



Hunting Effects on Favourable Conservation Status of Highly Inbred Swedish Wolves

LINDA LAIKRE,* ‡ MIJA JANSSON,* FRED W. ALLENDORF,† SVEN JAKOBSSON,*
AND NILS RYMAN*

*Department of Zoology, Stockholm University, SE-106 91, Stockholm, Sweden

†Division of Biological Sciences, University of Montana, Missoula, MT 59812, U.S.A.

Abstract: *The wolf (Canis lupus) is classified as endangered in Sweden by the Swedish Species Information Centre, which is the official authority for threat classification. The present population, which was founded in the early 1980s, descends from 5 individuals. It is isolated and highly inbred, and on average individuals are more related than siblings. Hunts have been used by Swedish authorities during 2010 and 2011 to reduce the population size to its upper tolerable level of 210 wolves. European Union (EU) biodiversity legislation requires all member states to promote a concept called “favourable conservation status” (FCS) for a series of species including the wolf. Swedish national policy stipulates maintenance of viable populations with sufficient levels of genetic variation of all naturally occurring species. Hunting to reduce wolf numbers in Sweden is currently not in line with national and EU policy agreements and will make genetically based FCS criteria less achievable for this species. We suggest that to reach FCS for the wolf in Sweden the following criteria need to be met: (1) a well-connected, large, subdivided wolf population over Scandinavia, Finland, and the Russian Karelia-Kola region should be reestablished, (2) genetically effective size (N_e) of this population is in the minimum range of $N_e = 500-1000$, (3) Sweden harbors a part of this total population that substantially contributes to the total N_e and that is large enough to not be classified as threatened genetically or according to IUCN criteria, and (4) average inbreeding levels in the Swedish population are <0.1 .*

Keywords: *Canis lupus*, conservation genetics, conservation policy, convention on biological diversity, FCS, genetic management, habitats directive, pedigree analysis

Efectos de la Cacería sobre el Estatus de Conservación Favorable de Lobos Suecos con Endogamia Alta

Resumen: *El lobo (Canis lupus) está clasificado como en peligro en Suecia por el Centro Sueco de Información de Especies, que es la autoridad oficial para la clasificación de amenazas. La población actual, que fue fundada a principio de la década de 1980, descende de 5 individuos. Esta aislada y tiene altos niveles de endogamia, y en promedio los individuos están más relacionados que los hermanos. Durante 2010 y 2011, las autoridades suecas han usado la cacería para reducir el tamaño de la población hasta su nivel superior tolerable de 210 lobos. La legislación de biodiversidad en la Unión Europea (UE) requiere que todos los países miembros promuevan un concepto denominado “estatus de conservación favorable” (ECF) para una serie de especies incluyendo al lobo. La política nacional sueca establece el mantenimiento de poblaciones viables, con niveles suficientes de variación genética, de todas las especies que ocurren naturalmente. La cacería para reducir el número de lobos en Suecia no se alinea con los acuerdos políticos nacionales y de la UE y es una limitante para que se cumplan los criterios para un ECF basado genéticamente. Sugerimos que para alcanzar el ECF para el lobo en Suecia se requiere cumplir con los siguientes criterios: (1) el restablecimiento de una población grande, subdividida y bien conectada en Escandinavia, Finlandia y la región Karelia-Kola de Rusia, (2) tamaño efectivo genéticamente (N_e) de esta población en el rango mínimo de $N_e = 500-1000$. (3) Suecia tiene una parte de esta población total que contribuye sustancialmente al N_e total, y que es lo suficientemente grande para no ser clasificada como amenazada genéticamente o de acuerdo con los criterios de la UICN, y (4) los niveles promedio de endogamia en la población sueca son <0.1 .*

‡email Linda.laikre@popgen.su.se

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Palabras Clave: Análisis de pedigrí, *Canis lupus*, Convención de Diversidad Biológica, Directiva de Hábitat, genética de la conservación, manejo genético, políticas de conservación

