Small Ruminant Research 253 (2025) 107650

Contents lists available at ScienceDirect

Small Ruminant Research

journal homepage: www.elsevier.com/locate/smallrumres

Inbreeding and population structure in the Swedish Landrace goat and a signature of selection in the region of the casein genes

Bernadett Hegedűs [a,b], Piter Bijma [a], Anna M. Johansson [b,*]

[a] Animal Breeding and Genomics, Wageningen University and Research, Droevendaalsesteeg 1, Wageningen 6708 PB, the Netherlands
[b] Department of Animal Biosciences, Swedish University of Agricultural Sciences, Box 7023, Uppsala 75007, Sweden

ARTICLE INFO

Keywords:
SNP
Genetic diversity
ROH
Casein genes

ABSTRACT

The Swedish Landrace goat is the most common dairy goat in Sweden. However, very few genetic studies have been done on this breed. This study therefore aimed to describe the population structure and the level of inbreeding. Forty-eight (48) samples from eight farms were studied with a medium density SNP chip. To study the population structure, a principal coordinate analysis and an admixture analysis were conducted. The level of inbreeding was investigated with three measures; observed heterozygosity, F_{ROH} and approximated coancestry. The results show that there is some structuring in the population and this structure is not solely due to the geographic location of these farms. The inbreeding level varies between the farms but is comparable to other European non-island goat populations. A potential signature of selection was identified on Chromosome 6 with ROH in the region of the casein genes. This is an important finding that shows that there have been selection for milk production.

1. Introduction

The Swedish Landrace goat is a dairy breed that is used in Sweden for milk and cheese production. It is the most common goat breed in Sweden. This goat breed has a high average milk yield which is about 700 kg per goat per year. However, there is also quite some variation regarding milk yield in this breed with some animals producing 2000 kg of milk per year (Svenska Getavelsförbundet, 2021). The Swedish Landrace goat is a breed without a uniform phenotype. This breed is known for its different colours and patterns. There is also variation when it comes to hair length as no selection has been conducted on this trait. Furthermore, this breed holds diversity regarding the presence, size and shape of horns (Svenska Getavelsförbundet, 2021).

The Swedish organization responsible for the Swedish Landrace goats is called Svenska Getavelsförbundet. However, this is a voluntary organisation, and the actual number of goats in Sweden is very likely higher than the number of registered animals. The organization currently uses the Elitlamm software which was originally developed for sheep breeders. The lack of a software specifically for goats sometimes causes difficulty when handling and collecting data which contributes to the difficulties of getting all goat owners to register the pedigrees of their goats.

The study by Manunza et al. (2023) showed that the Swedish Landrace goat is closely related to the Norwegian, Finnish and Icelandic goat breeds and most closely related to the Norweigian coastal goats. There is no reliable information on the number of breeding individuals currently or the sex distribution among the breeding individuals since not all goats are registered. Furthermore, there is no reliable information on the exact geographical distribution of this breed. There is a lack of studies concerning the Swedish Landrace goat (and Swedish goat breeds in general). The studies available mostly describe the milk quality, milk yield and milk compositions of this breed (Johansson et al., 2015; Yurchenko et al., 2018). A recent study looked into the prevalence of a deletion in the casein alpha s1 (*CSN1S1*) gene, (previously described by Hayes et al. (2006) and Dagnachew et al. (2011) in Norwegian populations), in Swedish goat herds and its relation to milk properties (Johansson et al., 2023). The results of that study show that the deletion that contributes to the reduced casein content in the milk is frequent in Swedish dairy goats, 59 % was homozygous for this deletion.

The FAO classifies the Swedish Landrace goat breed as endangered (FAO, 2025). The relationship to other European goat breeds have recently been studied (Manunza et al., 2023) but the genetic diversity and population structure among Swedish herds has not been investigated in detail and studies like the ones in the Swedish sheep breeds

* Corresponding author.
E-mail addresses: bernadett.hegedus@wur.nl (B. Hegedűs), piter.bijma@wur.nl (P. Bijma), anna.johansson@slu.se (A.M. Johansson).

https://doi.org/10.1016/j.smallrumres.2025.107650
Received 11 June 2025; Received in revised form 2 November 2025; Accepted 4 November 2025
Available online 6 November 2025

(Ghoreishifar et al., 2021; Rochus et al., 2020; Rochus and Johansson, 2017) are needed in order to make educated decisions on the conservation of this breed. This is especially needed as the Swedish goat breeding association (Svenska Getavelsförbundet) suggests selecting against the highly prevalent deletion in the *CSN1S1* gene. Strong selection for the absence of this deletion puts the population at risk of inbreeding. Thanks to the availability of a medium density SNP chip for goats (Tosser-Klopp et al., 2014) the genomic diversity of this livestock species can be characterised like other species. Therefore, the aim of this study was to study the genetic diversity in the Swedish Landrace goat. Firstly, we investigated whether there is a clear structure in this breed with regard to the herds and geographical locations. To answer this question, we used an admixture analysis and a principal coordinate analysis. Secondly, we investigated the inbreeding level of the Swedish Landrace goat with the help of the observed heterozygosity and compared the results to other European goat breeds. Furthermore, we estimated the coancestry both between- and within-herds. Lastly, we estimated the inbreeding coefficient based on runs of homozygosity.

2. Material and methods

48 Swedish Landrace goats were genotyped with the Goat SNP50 Bead Chip (Tosser-Klopp et al., 2014). This SNP chip includes the 29 autosomes and has an average spacing of markers of around 60 kbps. The 48 genotyped individuals were born in eight different herds in Sweden. The samples in this study are a subset of samples used in the study of (Persson et al., 2022) who looked at the prevalence of caseous lymphadenitis (CLA) and caprine arthritis encephalitis (CAE) in dairy goats Sweden. The choice of the selected 48 individuals was based on the consent from the owners for genetic studies and pedigree data to eliminate closely related individuals. The SNP genotypes were the same as those included in Manunza et al. (2023). Table 1 shows the number of individuals from each herd as well as the anonymized animals IDs and if the farm was in Northern or Southern Sweden. Three of the farms were in the Southern part of Sweden and the remaining five farms were located in the Northern part of Sweden.

