REF 4, 28). There has been a slow geographical expansion from the original breeding territory, and in 2002 the breeding range of wolves covered approximately 100.000 km^2, i.e. 15 % of the peninsula (fig. 3). The distance over land between the edge of this population and the source population in eastern Finland is approximately 800 km.

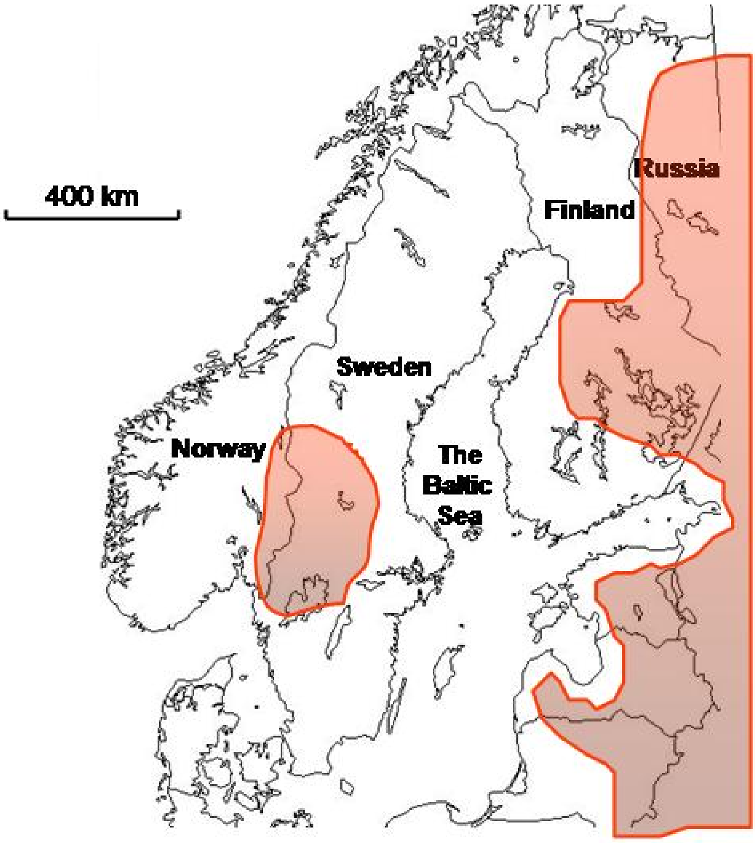

Figure 3. The breeding range of the isolated Scandinavian wolf population. Also denoted is the range of the large continuous East European wolf population in Finland, Russia and The Baltic states.

DNA-analyses of more than 100 wolves have demonstrated that the founders of the present Scandinavian wolf population were three wolves, all coming from the Finnish-Russian population (REF 26). Two of these founders started the population in 1983, and a third joined the population in 1991. The arrival of the latter sparked off a rapid increase in the population (fig. 2).

DNA-analyses coupled with field data have been used to establish a pedigree of the present wolf population. Average inbreeding coefficient for the youngest generation of wolves (born 2000 and later) in this population is 0,22 and increasing, while heterozygosity rate is 54 %, and since beginning of the 1990's is almost stable (fig. 4).

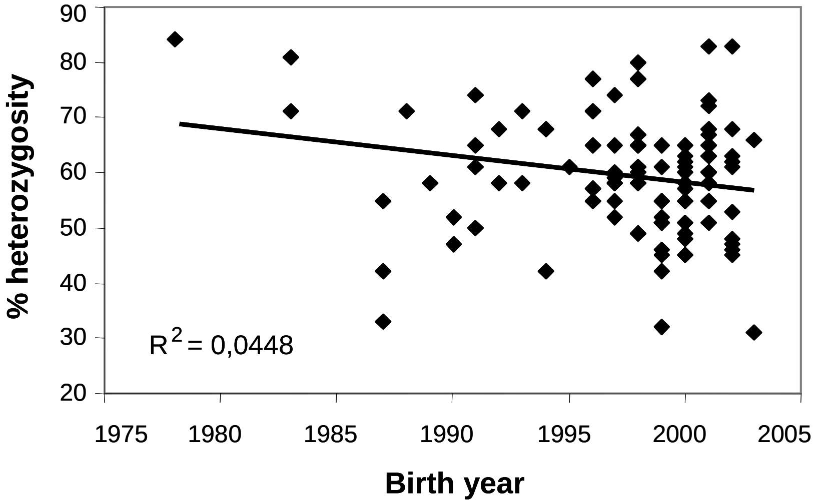

Figure 4. Degree of heterozygosity (%) in Scandinavian wolves in relation to birth year. Data are based on analysis of 31 nuclear microsatellites.

Wolf-human conflicts in Scandinavia

The nature of wolf-human conflicts in Scandinavia are typical for areas in western affluent countries where wolves recently have re-established a population after a long period of absence. Conflicts can be divided into five different categories: depredation on domestic reindeer, depredation on domestic stock other than reindeer (mainly sheep and cattle), killing of dogs (mainly hunting dogs), competition with human hunters for hoofed game, and human fear. They will here be briefly treated in turn.

Depredation on domestic reindeer is low, but this is a consequence of the official policy in both Norway and Sweden to keep wolves out of the reindeer management area. The Sami reindeer herders regard wolves as extremely detrimental to reindeer husbandry, not only because of depredation, but also due to their claimed tendency to scatter winter herds, thereby causing much extra work for the herders. According to most reindeer herders, modern reindeer management is almost impossible in areas where wolves occur regularly.

Depredation on sheep and cattle is low compared with southern and central Europe, but high compared with North America, and it is increasing. Table 1 gives the figures for the last few years in Norway and Sweden. However, the potential conflict with sheep husbandry in Norway is very high. The reason for depredation numbers so far being relatively low is that the Norwegian government in 2 – 3 years has spent more than NOK 30 million transferring sheep from forest and mountain habitats to fenced cultivated land away from two wolf packs which established in an important grazing area.

Table 1. Number of sheep reported killed by wolves and for which compensation has been paid, in Norway and Sweden 1997 – 2002. In the Swedish figures a few cases of killed cattle are included, but they never exceed 10 %. In Norway a large number (> 5 000) of sheep killed but not classified to a specific predator species are not included here, but most of those probably should be assigned to lynx, wolverine and bear.

Year	Norway	Sweden
1997	474	26
1998	422	18
1999	622	45
2000	827	90
2001	623	56
2002	1849	171

During the period 1997 – 2002 there was an increase in wolf attacks on dogs with as many as 27 attacks one year, mostly fatal (fig. 5). Killing of domestic dogs in most cases involved hunting dogs. In Scandinavia many of the traditional hunting methods, both for large and small game, includes use of dogs operating a distance from the hunter(s). Some of these dogs have very high market prices, and mostly they also have a high status in the owner family, treated and regarded almost as family members. The risk of losing a dog, although low, therefore is regarded by hunters as a very serious drawback.

Competition for game, foremost moose and roe deer, is possibly the least serious wolf-human conflict area. In large parts of the Scandinavian Peninsula, moose and roe deer are so numerous that even inside wolf territories there is still produced a surplus of these species that can be harvested by hunters. However, in areas with low productivity, there is a growing conflict between hunters and foresters on this issue. To minimize damage on young forest plants, forestry strives to reduce moose density to low levels whereby competition between hunters and wolves for moose may become acute.

Compared to other large carnivores of the same size and strength, the wolf seems unusually reluctant to attack human beings. Documented cases of fatal attacks in modern time are few (but not absent), considering the size of the world population of wolves (REF 22). Regardless of this there is a widespread personal fear of wolves among Scandinavians, as has been demonstrated by a number of questionnaires (REF 7, 12, 19). Often more than 50 % of the asked people declare that they are afraid of wolves. Typically women are more afraid than men, older people more than younger, and less educated persons more than higher educated.

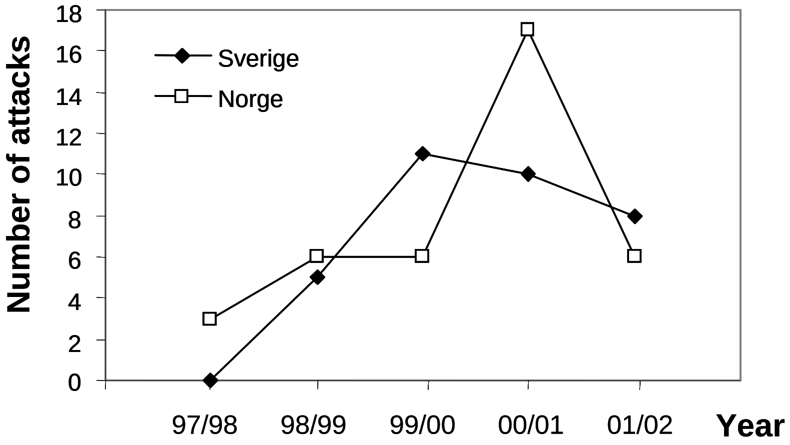

Figure 5. Documented wolf attacks on dogs in Sweden and Norway 1997 – 2002. Swedish data (filled symbols) from Viltskadecenter at Grimsö; Norwegian data (open symbols) are from local authorities (Fylkes-männen) in the counties Akershus, Hedmark and Östfold.