Introduction

The wolf (*Canis lupus*) is a native species in Sweden, but it was hunted to extinction in Sweden during the first part of the 20th century. It is currently classified as endangered by Swedish authorities (Swedish Species Information Centre 2012). In the mid-1960s individuals were observed only occasionally and the species was protected under Swedish law. In the winter 1982–1983, a breeding pair of wolves established in the border region between the provinces of Värmland in Sweden and Hedmark in Norway and provided the basis for the return of the species to Sweden (Liberg & Sand 2009). These 2 individuals, together with a male wolf that immigrated from Finland around 1990, constitute the primary genetic base of the current population of 200–300 wolves inhabiting the central part of the Scandinavian Peninsula. For over 18 years, none of the at least 10 wolves that immigrated via Finland to northern Scandinavia was able to reach the population in the middle of Scandinavia and contribute genes to the population (Liberg & Sand 2009). New genes were introduced in 2008 when 2 unrelated immigrating male wolves reproduced (Åkesson & Bensch 2010). Thus, there are only 5 founders of the existing Swedish wolf population, and the amount of genetic variation in the population cannot exceed that contributed by these founding individuals.

Inbreeding levels are high among living wolves; in 2010 the average coefficient of inbreeding (F) was 0.27 and the average mean kinship (MK) (Lacy 1995) among individuals was 0.28 (Laikre et al. 2011). These values imply that individuals on average are more related to each other than full siblings and that this situation will persist. The main reasons for the current situation are lack of management efforts to prevent genetic isolation (Swedish Ministry of Environment 1999) and rapid population growth. Early analyses of inbreeding effects in wolves bred in captivity and descending from wild wolves in Sweden and Finland revealed that deleterious recessive alleles are frequent and that inbreeding thus can result in both reduced fitness and hereditary disorders (Laikre & Ryman 1991; Laikre et al. 1993).

The difficult genetic situation (small population size, inbreeding, inbreeding depression, isolation, and low number of founders) for the Swedish wolves has been known for decades (e.g., Laikre 1999). Due to the population's narrow genetic base, rapid population growth and gene flow from neighboring populations are critical to achieving long-term population viability. Nevertheless, population levels have been kept low. Authorities have allowed individual wolves thought to be causing problems (e.g., injuring or killing livestock) to be killed, and poaching is

estimated to be substantial (Liberg et al. 2012). Poaching is regarded as the main reason for the very restricted gene flow from populations in Finland and farther east (Liberg & Sand 2009). In 2009 the Swedish Parliament decided that over the coming next few years (exact number of years not defined by Parliament) the population should be kept below 210 individuals (Swedish Government 2008/2009, p. 210). To achieve this, 28 wolves were culled in 2010 and 19 wolves were culled in 2011. This is in addition to almost 30 animals that were shot during these 2 years for other reasons.

The genetic problems of the wolf population are finally being recognized by authorities and include inbreeding depression (Liberg et al. 2005; Rääkkönen et al. 2006). The explicit goals of the Swedish Government now include that inbreeding levels should be reduced. Plans involve the introduction of up to 20 unrelated wolves. How this introduction is to be carried out in practice and where introduced wolves are to originate from have yet to be clarified. Our objective was to assess whether the Swedish wolf hunts in 2010 and 2011 were in line with national and international policy agreements (including agreements within the European Union [EU] of which Sweden is a part). In particular, we examined existing policy, the wolf hunt, and the situation of the wolf population with respect to its conservation genetic status.

Policy Relating on Swedish Wolf Management

A key question is whether current Swedish wolf management is in line with agreed national and international conservation policies and legislation. Within the EU the central biodiversity legislation is the Habitats Directive (92/43/EEC), which obliges all member countries to promote a “favourable conservation status” (FCS) for certain listed habitats and species, including the wolf. The FCS of a species is defined in Article 1*i* of the Habitats Directive and reads,

conservation status of a species means the sum of the influences acting on the species concerned that may affect the long-term distribution and abundance of its populations within the territory referred to in Article 2;

The *conservation status* will be taken as ‘favourable’ when:

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

- the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and
- there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis.