Plink 1.9 (Purcell et al., 2007) was used for the quality control on the raw data. There were three sets of quality controls. The details of each quality control can be found in Table 2 and will be explained below. A general quality control was used to filter out variants with a lower than 0.9 call rate and a minor allele frequency of 0.02 or lower (allele counts of 0 and 1). Furthermore, SNPs, where the p value of the Hardy-Weinberg equilibrium exact test was lower than 0.0001 were discarded. A 0.9 genotype call rate was also set on an individual level, but all 48 individuals passed this quality control. The dataset after this quality control was used for the calculation of observed heterozygosity and the PCoA. This quality control was followed up by LD- pruning for the admixture analysis.

The second quality control differed from the first one in the level of filtering on SNPs with missing values as the own function for calculating the approximated coancestry (see section 2.2.4) could not handle missing values. This extra filtering meant that SNPs that were not successfully genotyped in all the 48 individuals were removed from the dataset. The dataset after the second quality control was only used for the calculation of the approximated coancestries.

Table 1
Information on the number of samples from each herd with the corresponding animal IDs.

Herd ID	Number of samples	Animal IDs	Geographic location
Herd 1	9	Animals 1–9	Northern Sweden
Herd 2	8	Animals 10–17	Northern Sweden
Herd 3	7	Animals 18–24	Northern Sweden
Herd 4	4	Animals 25–28	Southern Sweden
Herd 5	1	Animal 29	Southern Sweden
Herd 6	7	Animals 30–36	Northern Sweden
Herd 7	5	Animals 37–41	Northern Sweden
Herd 8	7	Animals 41–48	Southern Sweden

Table 2
The parameters of the different quality controls. The first five column names refer to the commands in Plink. The last column states the number of SNPs left after the quality control.

	Geno[a]	Mind[b]	Maf[c]	Hwe[d]	Indep-pairwise[e]	Nr SNP
QC 1	0.1	0.1	0.02	0.0001	-	48,111
QC 1 (Admixture)	0.1	0.1	0.02	0.0001	50 5 0.2	9,839
QC 2	10^{-16}	0.1	0.02	0.0001	-	44,744
QC 3	0.1	0.1	-	0.0001	-	49,057

[a] Maximum missingness per SNP
[b] Maximum missingness per individual
[c] Minor allele frequency
[d] Hardy-Weinberg equilibrium exact test p-value
[e] Pruning for linkage disequilibrium, requires a window size in variant count, a variant count to shift the window at the end of each step and pairwise r^2 threshold, respectively.

A third quality control was needed for the calculation of the runs of homozygosity (ROH). There is no agreement in literature about the use of MAF filtering and LD pruning before ROH analysis. Meyermans et al. (2020) suggests using neither LD- pruning nor MAF filtering, as these might hinder the ROH detection by reducing the number of SNPs in the analysis too much. Therefore, in the third quality control neither of these filtering methods were used.

The observed heterozygosity was calculated with Plink 1.9 with the –het command (Purcell et al., 2007). In order to compare these results with published results of different goat populations in Europe the absolute number of heterozygous SNPs per individual was scaled by the total number of SNPs left after the quality control (see Table 2 QC 1).

The data used for the PCoA analysis was from QC 1. The PCoA was performed with the help of the –distance-matrix command in Plink 1.9 (Purcell et al., 2007), that created the similarity matrix as an input for the PCoA, and the function cmdscale() in R. For the plots presented in the Results section the first two principal coordinates are shown.

The genomic relationship matrix of the individuals with an allele frequency of 0.5 (p_i=0.5) was calculated with an own function. In this relationship matrix the diagonals represent the proportion of homozygous SNPs per individuals. The possible values for the relationship matrix range from -2 to 2, while negative values are not possible for the diagonals, as negative elements indicate opposite homozygotes. The used function was based on method 1 from VanRaden (2008) but with notation in **M** like in Hayes et al. (2009) and can be seen in Eqs. 1 and 2.

$$\mathbf{W} = \mathbf{M} - \mathbf{P} \tag{1}$$

$$\mathbf{G} = \frac{\mathbf{W}\mathbf{W}'}{2\sum_{i=1}^{nloc} p_i(1-p_i)} \tag{2}$$

M… matrix with the minor allele counts per individual with notation of 2, 1, 0 for 2, 1 and 0 copies of the minor allele, respectively

P… matrix with $2p_i$, as p = 0.5 the **P** matrix is an all-ones matrix

The **M** and **P** matrices had the dimensions of n*m, n being the number of individuals and m the number of markers. **G** had the dimensions n*n. The reason to choose p = 0.5 was that this way the elements of the **G** matrix are proportional to the expected heterozygosity of the offspring of any two individuals.

We approximated the population and herd specific coancestries with the average relatedness based on the relationship matrix mentioned above divided by two. These coancestries were calculated without the diagonals, as they would affect the results differently in each population given the small sample sizes.

The runs of homozygosity were calculated with the R package

detectRUNS (Biscarini et al., 2019). The function sldidingRUNS() was used, which resembles the method used by Plink. Table 3 shows the parameters used for slidingRUNS to run the analysis. The motivation for these parameters can be found in Appendix 1 and are based on work by Lencz et al. (2007), Purfield et al. (2012), Tosser-Klopp et al. (2014) and Meyermans et al. (2020).

The identified ROH were then used to calculate the inbreeding coefficient based on ROH. To calculate the inbreeding coefficient based on ROH the length of ROH segments is divided by the total length of the genome (Ceballos et al., 2018) (Eq. 5).

$$F_{ROH} = \frac{sum\ of\ ROH}{genome\ length} \quad (5)$$

For the admixture analysis the software Structure version 2.3.4 was used (Falush et al., 2007, 2003; Hubisz et al., 2009; Pritchard et al., 2000). For the input data for Structure the QC 1 (Admixture) (see Table 2) was used. The run length of the burn-in period was 10,000 iterations and the number of MCMC iterations after burn-in was also 10,000. The *admixture* model was used with the assumption of correlated allele frequencies between the populations. In the analysis the population IDs were used as sampling location indicators. The remaining settings were left to default. The choice of settings was based on the Structure documentation itself (Pritchard et al., 2010) and Wang (2017), who discusses common mistakes when choosing Structure parameters. The simulations were run for K 2–8 with 5 replicates for each K. For transparency reasons the exact input settings can be found in Appendix 2. To find the K that best describes the data the replicates from each K with the highest likelihoods were compared. For these seven chosen replicates the posterior probabilities were calculated, as suggested by the Structure documentation (Pritchard et al., 2010).

