

Panel review of genetic studies on the Scandinavian grey wolf

Panel Members in Alphabetical Order:

Fred W. Allendorf
Division of Biological Sciences
University of Montana
Missoula, MT 59812
USA
Email: fred.allendorf@gmail.com

Adam H. Freedman
Faculty of Arts & Sciences Informatics Group
Harvard University
Cambridge, MA 02138
USA
Email: adamfreedman@fas.harvard.edu

Robert K. Wayne
Ecology & Evolutionary Biology
UCLA
Los Angeles, CA 90095
USA
Email: rwayne@g.ucla.edu

The conclusions reached by the panelists are their own and do not reflect in any way the opinions of the institutions with which they are affiliated.

Report

The Norwegian Environment Agency asked the panel to conduct an independent investigation into the following two questions:

1. What is/are the genetic and biogeographical origins of the present Norwegian/Scandinavian population of grey wolves (*Canis lupus*)?
2. To what degree can historical and/or present hybridisation with domestic dogs (*C. l. familiaris*) be detected in the population?

We were unclear of the meaning of question 2 so we emailed Veronica Sahlén for clarification. She emailed that this question was asking if there is evidence for hybridization with domestic dogs in the Norwegian/Scandinavian population.

We followed the guidelines provided us by the Norwegian Environment Agency:

“The review should also assess the quality of the existing studies central to answering these questions and the overall result with respect to the technologies available and used at the time, as well as assess the validity of said results given technological and methodological developments and new knowledge.”

We concluded that the existing literature was sufficient to arrive at definite conclusions with regard to both questions. We believe that the existing literature as recently reviewed (Hendrikson et al. 2017), provides evidence that can be used as the basis for management plans.

1. What is/are the genetic and biogeographical origins of the present Norwegian/Scandinavian population of grey wolves (*Canis lupus*)?

We conclude that this population originated from founders from Finland and western Siberia (Aspi et al. 2006, 2009; Vila et al. 2003; Hindrikson et al. 2017). The population has been augmented by occasional natural migrants (Vila et al. 2002; Flagstad et al. 2003; Seddon et al. 2006).

There is no evidence, despite a large number of independent studies (Hindrikson et al. 2017), that the Scandinavian population is derived from captive wolves or from wolves transported from outside the current population independent of past migration from Finish or western Siberian source populations. Finally, one genetic study supports genetic differences between the historic and current south Scandinavian population (Aspi et al. 2006). However, these differences are not substantial and are similar to those found between historic and naturally re-established or re-introduced populations in the American west (Leonard et al. 2005; vonHoldt et al. 2008, 2010) and elsewhere where wolves have been extirpated.

2. To what degree can historical and/or present hybridization with domestic dogs (*C. l. familiaris*) be detected in the population?

We concluded that only one case of dog-wolf hybridization is well supported, and this is based on a single road-kill specimen in Norway (Vila et al. 2003). The individual appears to be a first-generation hybrid from a cross of a female wolf and male dog. Aside from this example, no other individual from the Scandinavian population shows evidence of admixture.

A caveat to this conclusion is that individuals with low levels of admixture derived from a cross many generations ago that backcrossed to pure wolf populations may not be detectable given past genetic techniques. However, if admixture has occurred recently, since the founding of the current population, then wolves with high and intermediate genomic signatures of introgression would be expected to be found. Alternatively, admixture may have occurred historically in the source population, prior to founding of

the current Scandinavian population. Further genomic studies may be able to test this idea, but current genetic analyses are sufficient to have detected recent admixture.

Recent studies based on whole genome data have found evidence for modest amounts of gene flow between wolves and dogs following domestication, particularly for wolf populations and breeds that have co-occurred historically (e.g., Freedman et al. 2014; Fan et al. 2016). Thus, it is possible that genomic analyses of Scandinavian wolves and breeds originating from western Eurasia may reach similar conclusions. Nevertheless, such low levels of admixture do not erode the genetic boundaries between species or the genetic distinctiveness of wolf populations any more than small fraction of Neanderthal ancestry detected in humans threaten their status as *Homo sapiens*. Future assessments of hybridization could be undertaken using an approach that leverages a modest number of ancestry-informative markers (e.g., VonHoldt et al. 2013).