Genetic concerns are of apparent importance to reach the FCS goal of long-term viability. A wealth of scientific reports provide information that shows that maintenance of intra- and interpopulation genetic diversity is of key importance for adaptive potential (Lacy 1995; Hoffmann & Sgrò 2011; Sgrò et al. 2011) and that negative effects of inbreeding on population viability are common (Schonewald-Cox et al. 1983; Allendorf & Ryman 2002; Frankham 2005). Genetic considerations are not explicitly mentioned in Article 1*i* of the Habitats Directive, but genetic concerns are necessary to include when implementing this policy (Laikre et al. 2009), and this is recognized in the most recent update of the EU Commission's Explanatory Guidelines on Implementing the FCS (Evens & Arvela 2011).

The Convention on Biological Diversity (CBD) explicitly states that ecosystem, species, and genetic levels of biological diversity should be maintained. The EU and Sweden are parties to this convention. In line with the CBD, Sweden has adopted national environmental goals that include maintenance of sufficient genetic variation within and between populations to assure long-term viability of naturally occurring species (Swedish Government 2006).

There is currently no established definition of what would be FCS for the Swedish wolf population or what would be sufficient genetic variation. However, from a conservation genetics perspective it is obvious that the current situation with high inbreeding levels, a very narrow genetic base, and genetic isolation cannot be regarded as either favorable or viable over the long term.

A national committee recently evaluated the management of large carnivores in Sweden, and this committee appointed an international scientific expert panel to assess the scientific basis of conservation genetic recommendations for managing Swedish wolves and to provide its own assessment of the population size needed for obtaining FCS (Hansen et al. 2011). This panel suggests that obtaining FCS will require a population size of at least 3000–5000 individuals and that these numbers could be achieved if a well-connected, large population, which existed historically, could be reconstructed throughout Scandinavia, Finland, and the Russian Karelia-Kola region. They also suggest that inbreeding levels be reduced to below 0.1 (Hansen et al. 2011). In an interim report (Liljelund 2011), the national committee adopted some of these ideas and suggests that inbreeding be reduced to below 10%, and as a preliminary goal that census size for the Swedish population increase to 450.

Genetic Effects of the Hunt

The Swedish Government allowed hunting of wolves during 2010 and 2011. This is the first time wolves have been allowed to be killed since the 1960s, except for hunting of particular individuals killing or injuring domestic animals. The hunts have raised the question of whether it is acceptable and legal, according to the Habitats Directive, to hunt a species that has not attained FCS. The EU Commission does not think it is legal and has taken legal action against Sweden. A final decision on these actions is pending.

The Swedish wolf population has been monitored closely over the years. Tracking data in combination with molecular genetic analyses of collected blood, hair, and other biological material including tissue from dead animals has resulted in an almost complete pedigree of the population. The pedigree is maintained by the Scanduly Project (Liberg et al. 2005). We analyzed the genetic effects of the 2010 wolf hunt by using the pedigree data as of November 2010 that we obtained from the Scanduly Project. We used the Population Management x software (PMx) (Ballou et al. 2011) to calculate inbreeding coefficients and MK and to assess founder contribution and loss of founder genetic variation. Prior to the 2010 hunt the population consisted of 209 individuals. Fourteen of these wolves were protected from hunting because they represented the territories of the 2 males that immigrated to Sweden in 2007 and 2008, including the 2 males themselves. The immigrant males and their offspring had inbreeding coefficients (F) of 0. This implies that 195 animals were subjected to hunting (209 living wolves minus the 14 wolves protected from the hunt).

The average distribution of inbreeding coefficients among the 195 animals on which the 2010 hunt focused was 0.29 (Fig. 1a). Among the 28 wolves killed the average inbreeding coefficient was 0.26 (Fig. 1b). This is statistically significantly less than what would be expected if the 28 killed animals had been selected at random among the 195 wolves subjected to the hunt (Fig. 1c).

Despite protecting the noninbred wolves ($F = 0$) and focusing on the major part of the population that is inbred ($F > 0$), the hunt did not reduce inbreeding levels in the population. In the population as a whole average F remained 0.27 after the 2010 hunt. If pedigree data had been used to identify the most inbred individuals, the average F could have been reduced to 0.25. The reason average inbreeding still decreased in the population as a whole is because the noninbred wolves were protected (the 2 immigrant males and their offspring); thus, the group of 195 wolves with $F > 0$ was reduced whereas the other group was not.

