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Faroese sheep expand overall global ovine genetic diversity



Eva Kjæld Hansen^{1,2}, Jens Ivan í Gerðinum³, Dag Inge Våge⁴ and Svein-Ole Mikalsen^{1*}

Abstract

Background Faroese sheep have an unclear history. While it is assumed that the Vikings brought sheep to the Faroes, traces of pre-Viking age sheep are also found. Historical sources cite disasters in a period around year 1600 that essentially eradicated the sheep population, and subsequent imports from Iceland to the northern part of Faroes, and from Shetland and Orkneys to the southern part of Faroes. We have here investigated the genetic relationship of northern Faroe sheep with other breeds.

Results A total of 359 sheep from four flocks from three Faroese islands (Streymoy, Eysturoy, Kalsoy) were genotyped using the GeneSeek Genomic Profiler Ovine 50K chip. The samples were clearly stratified into three groups corresponding to island of origin. This is likely due to the minimal transport of animals between the islands during extended periods of time. The Faroese samples were compared with the data from the Sheep HapMap database, representing breeds from different parts of the world, and, additionally, Norwegian White Sheep. The Northern European short-tailed breeds clearly stood out from the remaining global breeds, and Faroese sheep gained a peripheral position among the other North Atlantic short-tail breeds, with Icelandic sheep and Norwegian spael as their closest neighbors. The peripheral position suggests that the link to the surrounding breeds might be more distant than expected.

Conclusions Despite known imports of sheep from neighboring countries after the year 1600, this is poorly reflected in the genotyping data. One possible explanation could be that the present-day Faroese sheep have an unbroken genetic link to the pre-year 1300 Faroese sheep (which possibly were a mix of old-Norse and old-British/Irish animals), regardless of the presumed post-year 1600 influence from other breeds in the North Atlantic region.

Keywords Domestic animals, Faroe Islands, Genetic diversity, Genotyping array, North Atlantic short-tail sheep, *Ovis aries*, SNP genotyping

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Background

Despite that industrial agriculture and farming have generally pushed towards monocultures of both plants and animals, the UN Food and Agriculture Organization (FAO) has long had attention on the erosion of livestock genetic diversity [1]. Also the Biodiversity Convention of 1992 [2] includes genetic resources in Article 1 (Objectives). This has been further extended in detailed in the Kunming-Montreal Framework from 2022 [3]. In Goal A, it is clearly stated that"The genetic diversity within populations of wild and domestic species is maintained, safeguarding their adaptive potential". This is further repeated in Target 4 ("...maintain and restore the genetic diversity within and between populations of native, wild and domesticated species to maintain their adaptive potential..."). Thus, genetic diversity of domestic plants and animals has entered mainstream international biodiversity policy.

Genetic diversity can be assessed by several approaches. Whole-genome sequencing of each individual is by far the most comprehensive approach, as this allows the detection of essentially all individual genetic variations, whether they are previously known or not. However, extensive bioinformatic resources and infrastructures are needed to achieve proper analysis. A more affordable approach is genotyping microarrays, where oligonucleotides containing known genetic variations have been printed on a chip. A major drawback is that the number of species where such services are available is more limited. Nevertheless, genotyping microarrays are available for all major domestic species, including sheep.