Research on the Scandinavian wolf

When the first wolves established in mid-Scandinavia in the early 1980's, their activities were followed and documented by both volunteers and authorized personnel. The principal method of this work was snow tracking (REF 27). Formal scientific ecological fieldwork on the wolf however did not start until in 1997. The first radiomarking of wolves for scientific purposes was performed in December 1998. By March 2003, a total of 48 wolves have been equipped with radiotransmitters. In January 2000 the cooperation between Norwegian and Swedish wolf research was formalized by creating the umbrella project: The Scandinavian Wolf Research Project, SKANDULV. Field studies have a broad approach, including demography, population expansion, predator-prey dynamics, socio-biology, and questions related to depredation and other conflicts with humans.

Genetic studies on the wolves in Scandinavia started in the mid 90's (e.g., REF 11), and several PVAs have been presented (REF 3, 9, 10, 18). Studies of the human dimensions of wolf management started very early with a questionnaire in Sweden in the 70's (REF 2) but have intensified during the last ten years (REF 6, 12, 24).

A list of scientific reports dealing with Scandinavian wolves is presented in Appendix 5.

Swedish Wolf Policy

Since 1964 the wolf has been a protected species in Sweden, and the country has ratified the Bern convention. As a member of the European union, Sweden is also obliged to comply with the Union's Species and Habitat Directive, which is very restrictive regarding protection of the wolf. In 1998 the Government initiated an investigation of how the future policy for the large predators bear, wolf, lynx, wolverine and golden eagle (*Aquila chrysaetos*), should be formulated. Based on the report of this investigation ("Sammanhållen rovdjurpolitik", SOU 1999:146) a new large predator policy proposal by the Government was passed by the Parliament in 2000 (Prop. 2000/01:57). This Predator Act states that as a first step the wolf population in Sweden should be allowed to increase until there are at least 20 reproducing packs corresponding to 200 individuals. After this goal has been achieved, a new consideration of the situation should be made before next step will be determined. The ultimate goal however should be that wolves occur in a long-term viable population in the country. Wolves should be allowed throughout the entire country, but reproducing packs should not be accepted in the so-called year-round grazing grounds for reindeer husbandry (largely the alpine areas in the Scandinavian Mountain Range in the northwest, including a forest belt immediately to the east of the range, in all covering around 20 % of the country, see fig. 1).

Before the intermediate goal of 200 wolves is reached, allowances to control damage by taking wolves should be very restrictive. During 2000 – 2003, only two allowances were given, and no wolves were shot. Damage to domestic animals caused by wolves is compensated to farmers by the local authorities ("länsstyrelserna"), who also are responsible for subsidizing predator-proof fences and other protective measures. They also are responsible for the annual censuses of large predators. Ultimate responsibility for the management and conservation of the wolf lies with the central government organ Swedish Environmental Protection Agency SEPA, which also decides on control actions. The legislation against illegal killing of large predators was strengthened in the new predator policy. Despite this, there are indications that illegal killing of wolves is presently increasing.

Norwegian wolf policy

In Norway the wolf has been a protected species since 1971. Norway ratified the Bern convention, but because Norway is not a member of the European Union, it is not obliged by the Union's Habitat Directives. Norway has a somewhat different situation regarding predators than Sweden. The main reason for this is the large number of domestic sheep, around 2,1 million free ranging and 0,4 million fenced. This has forced politicians to a more restrictive predator management. At present, Norway has a zoned wolf policy. The wolf zone covers approximately 40.000 km^2 (13 % of the country) in the southeast, along the border to Sweden and in areas south and west of Oslo. Within the zone, a number of wolf packs should be accepted. Hence, livestock owners will have to accept a certain amount of damage to their animals, and control removal of wolves is restrictive. Outside the zone, reproducing wolves (pairs and packs) should not be accepted, and tolerance towards wolf-caused damage is generally low. Allowance to kill a damaging animal might be given promptly, depending on the total wolf population status. During the period 2000 – 2003 sixteen wolves were legally killed under control allowances in Norway. Most of these were taken out during winter 2001 in a control operation against one pack which had established in an important grazing area outside the management zone. All damage caused by large predators, both inside and outside the wolf zone, is compensated by the Norwegian government.

Norway has not yet defined a definite minimum level for its wolf population. Its policy at present is based on the principle that Norway and Sweden together shall have a long-term viable wolf population, and that Norway shall take responsibility for a lesser part of this population. Also, policy states that the predators must not jeopardize the sheep and reindeer husbandry. However, Norway is at present reconsidering its large-predator policy. The government has asked for a number of expert reports to use as a basis for its new white paper to the parliament. These reports were sent to the government during winter 2003 and the white paper is now under preparation. Norway's large-predator policy is expected to be treated by the parliament during spring 2004.

The problem

When determining so called Minimum Viable Population levels (MVP) one must consider both demographic and genetic risks for extinction in relation to population size. The demographic extinction risk is relatively straightforward to calculate if data on reproduction and mortality and their variances are available. Calculation of risk to extinction attributable to genetic factors is more complicated. The most accurate way to do this would require data on occurrence and frequency of all lethal and sub-lethal alleles present in the population, information that almost never is available. What is normally done instead is to make assumptions on this. The result thus is dependent on what assumptions are made. Another unfortunate consequence of small population sizes that can be calculated is loss of genetic variation to genetic drift. But still there is a lack of information on how extinction risk is correlated with loss of genetic variation. Instead conventions have been used. One such convention is that the inbreeding level should not increase more than 1 % per generation. Another more demanding convention is that the population should retain its full evolutionary potential, i.e. loss of genetic variation should not be faster that creation of new variation through mutations. The problem with such conventions is that they to some extent are arbitrary, and cannot be translated into hard figures on extinction risk.

These difficulties with calculating genetic criteria for MVP has led to practical problems for the management of the small Scandinavian wolf population in both Norway and Sweden. Because the wolf is an unusually controversial animal species which even at low numbers arouses resistance and non-acceptance especially among concerned local people, the level of MVP has become a hotly debated issue. The precaution principle (“försiktighetsprincipen”) means that to be on a safe level you add some extra individuals, or even double or treble the calculated viability level (REF 8). For a controversial species like the wolf however, there is probably less acceptance for such extra caution, and what is required is therefore a more exact calculation of the minimum needed for viability.

The MVP levels for Scandinavian wolves used so far by the authorities were calculated under great time pressure (REF 3). The demographic risks were based on earlier calculations when few data on Scandinavian wolves were available, and the genetic levels were based on the widely used so called “50/500-rule” (REF 13). Also missing is a proper analysis of risks of shooting animals in control operations, before the population has reached a viable level. A disagreement regarding risk assessment became apparent between population geneticists and wolf ecologists during the famous “Namsrett” court trial in Oslo (capital of Norway) in January 2001. Three ecologists from the Scandinavian Wolf Research Project SKANDULV, called in as expert witnesses, accepted a decision by the Norwegian government to take out a whole pack of wolves, while the single geneticist also called as witness, did not. Such an intra-scientific disagreement is of course unfortunate.

Because of this disagreement and because the level of the MVP for Scandinavian wolves, and the ability of the wolf population to withstand control reductions, will be questions of great concern for managing authorities for a long time to come, it was suggested by SKANDULV that these issues should be clarified by calling in international experts with the best competence available in the field. It was decided that the discussions should take the form of a workshop with a very strict agenda. The idea with this workshop was supported by the Coordination Group for Large Carnivore Research in Fennoscandia, and financed by The Environmental Protection Agency (Naturvårdsverket NV) in Sweden and The Directorate for Nature Management (Direktoratet för naturförvaltning DN) in Norway. Three well reputed and experienced conservation geneticists, Philip Hedrick, Fred Allendorf and Curtis Strobeck, one theoretical population ecologist, Mark Boyce, and two wolf biologists, David Mech and Ed Bangs, were invited from North America, the continent with the longest scientific experience with wolves. These six experts formed the so called "expert panel" (for full details about the panel see Appendix 3). A limited number of concerned Scandinavian experts and management officers, as well as a few representatives from NGOs also were invited. All participants are given in Appendix 3.

The workshop took place at Färna Herrgård in Västmanland, central Sweden during 1 – 3 May 2002. Chairman at the workshop was professor Per Lundberg, Dept of Theoretical Ecology at Lund University, and secretary was Jens Karlsson, Grimsö. Olof Liberg was coordinator at the meeting, and author of this report.

Aims of the workshop

1) To clarify and update the state-of art of conservation genetics with emphasis on wolves, especially the Scandinavian wolf population, and its role for determining the Minimum Viable Population size for wild wolves in Scandinavia.
2) To transfer the most recent international, especially North American, experiences with wolf conservation and management to Norwegian and Swedish scientists and managers.

Report of the discussions

A general introduction to the discussions

There might occur several different types of genetic problems for small populations. Perhaps the two most important categories, which also were those two focused on in this workshop, are inbreeding depression which has an effect in the short time horizon, and loss of genetic variation that might cause problems in the long run.