3. Results

3.1. Principal coordinate analysis

Fig. 1 shows the grouping of the 48 genotyped individuals regarding the first two principal coordinates. The first two principal coordinates together explained almost 15 % of the variance seen in these 48 individuals. Fig. 1 shows some grouping of individuals; some difference was visible between Herds 1, 2 and 7 (colours grey, orange and red in the figure). Herds 4, 5, 6 and 8 did not show a clear distinction (colours green, yellow, dark blue and pink). Furthermore, there was some distinction between individuals of Herd 2 (orange in the figure). One individual of Herd 3 (light blue in the figure) was grouped closer with individuals of Herd 1 (grey in the figure) than its own herd. One individual of Herd 1 also grouped closer to Herds 4 and 6 than to its own herd. When comparing Fig. 1 to the geographic location of the farms it is noticeable that the three herds that grouped more separately (Herds 1, 2 and 7) were herds that are located in the North of Sweden. The close grouping of Herds 4, 5, and 8, and Herds 3 and 6 cannot be explained by geographical proximity as Herds 4, 5 and 8 are located in the Southern part of Sweden while Herds 3 and 6 are in the Northern part.

Table 3
List of parameters for the ROH analysis with the package detectRUNS.

Parameter	Parameter name in detectRUNS	Value
Scanning window size	WindowSize	36
Scanning window threshold	Threshold	0.05
Minimal number of SNPs	minSNP	36
Minimal density	minDensity	1/70*
Maximal gap	maxGap	200 kb
Minimum length	minLengthBps	1000

* detectRUNS uses 1SNP/10 kb as their scale compared to Plink that uses distance between SNPs.

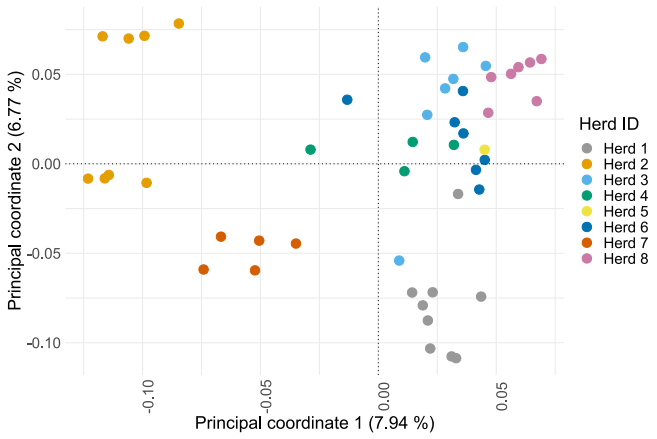

Fig. 1. Principal coordinate analysis of the Swedish Landrace Goat. All 48 individuals and 48,111 SNPs were used for the analysis presented here.

3.2. Admixture analysis

The admixture analysis run with the help of Structure showed some distinction but also similarities between the herds. Fig. 2 shows the proportions of ancestry in each individual for four assumed ancestral populations (K=4). For plots for K= {2,3,5,6,7,8} see Appendix 3 Figures S1-S6. K= 4 was the number of ancestral populations with the highest posterior probability and therefore it will be explained in more detail in the main text below. However, already the analysis with K= 2 showed some distinction between the herds; Herd 2 grouped mostly to a different ancestral population than the rest of the herds (Figure S1 in Appendix 3). As K was increased to 3 there still seemed to be a differentiation of Herd 2 from the other herds (Figure S3 in Appendix 3). Furthermore Herd 8 and Herd 3 showed a large proportion of shared assumed ancestral population.

The first thing that one might spot when looking at Fig. 2 where K= 4 is the uniqueness of Herd 2 when regarding proportions of assumed ancestral populations (see green colour in the plot for Goats 10–17). However, Herd 2 also showed some structuring within the herd; four individuals were also grouped close to Herd 7 (see grey colour both in Herd 2 and Herd 7). The 4 individuals from Herd 2 that grouped differently in the admixture analysis corresponded to the grouping seen in the PCoA (see Fig. 1 colour orange). Herds 1 and 8 were to a large proportion assigned to just one inferred population. Herd 1 also grouped separately in the PCoA; however, it was close to Herds 3, 4 and 5 when regarding the first principal coordinate (see Fig. 1). This close grouping was also visible in the proportion of the population indicated with blue in these populations (see the colour blue in Herds 1, 4, 5 and 6, Fig. 2). The shared ancestry described before (at K=3) for the Herds 3 and 8, is also visible in this plot (see the colour orange in Herds 3 and 8).

As K was increased during the analysis the rising number of assumed ancestral populations complicate the plots and make them more difficult to interpret. However, some characteristics that were mentioned with smaller K values are still visible in the plots with K= 8 (Figure S6 in Appendix 3). The uniqueness of Herd 2 is one example. The connection of Herd 2 and Herd 6 with regard to the 4 individuals in Herd 2 is also visible at K= 8. Lastly, the shared ancestry of Herds 4 and 6 also seemed constant.

3.3. Observed heterozygosity

The observed heterozygosities for the eight herds are illustrated in Fig. 3. This figure also contains mean observed heterozygosities of nine other European goat breeds as a reference. The nine additional goat breeds are Italian, Spanish and Norwegian goat breeds. Fig. 3 shows that the observed heterozygosities for the Swedish Landrace goat ranged