The Faroe Islands are an archipelago consisting of 18 islands (total land area 1395 km²) in the North Atlantic Ocean, midway between Scotland and Iceland. The Faroe Islands probably became populated by an early wave of people around year 400 to 500 [4, 5] (possibly coming from Ireland and/or Great Britain) and a later wave consisting of Nordic Vikings around year 750 to 850. It is likely that the first wave of settlers brought domestic animals, also sheep, as sedimentary ancient DNA and molecular fecal biomarkers identified sheep, and dated to around year 500 [5], well before the Viking arrival. The Vikings established their first settlements around year 825. In the same period, the Irish monk and geographer Dicuil wrote "Liber de mensura orbis terrae" where he mentioned some small islands in the north (probably Faroe Islands) that previously had been inhabited by people (monks?) from Scotia (Ireland/Scotland), and now were full of wild sheep and seabirds [6]. It is quite likely that the Vikings brought their own sheep, which may or may not have been hybridizing with the preexisting sheep. After year 1200, sheep became pivotal in maintaining people in the Faroe Islands [7, 8], and the first known written document from the Faroe Islands is"Seyðabrævið"("The Sheep Letter"), which in 1298 came as an amendment to the existing Norse law (the Gulating Law, also known as the "Landslov", by the Norse king Magnus Lagabøte, whose name literally translates to Magnus the Law Maker). Both the Norse law and the Sheep Letter can be found in modern Faroese translation in ref. [9]. The Sheep Letter describes the organization of sheep management and land ownership, which the present sheep and land management still, to some degree, rely on. A period with high sheep mortality occurred around year 1600, and nearly all animals died [10]. The period appears to coincide with a temperature minimum during the"Little Ice Age" [11], although it is not known whether there is any causal relationship. To replenish the sheep population, animals were presumably imported from the surrounding geographical areas. The scholar Jens Christian Svabo claimed the areas to be Iceland for the northern part of the Faroes, and Shetland and Orkneys for the southern part of the Faroes [10]. Subsequently, the active breeding of the old breed was probably abandoned. However, the old breed continued to exist for some time, and the last known animal was shot at the uninhabited island Lítla Dímun around year 1860. Svabo [12] specifically mentions the animals at Lítla Dímun as a "separate sheep species", but also notes the harsh conditions on this small and steep island. Three animals, shot at Lítla Dímun in 1844, are on display at the Faroese National Museum. There is little written documentation about sheep imports even in modern times [13, 14], but some animals were probably imported during the 1800s (three Merino(?) animals from Spain in 1821; a few Cheviot from UK in 1842 and 1850; a low number of Blackface from UK; and low numbers of Danish, Norwegian and Icelandic animals in uncertain years up to approximately 1950). In fact, the import of animals after 1908 should in principle only be permitted after allowance from the Faroese government and Chief Veterinary Officer [15]. The last known imports were one ram from Greenland in 1952 and another one in 1961, one ram from Scotland in 1960, and three Lantras animals from Gotland (Sweden) in 1967 [13, 14]. It is thus uncertain how strong the genetic link between the old and the new Faroese breed is, and also how much the Faroese sheep are genetically influenced by the surrounding breeds. We have here investigated sheep from the northern part of the Faroe Islands and their genetic relationship with other sheep breeds.

Methods

Animals

We performed a population genetic examination of Faroese sheep, collecting blood samples from more than 400 ewes taken from four flocks located on the three Faroese islands: Streymoy, Eysturoy, and Kalsoy. The total number of winterfed sheep in the Faroe Islands amounts to approximately 70 000 animals ([16] and Eyðfinn Magnussen, pers. comm.), a number that has remained quite stable for many years [16]. The northern region of the Faroe Islands consists of 13 islands, which our sampled animals represent, corresponding to approximately 48 000 winterfed animals. The three sampled islands have approximately 2/3 of the northern population of sheep ([16] and Eyðfinn Magnussen, pers. comm.), which are presumed to have their main influence of Icelandic sheep after the disasters around year 1600 [10]. We have not sampled any animals from the southern part of the Faroes, as the animals are claimed to have a different origin [10].

In the field, the blood samples were stored at 0-4 °C using cooling blocks, and subsequently frozen at -70 °C until DNA purification.

DNA purification and genotyping

DNA was purified with the DNeasy Blood and Tissue kit (Qiagen; Hilden, Germany) as described by the supplier. The samples for genotyping were prepared and handled as described by Neogen (Auchincruive, Ayr, Scotland), including heat treatment at 73 °C for 30 min to inactivate potential pathogens. Samples with sufficient purity and DNA amounts (362 individuals) were shipped to Neogen for genotyping with the GeneSeek Genomic Profiler Ovine 50K chip containing 51 646 SNPs.

Quality control and analysis of genotyping data

The data were analyzed using PLINK 1.9 [17]. All genotyping data was filtered with the parameters –geno 0.1, –mind 0.1, –maf 0.01 and –hwe 1e- 5. After quality filtering, 45,355 variants and 359 individuals remained in the Faroese dataset. The dataset was then pruned with the –indep-pairwise option in PLINK (r^2 -treshold 0.2) down to 30,885 SNPs. The Faroese dataset was analyzed by the –mds-plot function in PLINK to visualize the genetic relatedness of the Faroese sheep.