The problem with inbreeding is that harmful genes might have an increasing effect on the population. With the exception for genes on the sex chromosomes, genes always occur in pairs, sitting opposite to each other on the double-stranded DNA-string (also called the chromosome). Their place on the DNA-string is called the gene's locus (plural loci). The two corresponding genes of the same locus are also called alleles. As all sexually reproducing organisms inherit one half of the double DNA-string from the mother and the corresponding other half from the father, they always get one allele in an allele pair from mother and one from father Harmful genes, or rather alleles, are normally recessive, which means that they only express themselves (have effect) when they occur in double (homozygous) form, i.e. the animal has inherited them from both father and mother. In large outbred populations the risk of getting the same detrimental recessive allele from both father and mother is negligible, but in small populations where animals become increasingly related to each other this risk increases. The closer related the animals are, i.e. the stronger the inbreeding is, the larger this risk is. This situation will be aggravated in small populations by genetic drift. Genetic drift is a random process that affects the frequency of different alleles. In a very small population detrimental genes might by genetic drift increase in frequency and even become fixed (occur in homozygous form in all animals in the population and thus also affect all animals in the population) with no other possibility to get rid of them than by new mutations or new animals brought into the population.

The second genetic problem for small populations, dealt with in the workshop, is loss of genetic variation. There are two aspects of genetic variation. The primary aspect is the number of different alleles per gene locus in the population. Although each individual can carry only two alleles at each gene locus, there might occur many more than two alleles for each locus in the whole population. The secondary aspect of genetic variation, partly depending on the primary (see below), is degree of heterozygosity (a heterozygous locus is the opposite of a homozygous, i.e. the two alleles on the locus are different from each other). So, for a given sample of gene loci, genetic variation in a population can be expressed as either average number of alleles per locus, or percentage heterozygosity. Degree of heterozygosity of course is coupled to number of alleles. The fewer alleles at a certain locus, the lower the probability that an individual will be heterozygous at that locus. The extreme case is when there is only one allele left in the population. In that case all individuals are homozygous at that locus and the allele occurring there is fixed, as already described above.

In a newly established population, number of alleles is limited from the start by the number of founders. For the Scandinavian wolf population the number of founders was three individuals, which means that in the population there can exist maximum six alleles for any gene locus. For most loci the number is less. This is the immediate loss of genetic variation that will occur in all newly founded populations, or those that go through a narrow bottleneck. It only concerns number of alleles. Through genetic drift, and to some extent also selection, the loss of alleles will continue at a slow but steady pace, as long as the population remains "small". Degree of heterozygosity will not be affected directly during the bottleneck or founding event, but will after that also degrade slowly as long as the population stays "small" (what is regarded as small is discussed later in this workshop). This continuous loss of genetic variation is faster the smaller the population is. For this reason it is important to ensure that the population will grow as fast as possible to such size that this process has a minimal affect.

Loss of genetic variation is not necessarily dangerous for the immediate survival of the population. Everything might go well even for a very long time period until suddenly something changes, a new parasite or predator appears, or the climate changes. A population that has lost most of its genetic variation has a much lower probability to cope with such changes, i.e. its ability to genetically adapt to a changing world is reduced. This is what we call loss of evolutionary potential.

In this workshop we were dealing with these two categories of genetic problems in turn, beginning with inbreeding (after a short discussion of the general importance of genetics in conservation work). A third problem might be so called mutational meltdown which was dealt with very briefly, as it turned out that this might be a problem only in a time perspective of several hundreds of generations.

The workshop then went on to discuss the practical handling of a small population with a special eye on the Scandinavian wolf population. The so called 50/500 rule was scrutinized, and then the usefulness of the Minimum Viable Population (MVP) concept was discussed. Finally we also used some time to discuss risks and implications of culling individuals in a wolf population that is growing but still far below what can be regarded as a long-term viable level.

For clarification most sections are introduced by a short formulation of the question at issue. These parts are formulated by the author of this report, who takes the full responsibility for statements made there. In the Discussion parts, the report author, based on the official memo of the meeting, complemented by private memos taken by Scott Brainerd, Torbjörn Nilsson and Håkan Sand, have tried to recall the most important and relevant parts of the discussions. This means that the statements made during the workshop have been sifted through the mind of the author. To avoid important omissions and false accounts to what actually was said, this report has been reviewed in several steps by the members of the panel, and also by some experts in the audience. Especially Torbjörn Nilsson is thanked for a large effort in improving the report. The panel members have been asked to approve all statements made in their personal names, or as a group (e.g. the geneticists in the panel). Statements which are not attributable to any specific person or group, was not opposed by anyone during the meeting, unless explicitly written out. The conclusions have been approved by the entire panel, unless explicitly written out in each case.

During the course of the workshop, it turned out that it was not feasible to exactly follow the agenda and the work form lined out in the final invitation (see Appendix 1), although most of the themes listed there were treated.

As this is not a literature review, but an account of an oral expert meeting, literature references have been limited to a minimum. References are given as numbers within brackets (e.g. REF 1), and are listed in the end of the report.

What is the role of genetics in relation to other problems with conserving small populations?

The question

We began the workshop with a general discussion of how the different members of the panel viewed genetics in relation to other problems for small populations.

Discussion

There was a short discussion on this issue, and everybody in the panel agreed that genetics in principal indeed is important when working with conservation of small populations. Genetics contributes to the overall picture and should be included in the evaluation of the particular situation. It is possible that genetics may be of lower priority than, say protecting the animals from poachers if poaching is an acute danger threatening to eliminate the whole population within a short time. However, where the animals are protected from immediate threats like over-harvesting or poaching, introduced species or habitat destruction, but still are few in numbers, then genetics may become an important concern.

The panel also agreed that inbreeding is one factor of immediate concern in conservation of small populations.

However, it was stated that the magnitude of genetical problems for small populations vary from case to case, depending for example on number and genetic diversity of the founders of the population.

It was pointed out that genetic problems often cannot be entangled from other factors, like random demographic effects, as different negative effects may act synergistically (Phil Hedrick: “As the population gets smaller, inbreeding may reduce reproduction or survival and this in turn will reduce population further, which will aggravate the inbreeding and so on.”). This is what has been called the extinction vortex (REF 15).

What initial indications of inbreeding depression should we look for?

The question

If for some reason a population is kept at such low level that inbreeding occurs, are there any specific indications of beginning inbreeding depression that we should look for, as an “early warning”?

Discussion

The answer from the geneticists was that there are no specific diagnostic characters or traits, such as litter size or body measurement that will give “an early warning”. Detrimental effects of inbreeding could occur in any form and cannot be predicted. Therefore the experts recommended a broad continuous monitoring of life history traits and veterinary variables, like size and other body measurements, fecundity, survival, longevity, malformations, diseases, deficient immune reactions and other abnormal conditions. Urine can be collected from wild wolves to measure health parameters. So called "fluctuating asymmetries", i.e. asymmetries in bilateral traits like teeth or skull sutures, may be sensitive to inbreeding.

Continuing DNA-analyses, to detect changes in degree of heterozygosity and loss of alleles will supplement this monitoring.

Make sure that data are standardized so that comparisons can be made between individuals and over time.

Examples given of inbreeding effects found in large carnivores are reduced body size (captive Mexican wolf *Canis lupus baileyi*), blindness (captive Scandinavian wolves), deformities in vertebrae and other skeletal parts (wolves on Isle Royale), undescended testicles, reduced sperm quality, heart defects, fur malformations ("cow licks"), and kinked tails (Florida panther *Felis concolor coryii*). Further examples are given in REF 20 and 21.

It was pointed out that once effects are seen it might be too late to do anything about them, except to bring in new animals as fast as possible. Several times during the discussion it was stressed that the best way of avoiding problems with inbreeding is to ensure a gene flow from outside. One or two animals per generation that contribute significantly to the population will be enough (a wolf generation is approximately five years; ed.'s comm.).

How does inbreeding reduce population growth?

The question

The question was raised whether we can identify any specific mechanisms through which inbreeding reduces population growth.

Discussion

It is a general experience that the increasing degree of homozygosity which is an inevitable consequence of genetic drift in small populations, often is accompanied by lower population growth. As with signs of inbreeding depression, it is however impossible to point out any specific factor that is the prime mechanism through which inbreeding will lead to a retarded population growth. Sometimes it might be caused by the effect of one or a few strongly detrimental genes that have increased in frequency, but often it might as well be the consequence of the concerted effect of many genes each one with a small negative influence in homozygous form.

It was asked whether it is possible to define what is here meant by a "small population", whether it is possible to put any practical definition to this concept. The answer from the geneticists was that that it is not possible to give an exact definition of this concept. There are no magic thresholds or levels for any of the processes that makes small populations vulnerable to genetical problem, although there are some rather useful guidelines (these will be discussed further in the section on the 50/500 rules"). What exact problems we will get and how serious they will be, will vary from one population to another and from one situation to another. Maybe the only rule is "the smaller the worse, and the quicker the population grows out of its smallness the better". This discussion will also be extended in the section on Minimum Viable Populations. Dave Mech wanted to stress that we now have several examples of rather long records with small populations of large carnivores, including wolves, but yet no clear case where this has lead to the extinction of a population. Carles Vila however pointed to examples from other organisms like butterflies and possibly also from wolves (see next section).