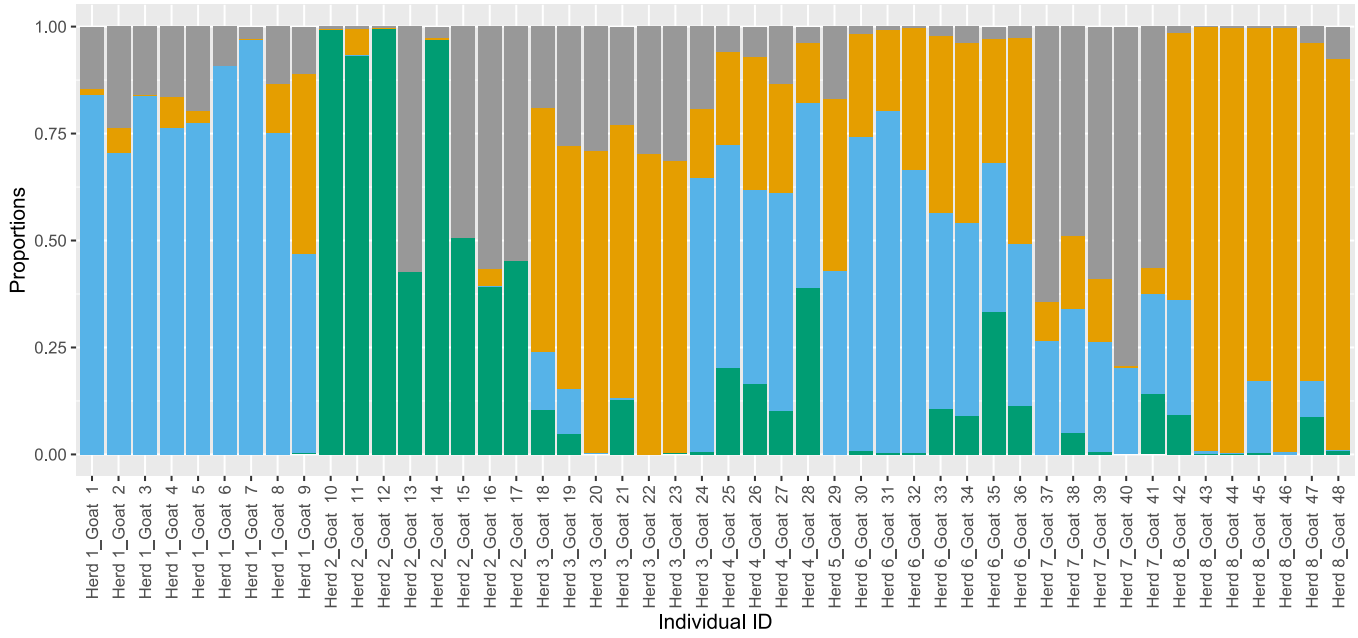

Fig. 2. Results of admixture analysis with K= 4. The proportion of the four assumed ancestral population in each individual is shown for all the 48 genotyped individuals. The colours in the plot refer to the four assumed ancestral populations and should not be confused with the colours used to indicate herds in other plots.

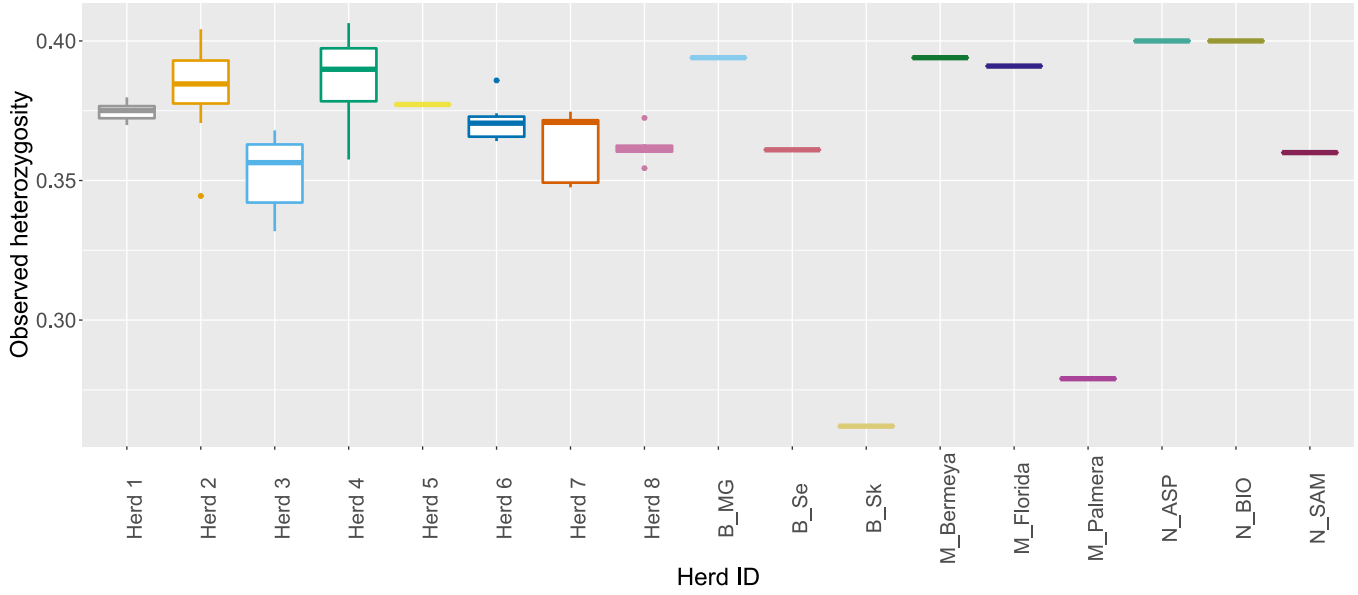

Fig. 3. Observed heterozygosities for herds of the Swedish Landrace goat (Herds 1–8) and for nine European goat breeds. The abbreviations B_MG, B_Se and B_Sk stand for the Norwegian Milk goat, Norwegian coastal goat Selje and the Norwegian coastal goat Skorpa (data from Berg et al. (2020)). The abbreviations M_Bermeya, M_Florida and M_Palmera stand for Spanish goat breeds investigated by Manunza et al. (2016). The abbreviations N_ASP, N_BIO and N_SAM stand for the Italian goat breeds Dell'Aspromonte, Bionda dell'Adamello, and Maltese sampled in Sardinia, respectively (data from Nicoloso et al. (2015)). The number of SNPs left after the quality control in the mentioned papers was 45772, 51136 and 39257 for Berg et al. (2020), Nicoloso et al. (2015) and Manunza et al. (2016), respectively. Note that both B_sk and M_Palmera are island populations. Note that the x axis does not start at 0.

from 0.33 to 0.41. This was comparable to other European non-island goat breeds, which were used as reference. The two goat breeds with a lower mean observed heterozygosity (B_Sk and M_Palmerain Fig. 3) were both island populations.