In addition, a 50K SNP dataset from 378 Norwegian White Sheep (NKS) [18] was included together with genotypes from 530 North-European sheep from the Sheep HapMap dataset generated by the International Sheep Genomics Consortium (ISGC) [19]. The three different SNP datasets (Faroese sheep, NKS and the subset of HapMap-breeds) were subsequently merged into a file containing 21 864 common markers and 1267 individuals. This dataset was then pruned down to 18,973 SNPs by the PLINK –indep pairwise option described above. The HapMap-breeds included in this study were (i) either known or assumed to have interbred with the Faroese sheep (Blackface from UK, two Spael breeds and NKS from Norway, and Icelandic sheep) [13, 14], (ii) belonging to assumed old breeds of short-tail sheep that may have relationships with the animals that presumably were brought to the Faroe Islands from UK/Ireland by monks pre-Viking age (Soay, Boreray), (iii) Finnsheep (an old Nordic short-tail sheep), and (iv) breeds with reference genomes in Ensembl (Rambouillet, Texel) [20, 21], giving ten breeds in this analysis. The Faroese and Icelandic animals, together with Norwegian Spael, Finnsheep, Soay and Boreray belong to the Northern European shorttailed sheep [22].

A global analysis was done by including the global dataset of sheep in the HapMap database together with Faroese sheep and NKS. The data were filtered and pruned in the same way as described above, giving 19 434 SNPs and 3694 animals.

Multidimensional scaling (MDS) plots were made from the pruned datasets for ten Northern European breeds and for the global breeds. Furthermore, weighted pairwise F_{st} -values [23, 24] was estimated for the ten Northern European breeds using the R-package StAMPP for and a corresponding neighbor-joining tree was constructed. Confidence intervals and p-values of pairwise F_{st} -values were estimated by performing 100 bootstraps. Inbreeding coefficient (F) for each individual of the ten Northern European breeds was calculated using the PLINK –het option.

Results

The Faroese animals showed distinct stratification corresponding to the island of origin (Fig. 1). The two flocks from Streymoy were closely located according to the 2-dimensional MDS-plot, while the pairwise F_{st} -values indicated significant (p < 0.01) differentiation between the 4 flocks (0.034—0.067), flock 1 and 4 being most different (Table 1). The stratification is likely due to relatively little transport of animals between the islands over many years, and further strengthened by the general prohibitions of interisland transport of sheep, which has been in place since 1990 as a part of the local action against scrapie [25]. If other Faroese islands had been included in the sampling, we would expect that further island-dependent stratification had been observed.

However, the stratification shown in Fig. 1 only indicates the internal diversity among Faroese sheep. SNP data for several North Atlantic and Nordic short-tail breeds, together with Scottish Texel, Scottish Blackface, and Rambouillet, were obtained from the Sheep HapMap database [19]. SNP data from Norwegian White Sheep breed (NKS) were also added [18]. The dataset contained ten breeds with a total of 1267 animals after filtering and pruning, and the number from each breed is shown in Table 1. The MDS plot (Fig. 2A) showed that the Faroese sheep located peripheral to, and surprisingly far away from, the other North Atlantic short-tail sheep, with Icelandic sheep and Spael as their closest neighbors. Note



Fig. 1 MDS plot showing the genetic relatedness of 359 Faroese sheep from four flocks on the three Faroese islands, Streymoy (black, 38 animals and red, 109 animals), Eysturoy (green, 83 animals), and Kalsoy (blue, 129 animals). Each circle represents one individual

that the number of Icelandic sheep is low (16 individuals), which might influence the estimated distance. The old breeds from the Hebrides, Soay and Boreray, located well away both from the Icelandic and Faroese sheep. The same conclusion was obtained from MDS plot where all breeds in the HapMap database were included (Fig. 2B), the main difference being Soay and Boreray locating closer to, and in the neighborhood of, Norwegian Spael. The Faroese animals still located peripheral to all other breed with Icelandic sheep as their closest neighbor.

It has previously been indicated that North Atlantic short-tailed breeds [22], such as Soay and Boreray, were clearly genetically distinct from other breeds [26, 27], and our results (Fig. 2B) fully corroborate this assertion. Soay and Boreray are old breeds from the Hebrides, and they clearly distinguished themselves by having much higher pairwise F_{st} values than any other pairwise comparisons (Table 1). This is likely caused by small population size and long-term isolation and thereby being subjected to inbreeding and genetic drift. This is further indicated by the very high inbreeding coefficient (F) for these two breeds (Fig. 3).