Can "purging" of detrimental genes by natural selection and/or genetic drift counteract negative effects of inbreeding?

The question

One problem with a small population is that detrimental genes might increase in frequency through genetic drift. The question was to what degree this might be counteracted by natural selection "purging" the population of such harmful genes.

Discussion

There are four forces that change frequencies of genes: selection, drift, mutation, and migration (REF 5). Mutation and migration can introduce new genetic variation into a population. Of interest here are the other two forces, selection and drift, which tend to reduce variation by making some alleles disappear and others to become fixed in the population. An important difference between these two forces is that natural selection has a direction while genetic drift has not. Natural selection by definition reduces or eliminates detrimental genes (unless these genes at the same time also have positive effects that might dominate in a certain environments) while having no effect on neutral genes. Genetic drift is a random process that affects all genes regardless of whether they are beneficial, detrimental or neutral. Natural selection thus is more important than genetic drift in purging a population but the outcome is determined by the relation between the size of the population and the strength of the selection pressure. The smaller the population, the larger the effect of genetic drift (random processes) and the less efficient is the process of natural selection, while on the other hand the more harmful a gene the stronger the selection pressure against it. The same principle determines whether a certain detrimental gene will become fixed which is the opposite from being purged (Kjell Wallin: "Really bad genes don't get fixed, slightly bad genes do."). However, in very small populations where random processes are important, even rather bad genes may become fixed. Genes that have only slightly negative effects in one environment might be more harmful if something changes in the environment.

There are few studies of purging in natural wild populations. Among these, there are examples that purging indeed might work, but also examples of the opposite. There are also examples that drift might eliminate harmful genes, just as there are cases where drift has fixed such genes (REF 16, 21).

In weighing the different possibilities against each other, the general conclusion of the geneticists in the panel was that purging does occur but it will be too weak to be of much importance in small populations of wild animals, including the present Scandinavian wolf population.

Is it likely that inbreeding is or will be a problem in the present Scandinavian wolf population?

The question

Here the workshop turned specifically to the Scandinavian wolf population, to discuss whether there already might be, or can be expected to appear any serious problems with inbreeding in this population.

Discussion

On this issue a clear dividing line appeared between the opinions of the ecologists and the geneticists in the panel. The ecologists pointed to the fact that the Scandinavian wolf population appears healthy in all aspects, body measurements show no abnormal deviations and the population growth rate is normal. They also claimed that inbreeding problems have not been observed in any of the small wolf populations of which we have records (Mech: “Wolves are one of the best studied wildlife species in the world. Still, there are no hard data indicating negative effects of inbreeding in wild wolf populations. The growth rate for the Swedish wolf population is acceptable. Is it showing any negative signs on its growth rate? No! This is an example of practical issues versus theoretical. Be pragmatic. What counts is the demographic picture. Genetics usually are not that important except in the long term.”). Against this optimistic view stood a more gloomy picture from the geneticists, who pointed out that even if no problems have been observed so far the danger is not over and there is no “either/or” between demographic and genetics but “both/and”. Serious inbreeding effects have been seen in captive wolves like the Swedish zoo population (REF 21).

Carles Vila also reminded of two small Spanish wolf populations that recently have gone extinct, possibly for genetic reasons. Mech responded by noting that there was great human pressure on these populations. Vila admitted that it is not known whether these populations died out primarily because of persecution and lack of habitat, or inbreeding problems, but his point was that we may not know all possible cases where small wolf populations have gone extinct due to genetic problems or not.

Fred Allendorf stated that there are methodological problems with measuring inbreeding effects and it is hard to study fitness differences in the wild (“You don’t have a control with which to compare population growth and morphology to be able to say whether these factors are affected or not. To observe inbreeding effects you need to introduce animals from outside into the same environment. You cannot compare between different populations.”). However, there was consensus by the entire panel on the opinion that the best way of avoiding future inbreeding problems is to ensure gene flow from outside (Bangs: “Promotion of dispersal in an early stage will save a lot of trouble in the future.” Allendorf: “These wolves are inbred. The question is, how connected are they with a larger population? Is there a gene flow from east? This is the key issue here.”).

Is retention of evolutionary potential important for conservation of the Scandinavian wolf population, and if so, how is it achieved?

The question

Now the workshop turned to questions regarding loss of genetic variation. This is one of the most controversial questions in the whole wolf conservation issue in Scandinavia. If it is considered necessary that the wolf population should be able to genetically adapt to unforeseen problems in the future, like new diseases or parasites, i.e. to have an evolutionary potential, it must not lose more of its present genetic variability, and preferably also obtain some new. If the population is isolated from other wolf populations, this means that it has to be large enough to compensate for loss of variation through drift and selection by creating new variation through beneficial mutations. This means a very large population size (exactly how large is discussed later). It has however become apparent in the Scandinavian wolf debate, that claims for a large wolf population tend to reduce acceptance of wolves in large sectors of the local human population in areas where wolves live, causing social and political tensions and conflicts.

Discussion

It was questioned from the audience whether it is reasonable to demand that every subpopulation of a large metapopulation, such as the world wolf population, should retain a full evolutionary potential. It was also claimed that "a metapopulation consisting of several small inbred populations may have greater evolutionary potential than one large with large variation" (Wallin). However, in answer to the latter, Torbjörn Nilsson pointed out that we should differentiate between "1. evolutionary potential to cope with environmental changes and 2. evolutionary potential that might lead to speciation". He claimed that it is the first mentioned that we are dealing with here, while the type Wallin was bringing up was of the latter kind.

The geneticists in the panel insisted in unison that if we want to maximize wolf survival in Scandinavia in the long time perspective, we must consider evolutionary potential. However, they agreed that ”Scandinavia is too small to have evolutionary potential in its own population, only by gene flow it is possible" (Allendorf). "The alternative is not a large population, but connection with a large population" (Curtis Strobeck).

To highlight this question, the geneticists in the panel were asked specifically which of the following two options they would recommend if there was a limited amount of money to spend on wolf conservation:

1) spend all the money on the costs of holding a large isolated population *or*
2) keep the population at a lower level where costs and conflicts were lower and instead use more resources on promoting a gene flow from outside.

The unanimous answer was that the latter option (the gene flow) absolutely was preferred. This was not only because the latter might be a more efficient use of managing resources but because the number of founders has been so extremely low (3 animals) that the genetic variation from the start was strongly limited, and from this low input of genetic variation we probably by now have lost another 20 – 25 %. So, even if all the variation that is still left could be conserved in the population, it might turn out not to be enough. This issue will be further discussed in the section on "Genetic bottleneck".

After this the discussion came to deal with immigration. It was agreed that swamping of local adaptations in Scandinavia by massive immigration or translocation of wolves from outside is not a problem at present. It is not likely that we yet have got any local adaptations in the population because of its recent origin, and it was founded by wolves from the same wolf population from where we can expect new immigrants. Thus, Mech failed to see how problems with swamping local adaptation would be an issue worth even to be raised or discussed. Still, Allendorf warned that it might be best not to wait too long before ensuring immigration of new wolves: "If we wait and then move in 10 – 20 wolves we might swamp the local adaptations. 1 – 2 immigrants per generation can preserve the possibility for local adaptations without disturbing it."

Mutational meltdown

The question was brought up whether so called "mutational meltdown" might become a problem to watch for in the Scandinavian wolf population. This phenomenon was first described by Wright in 1931 (REF 29) who suggested that small populations would continue to decline in vigor slowly over time because of the accumulation of deleterious mutations that natural selection would not be efficient in removing because of the overpowering effects of genetic drift. As deleterious mutations accumulate, population size might decrease further and thereby accelerate the rate of accumulation of deleterious mutations. However, it was clarified that the time scale is much longer than that for the impact of other factors and mutational meltdown would not, even in the most extreme case, be important even in the next few hundred of generations (next several centuries).

For how long time after a genetic "bottleneck" period can we expect to see effects from it?

The question

A genetic "bottleneck" here is defined as a limited period during which the population is so small that there is an immediate risk for inbreeding and loss of genetic variation through drift. The Scandinavian wolf population can be considered to recently have passed through a bottleneck (and possibly still be in it, as there is no universal definition of what constitutes the limits of a bottleneck).

Discussion

For most aspects "long-term effects of a bottleneck may not be so important" (Hedrick) and "if you have not seen any effect in 25 – 30 yrs it won't affect the population, just single individuals" (Strobeck). However, it also was pointed out that "possibly you might get late effects from unexpected environmental changes, e.g. increased stress as demonstrated by the Drosophila-temperature experiment" (Hedrick). Because the Scandinavian wolf population is based on only three founders, its members probably already are more sensitive to environmental changes than wolves in the source population. For example it was pointed out by Carles Vila that the variation in the so called Multi-Histocompatibility Complex MHC, i.e. genes involved in the animal's immune defence, is much lower in the Scandinavian wolf population compared with larger populations like the Finnish-Russian. This is a deficiency that cannot be cured by allowing the population to grow to a large size, as long as it is isolated. The only remedy is that these lost or missing genes are brought in from outside. Thus, again the importance of a gene flow from the east was stressed.

