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Genetic diversity in German Pomeranian Coarsewool sheep and the possibility of breeding for maedi-visna resistance

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Abstract. Knowledge of genetic diversity among sheep breeds is essential for conserving genetic resources, in particular when selective-breeding programs are taken into consideration, for example, to enhance disease resistance. Maedi-visna virus (MVV) is an incurable, progressive sheep disease caused by a small-ruminant lentivirus (SRLV) infection. In certain sheep breeds, MVV susceptibility has been associated with the allele E of the ovine transmembrane protein gene (*TMEM154*), whereas the allele K in a homozygous state is protective. The present study estimated the genetic diversity of the native German Pomeranian Coarsewool (RPL, "Rauhwolliges Pommersches Landschaf") sheep breed and evaluated the possibility of breeding for MVV resistance. A total of 185 RPL sheep were genotyped using the Illumina ovine 50K single-nucleotide polymorphism (SNP) BeadChip to calculate genetic diversity indicators such as effective population size ($Ne_{13} = 116$) and Wright's F statistical indices ($F_{IS} = 0.005$). The mean inbreeding coefficient based on runs of homozygosity (F_{ROH}) was 6.2 %, with a moderate correlation (0.42) with the pedigree-based coefficient (F_{PED}). Overall, the calculated genetic diversity parameters indicate that the diversity in the RPL breed is not at risk. Thus, breeding for MVV resistance would be possible without a major loss of genetic diversity due to the relatively high frequency of the allele K (54 %). However, selection for the *TMEM154* allele K across the entire breed is not advised until further studies confirm its protective effect against MVV in the RPL breed.

1 Introduction

Sheep (*Ovis aries*) are descendants of the wild Asian mouflon and were one of the first domesticated species around 10 000 years ago (Scherf and Pilling, 2015). Since domestication, 1500 unique sheep breeds have developed worldwide due to local environmental and human management adaptations (Scherf and Pilling, 2015; Yang et al., 2016). These various influences have resulted in great genetic diversity within the sheep population, but this diversity is currently threatened by economic forces and modernized agriculture (Tisdell, 2003). More than any other continent, Europe is home to almost half of all sheep breeds (Rischkowsky and Pilling, 2007). Of these European breeds, 14 % are already extinct, 43 % are at risk of extinction, and only 15 % are considered "safe" (FAO, 2024). The loss of this diversity is also leading to increased inbreeding, resulting in a higher risk of recessive genetic defects and jeopardizing genetic improvement and adaptation to future environmental, food production, and disease challenges (Keller and Waller, 2002; Rege and Gibson, 2003). The preservation of the genetic diversity of local breeds is considered imperative due to the role of this diversity as a genetic resource for potential future benefits and as cultural heritage (Mendelsohn, 2003). In this context, studying the genetic diversity of well-adapted local breeds is important to develop suitable breeding programs that will help to maintain and improve their genetics (Scherf and Pilling, 2015).

In Germany, 20 of the approximately 40 native sheep breeds are endangered, particularly the so-called "land sheep

Figure 1. Adult RPL ewes (blue-gray wool) with lambs (brown wool).

breeds" such as the Pomeranian Coarsewool sheep (RPL, "Rauhwolliges Pommersches Landschaf") (GEH, 2024; Scherf, 2000). The RPL is a medium-sized, polled sheep with gray to blue-gray wool on their bodies, whereas their heads and legs are black and free of wool (Gaede, 1926; Grumbach, 2002) (Fig. 1). This breed originated from the island of Rügen in Pomerania and resulted from crosses between the extinct German Zaupelschaf and Hannoversche Landschaf breeds (Gaede, 1926; Grumbach and Zupp, 2008). In 1936, the RPL population comprised 70 200 animals. This number increased to 110 000 after the Second World War due to the breed's high robustness and low maintenance requirements (Grumbach, 2002). However, as the economic situation stabilized, sheep breeds with higher productivity were favored, resulting in a decline in the RPL population (Grumbach and Zupp, 1992). In 1962, the last three registered RPL breeding sheep were shown at an exhibition (Grumbach, 2002).

Conservation efforts with respect to this indigenous German breed started in 1982, with 46 ewes, 7 rams, 8 female yearlings, and lambs, as part of a program that was initiated by the United Nations (UN) resolution for the protection of endangered cultural breeds (Grumbach, 2002; Grumbach and Zupp, 1992). Initially, there were seven original Pomeranian ram lines, and these lines were later supplemented by the S-line from a breeder in southwestern Germany (IGRPL, 2024). Due to the limited original population size and the occurrence of bottlenecks, a line-rotation breeding method was implemented to avoid further inbreeding (Grumbach, 2002). This method is still used today, maintaining almost 3500 herdbook-registered RPL sheep in Germany (VDL, 2023). Although the population size is increasing, the RPL breed remains at risk according to the German Society for the Conservation of Old and Endangered Livestock Breeds (GEH). This is because the GEH considers not only the current population but also other factors with an influence on the situation of a breed, e.g., the number of active breeders, offspring

rates, and the existence of state subsidy programs (GEH, 2024).