As could be expected, F_{st} indicated a quite low degree of differentiation within the Faroese animals, *i.e.*, between the Faroese flocks. When excluding Soay and Boreray from the pairwise F_{st} comparisons, the non-Faroese breeds had a mean pairwise $F_{st} = 0.102$, while the comparisons between Faroese animals vs. non-Faroese breeds gave a slightly higher mean pairwise $F_{st} =$ 0.123 (Table 1). The neighbor-joining tree based on the F_{st} values from the pairwise comparisons is shown in Suppl. Fig. 1.

The average inbreeding coefficient in the Faroese breed (F = 0.132) was comparable to several other breeds, like Finnsheep, Icelandic sheep, Rambouillet and Spael (Fig. 3), and clearly lower than Soay and

Boreray. The three breeds with F coefficient below 0.1 are all very populous breeds.

Discussion

A study of Northern European sheep using 25 microsatellites did not suggest that Faroese sheep were particularly different from other North European short-tail sheep, and they positioned close to Norwegian spael in an independent components analysis [28]. Furthermore, a recent conference abstract [29] suggested that the genetic diversity among sheep in the North Atlantic region has decreased from the Viking and Medieval period to the modern sheep breeds, specifically in Iceland and the Faroe Islands. One could imagine that high levels of inbreeding would occur among animals on small and quite isolated islands, explaining such a claimed loss of genetic diversity. Still, we here find that there is a considerable internal genetic diversity in both Faroese and Icelandic sheep, with inbreeding coefficients comparable to the levels in Finnsheep, Rambouillet and Norwegian Spael. On the other hand, the even smaller and isolated breeds of Soay and Boreray, have very high inbreeding levels, which potentially could be an explanatory factor for their "jump" in their relative position between the analysis of the North Atlantic animals (Fig. 2A) and the global breeds (Fig. 2B).

With the assumed import of Icelandic animals to the northern islands of the Faroes after the high sheep lethality around year 1600 [10, 12], we had expected the investigated sheep population to have high genetic connectivity to the Icelandic animals. It was therefore surprising that the Faroese sheep in the present study distinguished themselves so strongly, even from the Icelandic animals. During the last 200 years or so, a low number of animals have been imported from diverse breeds, mainly from the North Atlantic region, but also from elsewhere as

	Faroe1	Faroe2	Faroe3	Faroe4	NKS	Boreray	Finnsheep	lceland	Spael	Ramb	Scotb	Scott	# animals
Faroe1													38
Faroe2	0.038												109
Faroe3	0.049	0.034											83
Faroe4	0.067	0.050	0.047										129
NKS	0.114	0.101	0.101	0.111									378
Boreray	0.243	0.218	0.220	0.228	0.165								17
Finnsheep	0.129	0.115	0.114	0.125	0.065	0.188							66
Iceland	0.105	0.087	0.087	0.097	0.092	0.228	0.095						16
Spael	0.113	0.097	0.097	0.107	0.078	0.202	0.080	0.078					50
Ramb	0.149	0.136	0.135	0.146	0.083	0.196	0.100	0.125	0.113				102
Scotb	0.133	0.119	0.118	0.129	0.066	0.180	0.089	0.110	0.098	0.094			56
Scott	0.178	0.163	0.164	0.174	0.091	0.232	0.128	0.158	0.139	0.127	0.125		80
Soay	0.255	0.229	0.231	0.238	0.173	0.227	0.204	0.240	0.220	0.212	0.201	0.249	110

summarized in the Background [13, 14]. If these imports should have had significant impact on the genetic constitution, we would have expected the Faroese animals to locate closer to, or even in-between the other breeds. As the Faroese animals do not have any particularly high inbreeding coefficient (Fig. 3), we believe that inbreeding and genetic drift in a founder population is not the most likely explanation for the peripheral position and genetic distance to the other breeds. We will suggest two alternative hypotheses that may explain these results.