Are genetic risks for extinction possible to quantify in the same way as demographic risks?

The question

The risk (or probability) that an animal population will go extinct within a certain time period is the product of the interaction between environmental, demographic and genetic risks (REF 17, 23). Environmental risk can to some extent be calculated based on historical statistics of e.g. climate cycles and natural catastrophes like storms, earthquakes, forest fires, trajectories of habitat loss, etc. Demographic risks can be quantified more accurately once you have data on all the relevant demographic variables (age-specific fecundity and survival etc) and their standard deviations. Although not easy, these data are possible to collect. The question here was how far it is possible to quantify genetic risks, and their interaction with other risk sources, with hard figures.

Discussion

Again, there was some discord in the panel. Mark Boyce claimed that there is insufficient basis for connecting demographic and genetic extinction risks. Allendorf agreed that we cannot calculate genetic risk in the specific case unless we have very good information of the genetics of the founders, e.g. average number of lethal equivalents, which is rarely the case. But you can incorporate assumptions of inbreeding depression into demographic risk models, as for example is done in the computer program Vortex. Strobeck added that also demographic models usually are uncertain and putting in the genetics will not make them much worse. Hedrick claimed that even if we do not have a correlation between genetic variation or inbreeding coefficients and extinction risk, we know that inbreeding potentially may affect any of the demographic variables. Data from wild wolves have until now not been detailed enough to use but there is extensive data from livestock and laboratory animals suggesting that fitness components are generally reduced in a linear

way as inbreeding increases, so that an inbreeding coefficient of 0,1 will give a 10 % reduction in viability. This prediction is relatively straightforward.
It was asked whether inbreeding coefficients and viability data from the wild Scandinavian wolf population could be used to test this for wolves, to which Allendorf answered yes, and added that also data from captive wolf populations could be used here, assuming that detrimental effects (such as blindness) will have stronger impact on vitality in the wild than in captivity.

The general conclusion of the discussion, however, was that we still lack a mathematical function that explicitly describes the extinction risk in relation to genetic variation.

What is the present status of the “50/500 rule”?

The question

The so called 50/500 rule or principle (REF 14, 25) states that to ensure population survival in the short time horizon the genetically effective size of the population should be at least 50 to avoid serious inbreeding depression, while for survival in the long time horizon (100 years and more) the effective population size should be minimum 500 to ensure enough genetic variation to retain evolutionary potential. The 50/500 rule has now been in use for some time, and the questions posed here were what basis it has in real data, and whether it still is regarded as valid and useable in present day conservation genetics.

Important here is the ratio between genetically effective size of the population (N_e) and actual population size (N) and. The latter is normally between 2 and 10 times larger, dependent on species and situation. For calculation of N_e/N for wolves, see next section, and Appendix 3.

Discussion

From the start the geneticists made clear that the 50/500 principle should not be regarded as a “rule” or “law”, these figures are only guidelines, but as such quite useful when dealing with isolated populations. (Allendorf: “If N_e is larger than 500 no worries about genetics, if N_e is smaller than 50 it should raise a warning flag.”)
There seemed to be unanimous opinion in the panel that the 50 level for securing short time survival has a strong empirical basis from many different groups of animals, including large mammals, e.g. livestock and zoo animals.

For the 500 level, there was more disagreement. Boyce had no problem with the 50 level “because it has an empirical basis in livestock breeding as well as island studies of birds, but the 500 number is virtually pulled out of the air and has little to no basis in theory or empirical data”. Here he also referred to a review of the theory behind the 500 rule by Ewens 1990 (REF 13).

Professor Öje Danell with large experience from genetics of livestock also supported the 50 level from his and others work with captive animals, but explained that the 500 level is not used for livestock because of the long time horizon. To this it was argued that there indeed is some empirical evidence for the 500 level.

Allendorf stated: “the original 500 number was based on estimates of mutation rates and heritability in one Drosophila character. I believe that 500 is a helpful guideline regardless of Drosophila mutation rates and heritabilities”. Hedrick also stressed that “there is some empirical evidence for an effective population size of 500 being relevant. It was derived from the assumption that increase of genetic variation from mutation and loss of genetic variation from genetic drift would be nearly equal at this level so that future potential for adaptation would be retained”. He even claimed that new insights indicate that 500 is not enough (“further examination of the assumptions of this model suggests that to retain adaptive potential, an effective size even higher than 500 may be necessary”). To a question what assumptions were made in this model, Hedrick’s answer was: “All input variation from mutation is useful for future adaptation.” Allendorf and Hedrick were in agreement that these general guidelines are thought to be independent of species.

When Boyce persisted in his view that “for the 500 level there is no threshold or data to support it”, Hedrick admitted that “we would prefer to base Scandinavian wolf management on data more relevant to wolves than Drosophila studies, if such data had been available”, but he also claimed that there are more estimates done on mutational input from a number of different organisms and traits to generally support the 500 level since the original work on Drosophila. One problem here however is that variance estimates for mutational input are large and should be taken into account when applying the 500 level. In a later comment to the preliminary draft of this report, Boyce has developed his comment on this issue: “Given that empirical estimates of mutational input rates vary over at least 2 orders of magnitude, the implication is that this upper population guideline reasonably ranges somewhere between 50 and 5000. Therefore I do not find this to be a useful guideline that has any utility in conservation application.”

Allendorf also reminded that for large mammals empirical tests of the applicability of the 500 level would take hundreds of years.

However, regardless of the relevance of the 500 level, several members of the panel stressed that genetic input from outside is more important. Hedrick: “In particular situations, new variation just as well may be introduced from gene flow as from mutation. Actually, 4 or 5 immigrating animals over a 20 year period would be more important than mutations”. This was supported by Strobeck who claimed that immigration of new wolves from the east is so important that the 500 “rule” is not relevant for the Scandinavian wolf population.

Is the MVP concept useful for wolf conservation?

The question

The calculation of so called “Minimum Viable Population” estimates (MVP), has been a popular exercise within conservation biology for some years, and has been enhanced by the introduction of simulation computer programs for viability analyses, like Vortex. MVP is of course a handy tool for managers and politicians, giving them concrete figures to aim at in policy documents and management plans.

However, there are also several snags with using MVPs as management tools. The aim of the discussion here was to scrutinize problems with MVPs in an effort to evaluate the usefulness of this concept for the conservation of the Scandinavian wolf population, and see if there are alternatives.

Discussion

The panel agreed that one problem with MVP estimates is that the criteria they build on are arbitrary (time frame, acceptable levels for risk and retention of genetic variation, different assumptions of variation and of genetics, etc.). As Mech exemplified, this has led to a number of different answers from questioned experts of what constitutes an MVP for the small wolf populations that occur in USA south of the Canadian border. One common factor however that turned out in this questionnaire was that it is essential to keep a little bit of connectivity with the large Canadian wolf population.

Boyce pointed at the problem with variation when you extrapolate demographic variables far into the future. A time horizon of 100 years will give confidence intervals for extinction risk including 0 and 100 % which a number of ecologists have argued makes the function useless. Torbjörn Nilsson responded that conservation biology is faced with the question of how many animals are enough for long-term persistence, and we cannot get away from this question; therefore our responsibility as researchers is to suggest MVP criteria and make clear their arbitrariness, provide our best possible estimates of MVP under those criteria, and describe the uncertainty of those estimates.

A way to circumvent the problem with large confidence intervals, suggested by Henrik Andrén, would be to produce MVPs with much shorter time frames, say 10 or 15 years, and accept lower extinction risks, say 0,5 or 1 % instead of 5 or 10 %, which gained support by Boyce. However he also warned that “predicting such low probabilities of extinction might give managers the wrong message”. Allendorf also warned against short time frames, pointing at a recent grizzly bear study where extinction risk increased more than proportionally with increasing time span, suggesting that short-term predictions will be insufficient (REF 1).

Mech objected against the long time frames in many MVPs. He reminded of the enormous cultural, demographic, social, political and environmental changes that have occurred over the past 100 years, and found it naïve to plan for the next 100. Boyce did not entirely agree with this, pointing at the long planning periods within forestry. He also added that “ given historical trends, we have every reason to believe that society will be more sensitive to wildlife values in the future”. Ed Bangs thought that in the short term perspective it is biology that matters for viability of wolf populations, but socio/political aspects determine the long-term viability. He also pointed out that “once we start to manage the population, the parameters used in models for predictions are changed“. This was supported by Boyce who added that “with a species of high profile such as wolves, management intervention is quite certain”.

Boyce recommended habitat based viability analyses, to give reasonable measures on MVP. When several people both in the panel and audience objected that habitat is not a limiting factor for wolves in Scandinavia, Boyce's response was that "this is beside the point. Predicting the future distribution and potential abundance of wolves on the landscape can be exceedingly important in anticipating management alternatives".