Conclusions

The panel finds that the current literature is adequate to conclude that the existing Norwegian/Scandinavian population derives from immigration from Finland and Western Siberia. In addition, the existing population does not show evidence of hybridization with dogs.

We expect that future genetic results with greater genomic coverage will provide further evidence to address these questions. Specifically, we understand that ~100 Norwegian/Scandinavian wolf genomes will be available soon for analysis from researchers at Uppsala University (H. Ellegren and M. Kardos, personal communication). These results might be useful to more precisely localize the populations from which the current Scandinavian wolf population originated.

Literature Cited

Aspi, J., E. Roininen, M. Ruokonen, I. Kojola, and C. Vila. 2006. Genetic diversity, population structure, effective population size and demographic history of the Finnish wolf population. *Molecular Ecology* 15:1561-1576.

Aspi, J., E. Roininen, J. Kiiskila, M. Ruokonen, I. Kojola, L. Bljudnik, P. Danilov, S. Heikkinen, and E. Pulliainen. 2009. Genetic structure of the northwestern Russian wolf populations and gene flow between Russia and Finland. *Conservation Genetics* 10:815-826.

Fan, Z., and many others. 2016. Worldwide patterns of genomic variation and admixture in gray wolves. *Genome Research* 26:163-173.

Flagstad, O., C. W. Walker, C. Vila, A. K. Sundqvist, B. Fernholm, A. K. Hufthammer, O. Wiig, I. Koyola, and H. Ellegren. 2003. Two centuries of the Scandinavian wolf population: patterns of genetic variability and migration during an era of dramatic decline. *Molecular Ecology* 12:869-880.

Freedman, A. H., I. Gronau, R. M. Schweizer, D. Ortega-Del Vecchyo, E. Han, and P. M. Silva. 2014. Genome sequencing highlights the dynamic early history of dogs. *PLOS Genetics* 10(8): e1004631.

Hindrikson, M. and 22 others. 2017. Wolf population genetics in Europe: a systematic review, meta-analysis and suggestions for conservation and management. *Biological Reviews* 92:1601-1629.

Leonard, J. A., C. Vila, and R. K. Wayne. 2005. Legacy lost: genetic variability and population size of extirpated US grey wolves (*Canis lupus*). *Molecular Ecology* 14:9-17.

Seddon, J. M., A.-K. Sundqvist, S. Björnerfeldt, and H. Ellegren. 2006. Genetic identification of immigrants to the Scandinavian wolf population. *Conservation Genetics* 7:225-230.

Vila, C., A.-K. Sundqvist, O. Flagstad, J. Seddon, S. Björnerfeldt, I. Kojola, A. Casulli, H. Sand, P. Wabakken, and H. Ellegren. 2002. Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proceedings of the Royal Society of London B* 270:91-97.

Vila, C., C. Walker, A. K. Sundqvist, O. Flagstad, Z. Andersone, A. Casulli, I. Kojola, H. Valdmann, J. Halverson, and H. Ellegren. 2003. Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf-dog hybrids. *Heredity* 90:17-24.

vonHoldt, B. M., and 8 others. 2010. A novel assessment of population structure and gene flow in grey wolf populations of the Northern Rocky Mountains of the United States. *Molecular Ecology* 19:4412-4427.

vonHoldt, B.M., D.R. Stahler, D.W. Smith, D.A. Earl, J.P. Pollinger, and R.K. Wayne. 2008. The genealogy and genetic viability of reintroduced Yellowstone grey wolves. *Molecular Ecology* 17:252-74.

vonHoldt, B.M., J.P. Pollinger, D.A. Earl, H.G. Parker, E.A. Ostrander, and R. K. Wayne. 2013. Identification of recent hybridization between gray wolves and domesticated dogs by SNP genotyping. *Mammalian Genome* 24:80-88.