However, reducing the average level of inbreeding should not be the only objective of genetic management in a case like this. It is equally important to maintain as much as possible of the remaining allelic diversity of the

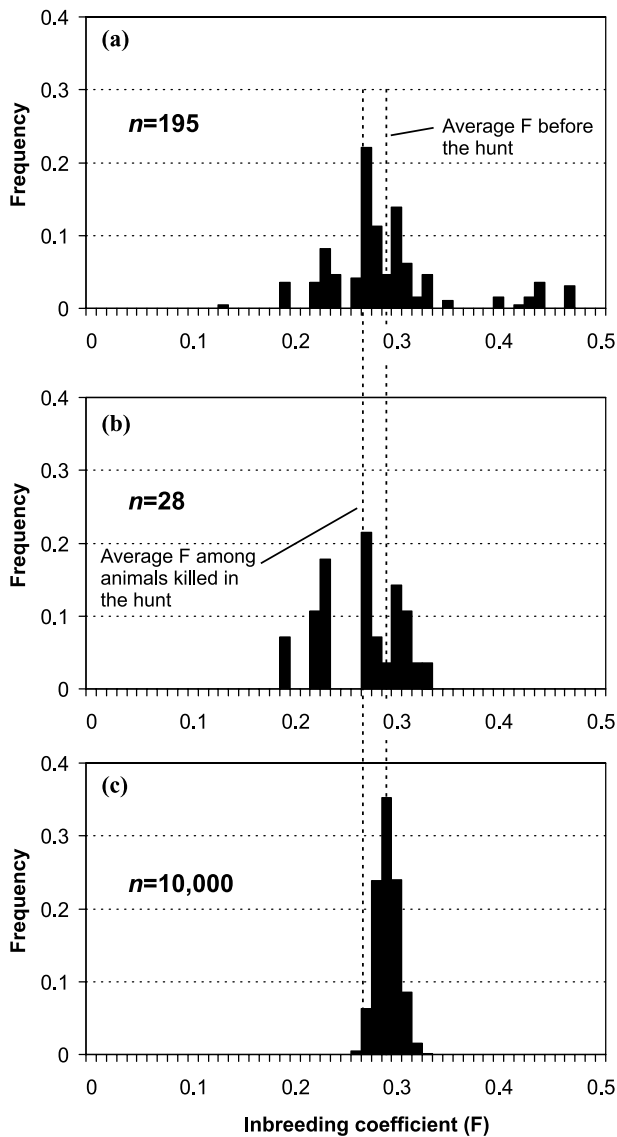


Figure 1. Distribution of inbreeding coefficients (F) among (a) 195 wolves alive prior to the hunt in 2010 and subjected to hunting (excluded from the hunt were 14 individuals that were the packs of 2 immigrating wolves) and (b) 28 wolves killed during the hunt (vertical dashed lines, average inbreeding coefficient among live wolves subject to the hunt [0.286, right line] and among killed individuals [0.262, left line]; difference statistically significant). Graph (c) shows average inbreeding coefficients in 10,000 computer simulated groups of 28 animals randomly drawn (without replacement) from the 195 animals subjected to the hunt.

population. It would be easy to reduce the mean level of inbreeding by just removing an even larger portion of the inbred wolves (in the most extreme case all the 195 wolves with $F > 0$), but this would also result in a further reduction of the genetic base of the population, which is

already very small. We think the risk of removing individuals representing potentially valuable genetic variation has not been adequately taken into consideration by the Swedish Government in the present case.

Several potentially inherited disorders have been observed in the Swedish wolf population. These include spinal disorders (present in 10% of wolves [Räikkönen et al. 2006]), chryptorchism, and heart and kidney problems (present in approximately 2–8% of wolves [Liberg & Sand 2009]). The wolf population at Isle Royale for many years was considered an example of how a viable wolf population could exist despite genetic isolation. In that population spine disorders, probably caused by inbreeding, are now common and occur at an estimated frequency of 60% (Räikkönen et al. 2009). Also, the rapid spread of genes from a new founder that immigrated to the Isle Royale population in the late 1990s further suggests higher fitness of descendants of this new founder than of the inbred animals. Genes from this new founder now dominate the population (Adams et al. 2011). Reduced fitness due to inbreeding and low levels of genetic variation is not always easily detected because population size can increase despite a poor relative fitness of the population.