The criterion that usually gives the highest estimates for wolf MVPs is the demand for conservation of genetic variation. The most commonly suggested levels here are retention of 95 % or 98 % of the variation for 100 years, but others are also possible. Hedrick recalled the, in population genetics well established, relation that an isolated population kept at $N_e = 100$, will retain 90 % of its start level of heterozygosity after 20 generations, a population of $N_e = 200$ will retain 95 % of heterozygosity after the same time and $N_e = 500$ will retain 98 %. Maybe the best thing to do is to present this to the politicians, and give them the choice. Hedrick himself suggested a 95 % retention, which with a N_e/N ratio of 0.25 – 0.33 (see below and Appendix 3) would mean a total wolf population of 600 – 800.

Bangs asked why just 95 %, he would be just as comfortable with 90 or 80 %, and Mech bade that he could go even for 75 %. Both Hedrick and Allendorf however claimed that there is empirical data from captive populations indicating a border line of 95 % retention of original level of heterozygosity, under which you will have detrimental effects. Strobeck then reminded that we probably already have lost 20 % of the original variation in the present Scandinavian wolf population, asking how much it then mattered whether we kept 90 or 80 % of the rest. Allendorf preferred to argue the other way round, concluding that this loss made it all so more important to keep as much as possible of what was left.

As the population levels discussed above are given as effective population sizes (N_e), not actual (N), it led to a short discussion of how to calculate the ratio between these two (N_e/N). It became apparent that there are several different ways to estimate the ratio between N_e and N. One can use a complete pedigree, where all fathers and mothers must be known. However, a complete pedigree is rarely available. Another way is to follow the loss of heterozygosity over several generations in a population of known size. This means a long-term study with very intensive data collection. This alternative is not suitable at the moment, but probably can be used in the future.

An alternative way to calculate the N_e/N ratio, that was suggested by Fred Allendorf, is to use an individually based simulation program. Such a program follows the life history of each individual, its survival and reproduction. The details of this procedure are presented in Appendix 4, in which Henrik Andrén has used this technique in the program Vortex to calculate the N_e/N ratio. Several calculations were performed, varying the input demographic parameters within limits set by field data from the present Scandinavian wolf population. Still the calculated ratios of N_e/N all fell within the narrow range of 0.34 – 0.35. An earlier attempt to calculate this ratio, using 12 different combinations of life history trait for Scandinavian wolves, gave the interval of 0,26 – 0,41 (REF 18). In examples given in this workshop we therefore have used a conservative span of 0.25 – 0.33 for the N_e/N ratio (which means that N_e should be multiplied with 3 or 4 to get N).

Several people in different ways stressed that regardless of MVP level chosen if any, it is important to monitor the population continuously and adapt the management along the way as new data are received. Per Lundberg suggested that we should develop risk analyses that are operational. This means that we must build 'decision trees' or 'decision tables' where all potential management actions (e.g., cull/not cull) and their consequences are contrasted. Such decision trees/tables should be continually updated as we gather more information about the system. Different management actions can be fed into the model and their consequences being evaluated, making it possible to chose between different scenarios, for chosen time periods and confidence limits.

What are the risks with culling in a population that not yet has reached a viable level

The question

The question whether it is possible to take out any wolves from the small Scandinavian wolf population without endangering its future has been haunting the wolf debate in this region for the last ten years. It will probably continue to be a controversial issue until the wolf population has reached a level that is considered safe by all actors in the field. As we can foresee an increasing frequency of depredation events in the near future with demands of control operations inevitably following en suite, guidelines for the responsible authorities however are badly needed.

Discussion

Specific recommendations regarding what level a small but increasing wolf population has to reach before animals can be taken out without seriously threatening its viability were not given. However, at the present level of the Scandinavian wolf population (approximately 100 animals) there was no principal objection against taking out one or a few animals (less than five) on an annual basis, if deemed necessary e.g. for socio-economic reasons. However, great precaution was strongly recommended. Preferably a viability analysis should forego removals of more animals per year. It was stressed that demographic and genetic monitoring should continue to give necessary background data, e.g. kinship and genetic variation in single individuals and packs. Hedrick: “You should use molecular data and kinship data, see if they are consistent, and use them to rank importance of individuals.” Allendorf: “The inbreeding coefficient is not as important as the genetic relationship (mean kinship) of the individual wolf to the rest of the population when judging which individual could be taken out. There is little correlation between kinship and inbreeding coefficient.”

Allendorf also pointed out that the worst thing that can be done genetically is to take out an entire pack. Strictly genetically you should spread the removals to as many packs as possible. But on the other hand you should be careful not to put such a hard pressure on dispersing animals that you might cause selective pressure against dispersal.

Conclusions

- The prime conclusion of the workshop was that the Scandinavian peninsula, including its biological, social and economic constraints on wolf distribution, is too small to carry a long term (> 100 years) viable wolf population on its own. Therefore the most important obligation for the wolf management in Norway and Sweden is to promote a genetic exchange with the nearest neighbouring wolf population, i.e. the Finnish/Russian population. This recommendation came up repeatedly during the discussions of several different themes.
- The need for a genetic inflow is aggravated by the fact that the present wolf population is founded by as few as three individuals, limiting its genetic variation from the very start. Further it is judged to have lost another 20 – 25 % of this variation up to present time. Even if it will reach a size where new mutations will balance further loss of genetic variations, it will continue to be genetically impoverished.
- One or two immigrating wolves per wolf generation should be enough to provide the Scandinavian wolf population with the genetic variation needed to keep the viability of the population. A wolf generation is approximately 5 – 6 years (see Appendix 3).
- The risk of swamping any possible local adaptations by allowing immigrating wolves into the Scandinavian wolf population is at present negligible because it is not likely there has been enough time for any such adaptations to evolve, and because immigrants are expected to come from the same area as the founders, and thus adapted to similar conditions as those occurring in Scandinavia. Still, to safeguard against this problem also in the future, it was suggested that promotion of immigration starts as soon as possible.
- Even when an appropriate genetic exchange has been secured, there is a minimum size under which the Scandinavian wolf population should not fall to avoid various short term demographic and genetic problems. An effective population size (N_e) of 50 was suggested to be such a minimum level. With an N_e/N ratio of 0.25 – 0.33, this means a population size of 150 – 200 wolves.
- There are no specific early warning signals that will indicate an ongoing inbreeding depression. A broad monitoring of demographic and life history variables should be performed parallel with a molecular monitoring. Reduced body size, undescended testicles and lowered sperm quality were given as examples of factors that should be especially watched out for.
- Once negative effects of inbreeding are detected, it might be too late to reverse a declining trend by allowing the population to grow. In that case the only remedy is to allow new animals from outside into the population.
- If the wolf population, despite all efforts, continues to be genetically isolated, it must conserve as much as possible of its present genetic variation. There was no consensus of levels, but a minimum seemed to be retention

of 95 % of the present degree of heterozygosity for the nearest 100 years, which means an effective population size of 200. With an N_e/N ratio between 0.25 – 0.33 (see Appendix 4), this means 600 – 800 wolves in total.

- Removal of one or a few wolves (less than five) per year, e.g. to control damage, is possible to perform in the present wolf population (approx. 100 wolves) without seriously threatening its viability. If the operation concerns specific individuals, try first to rank the importance of these individuals for the rest of the population by using demographic and molecular data. Kinship relations to the rest of the population is more important than inbreeding coefficients. If a planned control operation concerns more wolves, it was recommended that the culling should be foregone by a viability analysis, including evaluation of management alternatives. If several animals are to be taken out, it was recommended to distribute the culling over many packs, rather than taking all in one pack.

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Appendix 1

Abstracts of introductory talks

Inbreeding depression in conservation biology

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Inbreeding depression is of major concern in the management and conservation of endangered species. Reduction of fitness from inbreeding appears nearly universal although the extent is variable and depends upon the trait, the environment in which it is tested, the population, and the species. Further, statistically power may not be large both because of small sample size and the distribution of inbreeding coefficients. Recent experiments are consistent with greater inbreeding depression in more stressful environments. First, viability in *Drosophila melanogaster*, the fruitfly, is significantly lower in a stressful environments, such as high temperature, than in normal temperature. Lines with average fitness in normal temperatures may be lethal under stress. Second, white-footed mice show lowered fitness both when inbred and when in a stressful environment. However, the observed effect of inbreeding and stress is much greater than if the two acted independently, suggesting a synergistic effect. Finally, inbred endangered winter-run Chinook salmon from California have lower survival compared to non-inbred individuals when challenged by infectious disease, suggesting that inbred individuals may have greater disease susceptibility.

In endangered species, inbreeding depression may be expressed in a lower fitness of all individuals in a population due to genetic drift. Several recent introductions into populations with low fitness appear to have shown genetic restoration of fitness to levels similar to that before the effects of genetic drift. For example, the Florida panther, which exists only in one wild population of approximately 50 individuals, suffers from severe effects, such as over 60 % of the adult males have undescended testicles, and over 70 % of the adults have a kinked tail. Animals from Texas, over 1000 kilometers away, were introduced in 1995 in an attempt to genetically restore this population. Surveys show that none of the approximately 20 animals born recently with Texas ancestry have kinked tails and the five males examined with Texas ancestry have two descended testicles.