3.4. Inbreeding coefficient based on ROH

The inbreeding coefficients based on ROH for the 8 herds are illustrated in Figure S7 in Appendix 3. The inbreeding coefficients based on ROH were the highest in Herd 3. This is in line with what was visible in Fig. 3, as Herd 3 had the lowest observed heterozygosity. Note that whereas high values in Fig. 3 indicate higher diversity, high values in Figure S7 indicate lower diversity. A further difference between the Fig. 3 and Figure S7 is, that though in Fig. 3 all homozygous positions contributed to the observed homozygosity, not all homozygous positions contributed to the F_{ROH}, only the ones that are in longer segments.

3.5. Coancestry

As coancestry among individuals plays an important role in future

inbreeding, this was also investigated. Figure S8 in Appendix 3 shows the mean approximated coancestry in each herd. The mean approximated coancestry for all the sampled individuals is meant by the heading "all" in Figure S8. In Figure S8 it is visible that Herds 3 and 7 had the highest mean approximated coancestry and Herd 4 had the lowest mean approximated coancestry. The mean of approximated coancestry in Herd 4 was lower than the average of all the sampled individuals. The pattern visible in Figure S8 is in line with the plots for observed heterozygosity and F_{ROH} (compare Fig. 3 and Figure S7). An interpretation of the low value for Herd 4 could be that it is close to Stockholm and therefore there is a better infrastructure to trade animals. Furthermore, the mean approximated coancestry for all farms was lower than the mean of the individual within-herd values (see "all" in Figure S8). This shows that there is a structure present in the population; animals in farms were generally more related to individuals from the same farm than to individuals from other farms.

3.6. Runs of homozygosity

We created a plot for each chromosome showing the ROH found in the individuals. All the 29 plots can be found in Appendix 3 (Figures S9-S37). Note that only the individuals that had a ROH on the given chromosome show up on the y axis of these plots. So, if an individual is not present in a plot that means that that individual did not have a ROH on that chromosome. Chromosome 6 shows something unique; 41 of the animals (86 %) had a ROH in the region of 85–87 Mbps (see Figure S14 in Appendix 3). This was the only region with a ROH in so many animals. Fig. 4 zooms into this region of Chromosome 6 and shows the genes that can be found in this region and also all the individuals. The four casein genes that can be found in this region are *CSN1S1, CSN1S2, CSN2* and *CSN3*; the reference genome was ARS1 (Bickhart et al., 2017).

To investigate whether the ROH present in 41 of the individuals were the same haplotypes, a heatmap was created (Appendix 3 Figure S38). The heatmap confirms that there was indeed little variation in this region and opposite haplotypes were rare. An exception from this was Goat 42 from Herd 8 that showed the opposite haplotype at several loci. The prevalence of a one basepair deletion in exon 12 in *CSN1S1* (also studied by Hayes et al. (2006), Dagnachew et al. (2011), Johansson et al. (2023)) for 45 of the 48 goats studied in the current paper was studied in a master thesis (Gunnarsson, 2020) and the other three samples have been genotyped later. The genotype distribution was 30 DD (D meaning deletion), 9 DA, 4 DG, 3 AG, 1 AA, and 1 GG among the 48 goats in this paper. The deletion genotype of all the individuals was compared to the ROH presented in Figure S14 and Fig. 4. The comparison showed that the homozygosity status is mostly similar between the ROH plot and the deletion genotypes. The only difference was that all the goats with the genotypes DA (heterozygous for the deletion) showed up as having a ROH in the plot. The individuals in question were Goats 2, 10, 11, 13, 15, 16, 17, 38 and 43. The heterozygous individuals for the genotype DG did not show up as ROH. Furthermore, Goat 42 that had the opposite haplotype in the heatmap was also the individual that had the genotype GG at the position of the one base pair deletion in exon 12 of the *CSN1S1* gene. This pattern suggests that the deletion happened on the already existing ROH haplotype.

4. Discussion

The aim of this paper was to study the genetic diversity in the Swedish Landrace goat as there are very few genetic studies conducted on any of the goat breeds in Sweden. The results shown here indicate that there is some structuring among the sampled herds, as shown by the PCoA and the admixture plots (see Figs. 1, 2 and Appendix 3 Figures S1-S6). Among the herds there were also some that grouped closer together in the PCoA plot and showed a lot of similarity in the admixture plots indicated by shared proportions of the same ancestral population. The fact that individuals were asymmetrically assigned to the inferred populations in the admixture analyses indicates that the structure detected is real and not an artefact. In case of an artefact, one would expect the individuals to be assigned to the inferred populations to equal proportions (Pritchard et al., 2010). We would like to note that in order to find the true number of underlying ancestral populations probably more MCMC iterations would have been necessary in the admixture analysis, however finding the true number of ancestral populations was not the focus of the current paper.

The estimation of approximated coancestry also provides some information on the structure of the populations. The mean coancestry was