There are 5 founding animals of the Swedish wolf population. Maximizing the retention of their alleles includes reducing further loss of genetic variation and striving to spread the genes of the 2 most recent immigrant males so that their genetic contribution becomes similar to that of the 3 original founders. During the 2010 hunt, offspring from the 2 immigrant males were protected. Thus, the genetic contribution from these founders was not reduced, but the proportion of lost variation measured as founder allele survival as calculated from the pedigree increased from 18% to 20% for the 2 original founders and from 4% to 5% for the male that immigrated in 1990. To maximize retention of genetic variation in this population it is important that genes from the 2 recently immigrating males be allowed to spread in the population. This will be achieved if as many as possible of the descendants of these males are allowed to survive and reproduce.

It has been argued that the population size of Swedish wolves should be reduced because immigration will be more effective in reducing inbreeding in small populations as new genes may spread more rapidly in a small population than in a large one (Liljelund 2011). We disagree with this recommendation because a large population is better than a small one with respect to both demographic stochasticity and genetic considerations. In large populations the rate of inbreeding is lower, genotypic variability is greater, and selection will operate more effectively. Therefore, reducing the population size of Swedish wolves is not a good strategy even though the current population is highly inbred.

We conclude that the official hunts have not contributed to the genetic health of the population.

Furthermore, the hunt was not carried out in a manner that agrees with adaptive management because available pedigree information was not used in the best possible way by, for example, identifying and removing individuals with the highest MK, as is a common conservation genetic recommendation when genetically managing populations with a known pedigree (Lacy 1995). There is a risk that indiscriminate hunting (in this case only the noninbred wolves were protected) may result in removal of important genotypes because of the narrow genetic base (few founders and high inbreeding levels) of the population. Instead, rapid population growth is of central importance for a small, highly inbred population. Therefore, legal and illegal hunting prohibit genetic recovery.

Removing individuals and genes will imperil achievement of FCS as long as it is not clear whether the planned genetic supplementation of the population is possible to carry out or what effect it would have over various time scales. Similarly, hunting an endangered species challenges the precautionary principle and appears to be in conflict with implementing the CBD, the EU Habitats Directive, including achieving FCS, and national policy goals of maintaining genetic variation.

Criteria for a Genetically Viable Wolf Population in Sweden

In line with the suggestions of Hansen et al. (2011), we believe it is important to reestablish a large metapopulation throughout Scandinavia, Finland, and the Russian Karelia-Kola region. We suggest Sweden takes a leading role in the international efforts in this respect. We suggest that to reach FCS for the wolf in Sweden average inbreeding levels be <0.1 ; that the genetically effective population size (N_e) of the total wolf population of Sweden, Norway, Finland, and Russian Karelia-Kola be in the minimum range of $N_e = 500$ – 1000 ; and that Sweden harbor a substantial part of this metapopulation. The Swedish part of the metapopulation should at a minimum comprise a population that is large enough to not be classified as threatened according to International Union for Conservation of Nature (IUCN) Red List criteria (IUCN 2003) and should maintain genetic variation measured in terms of founder alleles.

A genetically effective population size of 500–1000, translates into 2500–5000 wolves on the basis of current estimates of the relation between effective population size and actual number of individuals (census size [N_c]) of approximately 0.2 (i.e., N_e is estimated to be about 20% of N_c [Forslund 2009]). This implies that the Swedish wolf population must increase substantially and gene flow must be created so that the Swedish segment of a total large wolf population is not isolated but contributes to the total population.

One question is what proportion of the total, interconnected population in this region should occur in Sweden. We propose that a minimum goal is to maintain a census size that results in the wolf no longer being on the Swedish Red List. The structure and necessary degree of gene flow among segments of a large population system remains to be addressed. Until this has been achieved FCS will not be reached for the Swedish wolves.

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