Examination of traits correlated to fitness in captive populations of Mexican and red wolves was also discussed to illustrate the approaches that can be used to detect inbreeding depression in wolves. There was no statistical association of viability or litter size with increased inbreeding in either species. However, there was an increase in viability over time. Because inbreeding has also increased over time, this confounding effect made it difficult to detect the effect of inbreeding on viability. There has been a decrease in body size in captive Mexican wolves as compared to wild wolves, and recent, more inbred wolves have lower body size than earlier, less inbred wolves.

Genetics and the persistence of small populations

Fred W. Allendorf
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The importance of the loss of genetic variation in decreasing the probability of persistence of isolated populations has been controversial in spite of abundant evidence for the detrimental effects of inbreeding on fitness-related characters. However, several recent studies have provided direct empirical evidence for the influence of genetics on population decline and recovery. Many population viability models that have included genetics may have underestimated the effects of inbreeding for two reasons. First, they have used estimates of inbreeding depression derived from captive populations, and inbreeding depression is likely to be more severe in the wild. Second, effects of inbreeding depression usually have been incorporated in only one aspect of life history (usually juvenile survival) whereas inbreeding depression can affect many other attributes as well (e.g., litter size, adult survival, etc.). In addition, the loss of phenotypic variation in small populations may reduce population viability in the absence of inbreeding depression.

The incorporation of genetics into PVA is problematic for many species because of unreliable estimates of demographic effects and genetic parameters related to inbreeding depression. Perhaps the best way to incorporate inbreeding depression is to use a range of values that span the likely effects of inbreeding depression to investigate how likely it is that inbreeding depression will affect absolute or relative population viability. It is important that the effects of inbreeding depression be examined on many vital rates, not just juvenile survival. Some have suggested that it may not be important to include genetic concerns in relative applications of PVA because any management option that minimizes the probability of extinction is also likely to minimize the effects of inbreeding. However, there is no way to know whether or not this assertion is true without testing it by incorporating genetics into the models.

Consideration of genetic effects over longer time frames is important for the long-term viability of populations and species. Recent considerations of this problem have led to the recommendation that an effective population size of approximately 1,000 individuals is needed to allow continued adaptive evolution and to avoid the accumulation of new harmful mutations. Such large populations will not be possible for many species (e.g., wolves in Scandinavia) except by increasing the connectivity among geographically separated populations over a wide area.

A pragmatic perspective on the genetic and demographic basis for conservation

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CANADA

The utility of population genetics in conservation biology has been the source of considerable debate. In his provocative essay, Graeme Caughley (1994, J. Anim. Ecol.) noted that not a single extinction can be attributed to genetic malfunction. Russell Lande (1988, Science) has noted that demography and environmental stochasticity are more likely than genetics to be of immediate importance in determining the minimum viable sizes of wild populations. We know of many examples of insular populations that have persisted at low population sizes with low levels of genetic variability for thousands of years and still remain viable. Yet, the fundamental motivation behind conservation biology is a desire to preserve genetic diversity, so one would expect population genetics to play a pivotal role in the practice of conservation. Population genetics offers general guidelines of conservation significance. For example, larger populations are less likely to suffer inbreeding depression and genetic drift thereby retaining genetic diversity to permit evolutionary response to environmental change. But recognizing the value of larger populations does not give us much direction beyond that afforded by ecology. Genetic studies have demonstrated complex spatial structure in and among populations arguing for the significance of preserving spatial isolates and variants. Also, dispersal has been shown to be a powerful force in the maintenance of genetic variation. But generally, the guidance offered by population genetics for conservation application is disappointing.

Conservation biologists also have struggled with practical applications for demography and ecological models. Population viability analysis has been criticized repeatedly because of huge uncertainty associated with predicting the future (see Ludwig 1999 Ecology). Estimates of vital rates of fecundity and survival vary temporally but also are burdened with large sampling and measurement errors. Consequently, it is difficult to reach sound conclusions about the future viability of a population based on the observed demographic status of a population.

More powerful than genetic or demographic models is to use resource selection functions to develop habitat-based population viability analyses. Habitat management, e.g., related to land uses such as forestry, is often done on long time horizons and can be highly predictable based on active management. Likewise, resource selection functions can be reliable predictors of the distribution and relative abundance of a species. Interfaced with geographical information systems (GIS), habitat-based PVA can thus be used to anticipate the consequences of alternative land management decisions. Indeed, I argue that being able to anticipate the future distribution and abundance of a species, e.g., wolves in Scandinavia, will have more direct ramifications for management of the species than we can glean from genetics or demography.

Wolf restoration and management in the northwestern United States

Ed Bangs
U.S. Fish and Wildlife Service, Helena, Montana

Gray wolf (*Canis lupus*) populations were eliminated from the western United States by 1930. Naturally dispersing wolves from Canada first denned in Montana in 1986. In 1995 and 1996 wolves from western Canada were reintroduced to central Idaho and Yellowstone National Park, Wyoming. Between natural wolf dispersal and reintroduction of wolves from several areas in Canada genetic diversity is not a conservation issue. By December 2002 nearly 700 wolves were being managed in those three states under the federal Endangered Species Act. Wolf restoration has proceeded more quickly, with more benefits (public viewing and restoration of ecological processes), and fewer problems (livestock and pets depredations) than predicted. However, between 1987 and December 2001, a minimum of 188 cattle, 494 sheep, 43 dogs, and 5 llamas were killed by wolves and nearly $250,000 was paid from a private damage compensation fund. The U.S. Fish and Wildlife Service relocated 117 wolves but most relocated problem wolves did not survive long enough to reproduce. One hundred and fifty problem wolves were killed but this level of removal did not stop growth and expansion of the wolf population. Wolf management also includes preventative and non-lethal tools such as injurious [i.e. rubber bullets] and non-injurious [i.e. light and siren devices] harassment, barriers [i.e. fencing, fladry, scents, herders, guard animals], altering wolf activity patterns [supplemental feeding, moving dens and rendezvous sites away from livestock], livestock management [i.e. confinement, alternative pasture, later turn-out, closer surveillance, discouraging range sheep or other types of livestock that are highly vulnerable to predation], and practical research [i.e. livestock death and movement caused by wolves, aversive conditioning]. Livestock losses by wolves remain rare compared to other causes of livestock death but are inordinately controversial. Because over 85 % of adult wolf mortality is human-caused, the interagency recovery program focuses its efforts on addressing the concerns of people who live near wolves to increase their tolerance of non-depredating wolves. Wolf restoration efforts attempt to empower local people in wolf management and minimize conflicts while allowing wolf population expansion in areas where conflicts are rare enough to be tolerated.

Wolf population persistence in real life

L. David Mech
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Wolf (*Canis lupus*) populations tend to be resilient and to persist for long periods, and several characteristics contribute to their resilience and persistence: (1) age of first reproduction (2 – 3 years), (2) high annual litter size (mean = 6), (3) low dispersal age (1 – 3 years), and (4) long potential dispersal distance (< 880 km). The only documented factor leading to extinction of well established wolf populations with sufficient food is deliberate poisoning, although conceivably disease could have such an effect.

When possible, wolves tend to avoid close inbreeding (based on 3 of 3 populations), but parent/offspring and sib/sib matings do occur when no other mates are available. Deleterious inbreeding effects are documented in 2 of 2 captive wolf populations studied. Nevertheless, several relatively isolated but protected wild wolf populations of < 100 have persisted for many decades, including the highly inbred Isle Royale (Michigan, USA) population that has persisted for 50 years and has withstood an outbreak of canine parvovirus.

Conservation genetics theory, population viability analyses (PVAs), and the minimum viable population (MV) concept are too nebulous to apply with confidence to wild wolf populations because they are (1) too new, (2) untested, (3) not specific, and (4) lack scientific consensus.

Appendix 2

Final invitation to the workshop

Workshop to discuss Conservation of small wolf populations with special emphasis on genetics and MVP.

Aims of the workshop

1) to clarify and update the state-of-art of conservation genetics with special emphasis on wolves and its role for determining MVP in wolves
2) to transfer international, especially North American, experiences of wolf conservation and management to Norwegian and Swedish scientists and managers

The workshop procedure

1) The six invited foreign experts (the panel) all give a 30 min. presentation on the theme ”Small population conservation, with emphasis on the role of genetics”. They are free to choose the details of the topic, although such issues as "inbreeding depression", "evolutionary potential", "extinction risk", "effective population size", ”genetic bottlenecks” and "MVP" probably are unavoidable. They are also free to choose how much emphasis they will put on wolves in this presentation, although this species should be on their mind in their presentation. The three non-geneticists in the panel (Mech, Boyce and Bangs) are of course not expected to go into depth of theoretical genetics, but are free to put their emphasis on any issues they find important in the context of this workshop. We urge the experts to make an effort to be pedagogic and make their presentations intelligible also for non-experts, considering that the participants at the meeting have a mixed background.

2) The panel and the other participants engage in a round table discussion, led by the chairman, on the issues brought up in the presentations. Special emphasis should be given to the following topics (with special reference to wolves):
   - How does inbreeding relate to extinction risks and population viability?
   - Importance of genetic drift, and loss of “valuable genes”
   - Mutational meltdown – fact or fiction?
   - What is "evolutionary potential" and is it a useful concept in PVAs?
   - Genetic bottlenecks
   - Are genetic risks for extinction possible to quantify in the same way as demographic risks?
   - What is the present status of the 50/500 rule
   - The potential role of immigration

   For each issue we find out where there is consensus (in the panel), where there are disagreements and which they are, and where you think there are gaps in our knowledge. These conclusions are noted by the secretary and will be read for acknowledgement, before next issue is approached.