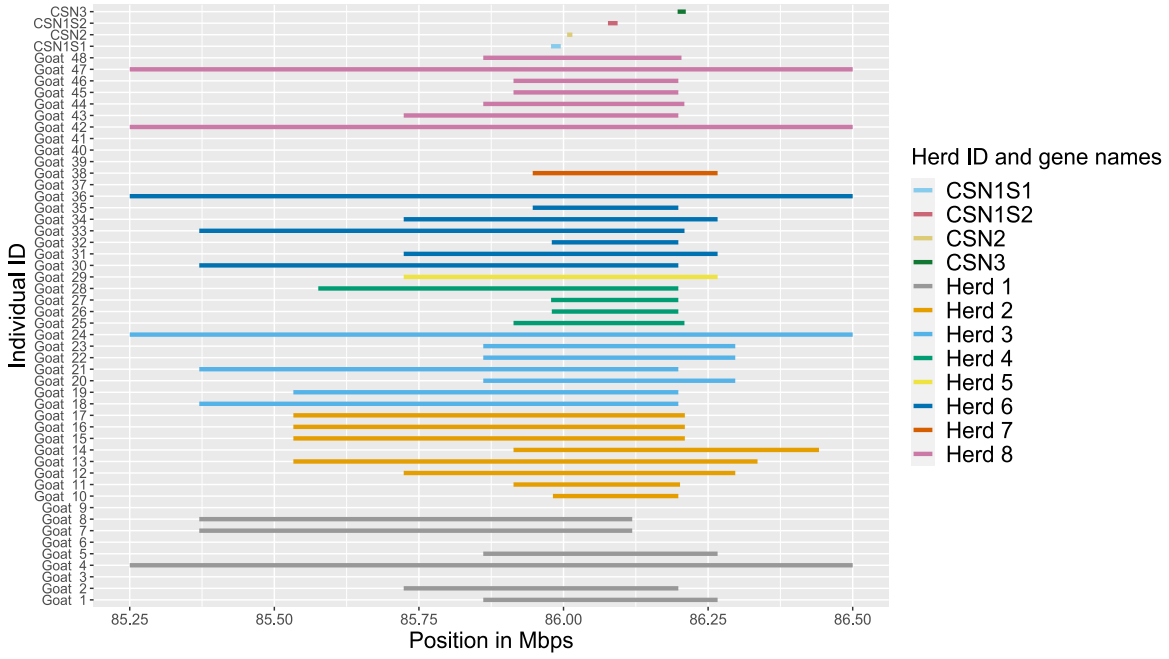

Fig. 4. ROH segments per individual at 85.25–86.5 Mbps on Chromosome 6. Note that for illustration in this figure all individuals are present on the y axis, even if they do not have a ROH in this region. The four casein genes are marked in the first four rows.

lower than the averages of all the within-herd coancestries (see Figure S8), indicating structuring between farms. Regarding the inbreeding some difference was visible between the herds, however, all the herds were in the range of the values that had been observed in other European non-island goat populations (see Fig. 3 regarding observed heterozygosities). Both the inbreeding measures, observed heterozygosity and F_{ROH}, gave the same picture when ranking the herds of the Swedish goat with regard to level of inbreeding.

The range of F_{ROH} calculated for the Swedish Landrace goat was similar to the values observed in the study of Berg et al. (2020) where the means for the two non-island populations were 0.074 and 0.115 for MG and Se respectively (for explanation about the breed abbreviations please refer to the legend of Fig. 3). The F_{ROH} for the island population (Sk) was higher (0.347) than the values observed in in Figure S7. The study of Berg et al. (2020) used the same SNP chip as the one used in this study. However, it is difficult to compare results based on identified ROH as often not all the input parameters are published.

The calculation of coancestry between and within herds aimed to assess the risk of future inbreeding. It showed that the herds, currently having a higher level of inbreeding are expected to follow the same trend unless new less related animals are introduced into these herds. Furthermore, we showed that the average coancestry between all the sampled individuals was lower than of all but one individual herds. This result shows that future inbreeding could somewhat be avoided by trading more animals among farms.

The ROH found on Chromosome 6 is a very interesting aspect of this study. The ROH found in the region of 85.25–86.50 Mbps on chromosome 6 could indicate the history of selection on the casein genes in this region. As the casein genes are responsible for more than 80 % of the protein content in the milk (Ceballos et al., 2009) and the goats in question are dairy goats, this is a logical finding. Furthermore, here we compared the ROH found in this study with genotypes for a deletion on exon 12 of *CSN1S1* described to reduce protein and fat yield and increase milk yield (Hayes et al., 2006, Dagnachew et al., 2011, Johansson et al., 2023). This mutation was found to have a high frequency both in Norway and Sweden (Hayes et al., 2006; Johansson et al., 2023), which could mean that the selection of the goats in the past was based on the quantity of the produced milk. In the comparison of the deletion genotypes of exon 12 in *CSN1S1* and the ROH detected with the medium density SNP chip it was seen that all of the individuals that were heterozygous for the deletion and the ancestral A allele had a ROH at this position. These findings indicate that before the deletion occurred there were two haplotypes, one with the A allele and one with the G allele, and that the mutation with the deletion occurred on the haplotype with the A allele. Since the deletion and the A allele have identical haplotypes for the SNP markers in the region of the casein genes, the SNP array used in the present study cannot be used for selecting goats that have the favourable A allele (and thereby produce milk with increased protein content). To be able to distinguish the goats with the A allele, Sanger sequencing will be needed (as has been done in Johansson et al. (2023). In addition to *CSN1S1* also the genes *CSN2* and *CSN1S2* are within the region of the ROH (Fig. 4) and there could also be unknown mutations in one of these genes that have been the target of selection. It should be noted that *CSN3* was outside the ROH in a few of the goats.

A recent study looking into the signatures of selection in Swiss goat breeds with whole genome sequencing data did not find any ROH on Chromosome 6, which was present in at least 80 % of their samples (Signer-Hasler et al., 2022).

In addition to geographic distance, there is another factor that might have an effect on the structuring and exchange of animals; the caprine arthritis encephalitis (CAE) status of the farms. CAE is disease that have been found in 14.6 % of goats and in 50 % of the investigated goat farms in Sweden (Persson et al., 2022). Farms that are classified as CAE-free in the control program in Sweden can only keep this status if the animals they add to their herds are also from CAE-free farms. On the other hand, if a farm is not classified as CAE-free then it can purchase individuals from any farm regardless of the CAE status. This structuring of farms could potentially have an effect on the inbreeding level of the individuals in farms, if for example the number of farms that are CAE-free is low. This status was not easily accessible for the animals used in this study.

There are some risks that should be considered when breeding the Swedish Landrace goat in the future. Firstly, the Swedish goat breeding organization emphasizes the breeding against the deletion on exon 12 of *CSN1S1* in order to increase the protein yield of the milk produced (Svenska Getavelsförbundet, 2021). Given the potential high prevalence of this mutation shown by Johansson et al. (2023), breeding against this mutation with a high intensity could result in a high level on inbreeding in the future. A possible solution could be to include the mutation into an index in combination with the other breeding goal traits and make use of optimal contribution selection (Meuwissen, 1997) to control the rate of inbreeding while simultaneously reducing the prevalence of the mutation and improving the breeding goal. Optimal contribution selection is a method to balance the genetic change and the rate of inbreeding based on preferred constraints by calculating contributions with which an animal should contribute to the next generation. Secondly, a potential risk for inbreeding is posed by the grouping of farms in CAE-free and not CAE-free. This grouping is epidemiologically relevant, however it should be closely monitored and studied how this grouping affects the within group coancestry of the CAE-free farms and the not CAE-free farms. These coancestries should be compared to the overall coancestry of the whole Swedish Landrace goat population and monitored over time. Furthermore, this analysis would answer the question to what extent the CAE status of the farms affects the structure visible in this goat breed. Thirdly, there is a lack of funding in the Swedish Goat Association which is a voluntary organization. This leads to problems when it comes to data organization and handling. It would benefit the Swedish goat breeders, if projects were created to store phenotypic and genotypic data for the Swedish goat breeds. This would be a prerequisite of a more organized breeding programme for the farmers. A breeding programme with the goal of improving the production traits in the Swedish Landrace goat would help it to survive in the market for longer, and thereby secure the population.