Our main suggestion for the genetic separation between the Faroese sheep and all other breeds is an unbroken genetic line from the pre-year 1600 sheep to the present-day Faroese sheep, combined with genetic drift in a small and isolated population. The strong genetic separation in Fig. 2A and B may suggest that imports in the early 1600s and later have only slightly influenced the genetic constitution of Faroese sheep. To what degree the old Faroese lineage is a mix of old-British/Irish and old-Norse sheep is unknown. According to Øye [7], other domestic animals, such as cattle and pigs, together with fish, birds and other wild animals, were more important in the first period after the Norse settlement in the Faroe Islands, as evidenced by archaeological excavations [8, 30, 31]. Domestic sheep gained more importance during the 1200s [7]. Speculatively, this may imply that the presumed old-British/Irish sheep roamed the islands in the 200-300 years after the Norse settlement, and they became gradually absorbed into the domestic old-Norse sheep, and by year 1200-1300 a unique breed had been settled.

Alternatively, and probably less likely, one could imagine that the sheep in Shetland, the Orkneys and/or Iceland have been genetically more influenced by other breeds in the last 400 years than the sheep in the Faroe Islands. Theoretically, it could be possible to distinguish between the two alternative hypotheses by taking samples from the three animals of the old Faroese breed on display at the National Museum in Tórshavn. It will weigh strongly towards the first alternative if the presentday Faroese animals show a closer genetic relationship to the old Faroese sheep than to any other present-day breeds. However, it should be noted that we do not know how long these sheep had been isolated at the small island of Lítla Dímun, and whether they had any genetic inflow after the high sheep mortality around year 1600. It would also be interesting to make a genetic comparison with the Old Norse Sheep ("Gammelnorsk sau"; also called"Utegangarsau"or"Norsk Villsau" [32]), which is assumed to be of old Norse origin with little crossbreeding involved [22]. This breed was close to extinction but has gained popularity during the last five decades or so due to its self-sufficiency and excellent meat guality. This breed may give a link to the sheep that the



Fig. 2 A MDS plot indicating the genetic relationship between Faroese sheep and nine other Northern European breeds with genotyping data in the Sheep HapMap database. Faroese and Icelandic animals, together with Norwegian Spael, Finnsheep, Soay and Boreray belong to Northern European short-tailed sheep. **B** MDS plot including all sheep breeds in the HapMap database, together with Faroese sheep and the Norwegian White Sheep (NKS). Note how the Northern European short-tailed sheep stand out from the remaining global breeds, and that Faroese animals keep their peripheral position, while Soay and Boreray moved closer to Norwegian Spael





Conclusions

Faroese sheep positioned their genetic variations well outside the geographically surrounding sheep breeds and thus extended the known global genetic variation in sheep. The main hypothesis for this result is the possibility of an unbroken genetic line from the present animals to pre-year 1600 animals, possibly also pre-year 1300 animals, which might have consisted of ancient Norse sheep with British/Irish sheep inbred into the population.

Abbreviations

F	Inbreeding coefficient
F _{st}	Fixation index
MDS	Multidimensional scaling
NKS	Norsk Kvit Sau (Norwegian White Sheep)
SNP	Single nucleotide polymorphism

Supplementary Information

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Supplementary Material 1.

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Authors' contributions

EKH contributed to designing the work, acquired the blood samples together with the veterinarian, performed all the experimental work, analyzed the data, and edited the manuscript; JIG contributed to designing the work, had all the contacts with the funders, and contributed to editing the manuscript; DIV contributed to designing the analytical work, supervised EKH in setting up the data for analysis, analyzed the data, created the figures, and contributed to editing the manuscript; SOM contributed to designing the work and supervised the experimental part of the work, drafted the manuscript, and edited the manuscript. All authors have read and approved the final manuscript and consent in submitting to BMC Genomic Data.

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Data availability

The microarray datasets for Faroese sheep and Norwegian White Sheep are available in the European Variation Archive under the accession numbers PRJEB81861 (https://www.ebi.ac.uk/ena/browser/view/PRJEB81861) and PRJEB82836 (https://www.ebi.ac.uk/ena/browser/view/PRJEB82836), respectively.

Declarations

Ethics approval and consent to participate

This project complies with all national guidelines and laws, including those concerning ethics, by being permitted by the Chief Veterinary Officer of the Faroe Islands. The blood samples were drawn by a certified veterinarian as required by the Chief Veterinary Officer. The authors declare that the practical execution of the project complies with all relevant and accepted international guidelines, including the ICLAS Ethical Guidelines for Researchers. The informed consent was obtained from the animal owners, and they made their animals available for this project without any payment or compensation.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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