3) After having reviewed the conservation genetics from a more scientific point of view, the efforts are now turned to the management implications and the more operational side of the problem. In the same format as above, the panel and other participants attempt to reach conclusions on how the genetics can be integrated into management plans for the Scandinavian wolf population. This involves a discussion on how an operational risk analysis (decision table) should be devised.
    - Is MVP a useful concept in wolf conservation?
    - How do we calculate a genetical MVP for wolves?
    - Is an operational risk analysis (decision table) an alternative to MVP, and how should it be devised?
    - How do we calculate ratio genetically effective population/total population (N_e/N) in wolves, and what measures of this ratio do we already have?
    - Is retention of "full evolutionary potential" a criterion for MVP in each wolf subpopulation?
    - How long time after a passed population bottleneck is it reasonable that the risk for inbreeding depression persists (i.e. when is the risk over), and what signs should we look for?
    - How do we evaluate genetical risks of taking out animals (because of extensive depredation or some other reason for a preventive shooting) from a growing population before it has reached MVP?
    - Is artificial introduction of animals from outside an option if genetical problems are detected in a small wolf population? How many animals, from where, how often? What are the experiences from other places in the world?

4) In the end of the workshop we investigate if there are general conclusions to be drawn. These are stated in written by the secretary in the same way as before.

Report

On the basis of the memo written down by the secretary (we will probably also tape the discussions), Olof Liberg will have the responsibility to write up a preliminary report, where the workshop conclusions will be the body of the report, divided into two parts: Conservation genetics and Management implications. This draft will then be sent to the panel members for corrections, comments, and finally (if necessary after several revision rounds) approval. The report will be published (in English) in an institutional report series, either by Swedish University of Agricultural Sciences or the National Environment Protection Board (not yet decided). If possible we will also try to get it published (in a shortened form) in an international journal, like TREE or Wildlife Society Bulletin.

Invited participants

Secretariat

Chairman: Dr Per Lundberg, Dept of Theoretical Ecology. University of Lund
Coordinator: Dr Olof Liberg, Grimsö Wildlife Research Station, SKANDULV
Secretary: Jens Karlsson, Grimsö, SKANDULV

The panel

Dr Fred Allendorf, University of Montana
Dr Ed Bangs, Coordinator Yellowstone Wolf Project, Montana
Dr Mark Boyce, University of Alberta
Dr Philip Hedrick, Arizona State University
Dr David Mech, University of Minnesota
Dr Curtis Strobeck, University of Alberta

Experts and organizations

Dr Henrik Andrén Grimsö, SKANDULV
Dr Staffan Bensch, Lund University
Dr Luigi Boitani, University of Roma
Dr Öje Danell, Swedish Universtiy for Agricultural Sciences
Dr Torbjörn Ebenhardt, Center for Biodiversity Uppsala
Dr Hans Ellegren, Uppsala University
Dr Kjetil Hindar, Norwegian Institute for Nature Research NINA
Dr Linda Laikre, Stockholm University
Dr Lennart Nyman, World Wide Fund WWF
Dr Hans-Christian Pedersen, Hedmark Höjskole SKANDULV
Dr Nils Ryman, Stockholm University
Dr Bernt-Erik Saether, Trondheim Universtiy for Tech. and Nat. Sciencies
Dr Håkan Sand Grimsö, SKANDULV
Dr Petter Wabakken, Hedmark Höjskole, SKANDULV
Dr Kjell Wallin, Gothenburg University

There will also be invited a few officials from the Norwegian and Swedish Wildlife Management authorities.

Appendix 3

Final list of participants

Participants at Workshop on wolf PVA at Färna, Sweden 1 – 3 May 2002

Name	Function	Organization and Address	e-mail
The panel			
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Appendix 4

Calculation of the ratio between N_e (effective population size) and N_c (census population size)

Henrik Andrén

There are several different ways to estimate the ratio between N_e and N. One can use a complete pedigree, where all fathers and mothers must be known. Although we know most of the relationships among wolf individuals in the Scandinavian wolf population, we do not have a complete pedigree. Another way is to follow the loss of heterozygosity over several generations in a population of known size. This means a long-term study with very intensive data collection. This alternative is not suitable at the moment, but can probably be used in the future.

An alternative to calculated the N_e/N ratio, that was suggested by Fred Allendorf, is to use an individually based simulation program. In an individually based simulation program one follows the life history of each individual, its survival and reproduction. Each individuals is given a specific genetical code and the genetical contribution to future generations is known. The simulation program summarize the total genetical variation over all individuals in each time step, which means that the loss of heterozygosity can describe in each time step. However, a simulation will only give an approximate value of the N_e/N ratio. On the other hand, one can easily test the sensitivity of different life history traits on the N_e/N ratio. N_e can be obtained using the rate of loss of heterozygosity per generation. The ratio can be estimated, if the total population size is known (Harris & Allendorf 1989):

$$N_e = 1 / (2 \text{ x } H_{\text{Loss}})$$

Or more general, the remaining heterozygosity after a certain number of generations and the ratio N_e/N can be calculated if the total population size is known:

$$N_e = 1 / (2 \text{ x } (1 - H_{\text{Remaining}}{}^{(1/\text{number of generations})}))$$

The second formula in combination with a stochastic individually based simulation program can be use to obtain an approximate ratio between N_c (census population size) and N_e (effective population size). The simulation program will give data on total population size, generation time, time frame of the simulation and loss of heterozygosity. Thus, one will have all necessary information to calculate N_e according to the second formula and therefore also the ratio N_e/N.

We used the simulation program VORTEX (Lacy 1995). To run VORTEX one has to specify several different life history traits and we use five different combinations of survival and reproduction, all possible for a wolf population, to get a possible range of output. As a result the growth rate varied between 1.06 and 1.35, which represents a large variation, but all possible for a wolf population. From 1991 to 1998 the mean yearly growth rate for the Scandinavian wolf population was 1.29 (±0.035 S.D.; Wabakken et al. 2001).

One also has to specify the number of years (time steps) in VORTEX, as well as the carrying capacity and initial population size. The output includes generation time, mean population size (i.e. N_c) and the remaining degree of heterozygosity. From generation time, one can calculate the number of generation by: time/generation time. Thus, one has all necessary data to calculate N_e according to the second formula.

The ratio N_e/N_c varied between 0.34 and 0.35 (Table 1). The ratio was very robust the large changes in growth rate. Assuming that an N_e of 50 individuals is necessary for the preservation of genetic variation, the census population should be between 144 and 148 individuals (Table 1). The ratios N_e/N_c in our simulations were fairly stable in spite of quite large variation in the growth rate due to variation in mortality and reproduction. Furthermore, Johansson and Ebenhard (1996) got N_e/N_c ratios between 0.26 and 0.41. They had 12 different combinations of life history trait and again, the results were very robust to changes in growth rates. Their data results in census population of 122 to 192 for an N_e of 50 individuals. Thus, the ratio N_e/N in the present Scandinavian wolf population most probably falls somewhere between 0.25 and 0.40. A ratio of 0.25 could be regarded as conservative. Observe that we regard N_c (the censused population) as an approximation of N (the actual population).

Table 1. Results from the VORTEX simulations and calculations of N_e (according to the equation above) and the ration N_e/N_c. The number of time step was 100 years, the initial population was 50 individuals and the carrying capacity was 200 individuals in all simulations.

Data from the VORTEX simulations					Calculated		
Growth rate (λ)	**Mean pop.size (N_c)**	**Generation time (years)**	**Number of generations per 100 yrs**	**Remaining heterozygosity after 100 yrs**	**N_e**	**Ratio N_e/N_c**	**N_c if N_e is 50**
1.06	155	6.47	15.5	86.5 %	53.54	0.35	145
1.09	186	6.41	15.6	88.4 %	63.51	0.34	146
1.15	191	5.62	17.8	87.4 %	66.31	0.35	144
1.22	197	5.47	18.3	87.1 %	66.43	0,34	148
1.32	199	5.26	19.0	86.8 %	67.40	0,34	148

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Genetic aspects of viability in small wolf populations

- with special emphasis on the Scandinavian wolf population

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In our crowded world, populations of large carnivores like tigers, cougars, bears and wolves often are fragmented into small subpopulations which might cause problems with inbreeding and loss of genetic material. Conservationists therefore want to keep these subpopulations as large as possible, which is in conflict with local intereststof farmers and big game hunters. The Scandinavian wolf population is a typical exponent of this dilemma, that came to its peak during a court trial in Norway, where different scientists took different sides. To resolve this intra-science controversy and generally clarify the role of genetics in conservation biology, a group of international experts in genetics and wolf ecology were invited to discuss these issues with Scandinavian colleagues and managers during three days. Here is the report of this seminal meeting, indispensable to anyone interested in the conservation of large carnivores.

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