Lastly, the finding of the ROH segment on Chromosome 6 opens up the question of looking for patterns of selection in the Swedish Landrace goats. As the Scandinavian goat breeds are closely related (Svenska Getavelsförbundet, 2021) it would be interesting to see if there are any region-specific selection patterns.

5. Conclusion

We found some population structure in the Swedish Landrace goat and this structure was not solely due to the geographic location of the sampled farms. The inbreeding level of the farms was comparable to other European non-island goat populations. In case of a strong selection against the deletion in exon 12 of the *CSN1S1* the inbreeding could increase and therefore, the use of optimal contribution selection is recommended. The inbreeding level could also be affected by the restricted trading of the animals due to the CAE status of the farms, which needs to be monitored.

Funding

This work was supported by The Swedish goat breeding association (Svenska getavelsförbundet) and The Swedish board of Agriculture.

CRediT authorship contribution statement

Bernadett Hegedűs: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis. **Piter Bijma:** Writing – review & editing, Supervision. **Anna M Johansson:** Supervision, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no competing interests

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.smallrumres.2025.107650.

References

Berg, P., Groeneveld, L.F., Brekke, C., Våge, D.I., Sørheim, K.M., Grøva, L., 2020. Genetic characterization of a small closed island population of Norwegian coastal goat. Acta Agric. Scand. A Anim. Sci. 69, 47–52. https://doi.org/10.1080/09064702.2020.1729852.

Bickhart, D.M., Rosen, B.D., Koren, S., Sayre, B.L., Hastie, A.R., Chan, S., Lee, J., Lam, E. T., Liachko, I., Sullivan, S.T., Burton, J.N., Huson, H.J., Nystrom, J.C., Kelley, C.M., Hutchison, J.L., Zhou, Y., Sun, J., Crisà, A., Ponce de León, F.A., Schwartz, J.C., Hammond, J.A., Waldbieser, G.C., Schroeder, S.G., Liu, G.E., Dunham, M.J., Shendure, J., Sonstegard, T.S., Phillippy, A.M., Van Tassell, C.P., Smith, T.P.L., 2017. Single-molecule sequencing and chromatin conformation capture enable de novo reference assembly of the domestic goat genome. Nat. Genet 49, 643–650. https://doi.org/10.1038/ng.3802.

Biscarini, F., Cozzi, P., Gaspa, G., Marras, G., 2019. detectRUNS: Detect Runs of Homozygosity and Runs of Heterozygosity in Diploid Genomes.

Ceballos, F.C., Joshi, P.K., Clark, D.W., Ramsay, M., Wilson, J.F., 2018. Runs of homozygosity: windows into population history and trait architecture. Nat. Rev. Genet 19, 220–234. https://doi.org/10.1038/nrg.2017.109.

Ceballos, L.S., Morales, E.R., de la Torre Adarve, G., Castro, J.D., Martínez, L.P., Sampelayo, M.R.S., 2009. Composition of goat and cow milk produced under similar conditions and analyzed by identical methodology. J. Food Compos Anal. 22, 322–329. https://doi.org/10.1016/j.jfca.2008.10.020.

Dagnachew, B.S., Thaller, G., Lien, S., Ådnøy, T., 2011. Casein SNP in Norwegian goats: additive and dominance effects on milk composition and quality. Genet Sel. Evol. 43, 31. https://doi.org/10.1186/1297-9686-43-31.

Falush, D., Stephens, M., Pritchard, J.K., 2003. Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164, 1567–1587. https://doi.org/10.1093/genetics/164.4.1567.

Falush, D., Stephens, M., Pritchard, J., 2007. Inference of population STRUCTURE using multilocus genotype data: dominant markers and null alleles. Mol. Ecol. Notes 7, 574–578. https://doi.org/10.1111/j.1471-8286.2007.01758.x.

FAO. (2025). *Domestic Animal Diversity Information System (DAD-IS): Browse by country and species*. Retrieved November 10, 2025, from https://www.fao.org/dad-is/browse-by-country-and-species/en/.

Ghoreishifar, S.M., Rochus, C.M., Moghaddaszadeh-Ahrabi, S., Davoudi, P., Salek Ardestani, S., Zinovieva, N.A., Deniskova, T.E., Johansson, A.M., 2021. Shared ancestry and signatures of recent selection in Gotland Sheep. Genes 12, 433. https://doi.org/10.3390/genes12030433.

Gunnarsson, S. 2020. Resistens mot Caprin artrit encefalit och genetisk variation i αS1-kasein genen (CSN1S1) hos svenska getter. Second cycle, A2E. Uppsala: SLU, Dept. of Animal Breeding and Genetics. ⟨https://stud.epsilon.slu.se/16330/⟩.

Hayes, B.J., Bowman, P.J., Chamberlain, A.C., Verbyla, K., Goddard, M.E., 2009. Accuracy of genomic breeding values in multi-breed dairy cattle populations. Genet Sel. Evol. 41, 1–9. https://doi.org/10.1186/1297-9686-41-51.

Hayes, B., Hagesæther, N., Ådnøy, T., Pellerud, G., Berg, P.R., Lien, S., 2006. Effects on production traits of haplotypes among casein genes in Norwegian Goats and evidence for a site of preferential recombination. Genetics 174, 455–464. https://doi.org/10.1534/genetics.106.058966.

Hubisz, M.J., Falush, D., Stephens, M., Pritchard, J.K., 2009. Inferring weak population structure with the assistance of sample group information. Mol. Ecol. Resour. 9, 1322–1332. https://doi.org/10.1111/j.1755-0998.2009.02591.x.

Johansson, M., Högberg, M., Andrén, A., 2015. Relation Between αS1-Casein content and coagulation properties of milk from Swedish dairy goats. TOFSJ 9, 1–4. https://doi.org/10.2174/1874256401509010001.

Johansson, M., Lundh, Å., Johansson, A.M., 2023. Relation between αS1-casein, genotype, and quality traits of milk from Swedish dairy goats. J. Dairy Sci. 106, 5582–5592. https://doi.org/10.3168/jds.2022-22857.

Lencz, T., Lambert, C., DeRosse, P., Burdick, K.E., Morgan, T.V., Kane, J.M., Kucherlapati, R., Malhotra, A.K., 2007. Runs of homozygosity reveal highly penetrant recessive loci in Schizophrenia. Proc. Natl. Acad. Sci. USA 104, 19942–19947. https://doi.org/10.1073/pnas.0710021104.

Manunza, A., Noce, A., Serradilla, J.M., Goyache, F., Martínez, A., Capote, J., Delgado, J. V., Jordana, J., Muñoz, E., Molina, A., Landi, V., Pons, A., Balteanu, V., Traoré, A., Vidilla, M., Sánchez-Rodríguez, M., Sànchez, A., Cardoso, T.F., Amills, M., 2016. A genome-wide perspective about the diversity and demographic history of seven Spanish goat breeds. Genet Sel. Evol. 48, 52. https://doi.org/10.1186/s12711-016-0229-6.

Manunza, A., Ramirez-Diaz, J., Cozzi, P., Lazzari, B., Tosser-Klopp, G., Servin, B., Johansson, A.M., Grøva, L., Berg, P., Våge, D.I., Stella, A., 2023. Genetic diversity and historical demography of underutilised goat breeds in North-Western Europe. Sci. Rep. 13, 20728. https://doi.org/10.1038/s41598-023-48005-8.

Meuwissen, T.H.E., 1997. Maximizing the response of selection with a predefined rate of inbreeding. J. Anim. Sci. 75, 934–940.

Meyermans, R., Gorssen, W., Buys, N., Janssens, S., 2020. How to study runs of homozygosity using PLINK? A guide for analyzing medium density SNP data in livestock and pet species. BMC Genom. 21, 94. https://doi.org/10.1186/s12864-020-6463-x.

Nicoloso, L., Bomba, L., Colli, L., Negrini, R., Milanesi, M., Mazza, R., Sechi, T., Frattini, S., Talenti, A., Coizet, B., Chessa, S., Marletta, D., D'Andrea, M., Bordonaro, S., Ptak, G., Carta, A., Pagnacco, G., Valentini, A., Pilla, F., Ajmone-Marsan, P., Crepaldi, P., 2015. Genetic diversity of Italian goat breeds assessed with a medium-density SNP chip. Genet Sel. Evol. 47, 1–10. https://doi.org/10.1186/s12711-015-0140-6.

Persson, Y., Andersson, E., Frössling, J., Wensman, J.J., 2022. Occurrence of CAE and CLA in Swedish Dairy Goats and comparison of serum and milk as sampling material. Dairy 3, 190–198. https://doi.org/10.3390/dairy3010015.

Pritchard, J.K., Stephens, M., Donnelly, P., 2000. Inference of population structure using multilocus genotype data. Genetics 155, 945–959.

Pritchard, J., Wen, X., Falush, D., 2010. Documentation for structure software: Version 2.3.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M.A.R., Bender, D., Maller, J., Sklar, P., de Bakker, P.I.W., Daly, M.J., Sham, P.C., 2007. PLINK: A Tool Set for Whole-Genome Association and Population-Based Linkage Analyses. Am. J. Hum. Genet 81, 559–575. https://doi.org/10.1086/519795.

Purfield, D.C., Berry, D.P., McParland, S., Bradley, D.G., 2012. Runs of homozygosity and population history in cattle. BMC Genet 13, 70. https://doi.org/10.1186/1471-2156-13-70.

Rochus, C.M., Johansson, A.M., 2017. Estimation of genetic diversity in Gute sheep: pedigree and microsatellite analyses of an ancient Swedish breed. Hereditas 154, 4. https://doi.org/10.1186/s41065-017-0026-4.

Rochus, C.M., Jonas, E., Johansson, A.M., 2020. Population structure of five native sheep breeds of Sweden estimated with high density SNP genotypes. BMC Genet 21, 27. https://doi.org/10.1186/s12863-020-0827-8.

Signer-Hasler, H., Henkel, J., Bangerter, E., Bulut, Z., Drögemüller, C., Leeb, T., Flury, C., 2022. Runs of homozygosity in Swiss goats reveal genetic changes associated with domestication and modern selection. Genet Sel. Evol. 54, 1–11. https://doi.org/10.1186/s12711-022-00695-w.

Svenska Getavelsförbundet, 2021. Avelsprogram för getter av svensk lantras från år 2020.

Tosser-Klopp, G., Bardou, P., Bouchez, O., Cabau, C., Crooijmans, R., Dong, Y., Donnadieu-Tonon, C., Eggen, A., Heuven, H.C.M., Jamli, S., Jiken, A.J., Klopp, C., Lawley, C.T., McEwan, J., Martin, P., Moreno, C.R., Mulsant, P., Nabihoudine, I., Pailhoux, E., Palhière, I., Rupp, R., Sarry, J., Sayre, B.L., Tircazes, A., Wang, J., Wang, W., Zhang, W., Consortium, the I.G.G., 2014. Design and characterization of a 52K SNP chip for goats. PLOS ONE 9, e86227. https://doi.org/10.1371/journal.pone.0086227.

VanRaden, P.M., 2008. Efficient methods to compute genomic predictions. J. Dairy Sci. 91, 4414–4423. https://doi.org/10.3168/jds.2007-0980.

Wang, J., 2017. The computer program structure for assigning individuals to populations: easy to use but easier to misuse. Mol. Ecol. Resour. 17, 981–990. https://doi.org/10.1111/1755-0998.12650.

Yurchenko, S., Sats, A., Tatar, V., Kaart, T., Mootse, H., Jõudu, I., 2018. Fatty acid profile of milk from Saanen and Swedish Landrace goats. Food Chem. 254, 326–332. https://doi.org/10.1016/j.foodchem.2018.02.041.