An additional challenge in the conversation of genetic diversity is selective breeding for phenotypic traits or for functional traits, e.g., disease resistance. The RPL breed is known to be less susceptible to certain diseases, such as foot rot and scrapie (Drögemüller et al., 2004; Grumbach and Zupp, 2008; Rischkowsky and Pilling, 2007). For several years, prion protein gene (*PRNP*) alleles associated with scrapie resistance have been considered in the selection of sires (Grumbach, 2002). In the future, breeding for maedi-visna virus (MVV) resistance could be an additional opportunity. In many breeds, the susceptibility to MVV is associated with the ovine transmembrane protein 154 gene (*TMEM154*) (Heaton et al., 2012). At position 35 of the TMEM154 protein, the amino acid lysine (K allele) has a protective effect in certain sheep breeds in the homozygous form, while the presence of the amino acid glutamate (E allele) is associated with susceptibility. In the RPL breed, this association between *TMEM154* genotypes (hereafter always referring to the variation at position 35 of the protein) and MVV seropositivity showed a trend towards significance ($p = 0.09$) (Frölich et al., 2024). One discussed reason for the lack of significance was the low number of serologically MVV-positive sheep (30 out of 849), of which 26 RPL sheep carried the *TMEM154* genotype EK/EE and four exhibited the genotype KK. As the putative protective genotype KK and allele K were present in 28 % and 53 % of the genotyped RPL population, respectively, selective breeding could be an additional tool to eradicate MVV in infected flocks or even in the whole breed.

Before considering selective breeding for the *TMEM154* allele K, it is crucial to assess the current genetic diversity of this breed and understand how it might be influenced by selection. Various studies have calculated population genetic parameters such as effective population size (Ne), expected heterozygosity (He), observed heterozygosity (Ho), and Wright's F statistical indices (F_{IS}) to describe the genetic diversity of different sheep breeds (Adeniyi et al., 2022; Al-Mamun et al., 2015; Sveistiene and Tapio, 2021). However, the state-of-the-art method for inbreeding analysis using genotyping data is the calculation of the inbreeding coefficient (F_{ROH}) based on runs of homozygosity (ROH) (Peripolli et al., 2017). Many studies have shown that this coefficient is more accurate than the pedigree-based inbreeding coefficients (F_{PED}) (Burren et al., 2016; McQuillan et al., 2008; Meyermans et al., 2020a; Wiener et al., 2017).

The aim of the present study was to analyze the genetic diversity of the native German RPL breed and to investigate the possibility of selection for the *TMEM154* allele K without compromising genetic diversity by generating and analyzing Illumina ovine 50K single-nucleotide polymorphism (SNP) chip genotyping data of this breed. Various diversity parameters were calculated not only for the entire RPL breed but also for different ram lines, to assess the effect of the registration and consideration of ram lines in breeding decisions,

Table 1. Selection of RPL sheep for the SNP chip divided by ram lines, sex, and *TMEM154* genotype results.

Ram line	Sex		*TMEM154* genotype			Total
	Male	Female	EE	EK	KK	
Line 1	3	13	5	8	3	16
Line 2	7	10	8	5	4	17
Line 3	3	16	4	8	7	19
Line 4	9	20	6	12	11	29
Line 5	10	20	5	18	7	30
Line 6	7	10	2	12	3	17
Line 7	10	20	3	18	9	30
Line S	5	6	2	5	4	11
Unknown line	4	19	4	13	6	23
Total	58	134	39	99	54	192

and for *TMEM154* genotypes, to evaluate the potential loss of genetic diversity if sheep with certain genotypes were to be selected in the future.

2 Methods and materials

2.1 Animal sampling and genotyping

As part of this and a related project (Frölich et al., 2024), veterinarians collected ethylenediaminetetraacetic acid (EDTA) blood samples from 54 RPL flocks on voluntarily participating farms across nine German federal states (Baden-Württemberg, Brandenburg, Hesse, Lower Saxony, Mecklenburg–Western Pomerania, North Rhine-Westphalia, Saxony, Saxony-Anhalt, and Schleswig-Holstein). A representative set of not closely related RPL sheep (no first- or second-degree relatedness) was chosen for genotyping based on pedigree information. Sheep from all eight ram lines were included in the sample set; for details, see Table 1. The number of sampled sheep per flock ranged from one to nine, proportional to the flock size. A total of 192 samples from RPL sheep (187 purebred and 5 crossbred) born between 2013 and 2022 were sent to Neogen (Ayr, Scotland, UK) for genotyping using the OvineSNP50K BeadChip v.3 (Illumina, San Diego, CA, USA).

2.2 Genome-wide SNP and *TMEM154* genotyping

All 192 samples were genotyped with the OvineSNP50K BeadChip. OvineSNP50k BeadChip results for SNP OAR17_5388531 were checked for the nucleotide substitution G>A in the coding region of *TMEM154*, resulting in the amino acids glutamate (E) or lysine (K) at position 35 in the protein. Except for one, the samples were additionally genotyped for the *TMEM154* genotypes using KASP technology (LGC, Hoddesdon, UK), as previously described by

Frölich et al. (2024) and Molaee et al. (2018), to check the reliability of the SNP chip data.

2.3 Quality control analysis

A total of 192 animals and 61 918 SNPs were available for analysis. Prior to quality control (QC) analysis of the data, the "–related" function in KING version 2.2.4 was used to check the relatedness of the animals (Chen, 2024). One of each related animal of pairs with an identify-by-descent (IBD) value > 0.177 (second-degree relationship) was removed, resulting in the exclusion of three animals. After that, QC was performed using PLINK version 1.9 (Chang et al., 2015). SNPs genotyped in less than 95 % of the animals or with a minor allele frequency (MAF) lower than 5 % were removed. Additionally, only autosomal SNPs and animals with less than 5 % of missing genotypes were retained. The final dataset for genomic-based diversity analysis included 185 individuals and 52 016 high-quality SNPs.

2.4 Genetic diversity assessment

After passing QC, the "–indep-pairwise" function in PLINK version 1.9 was used to prune SNPs for linkage disequilibrium (LD) by removing one of each pair of SNPs in high LD ($r^2 > 0.5$) within a window size of 50 SNPs and with a window slider of 5 SNPs. Principal component analysis (PCA) was performed with PLINK to visualize the breed structure and to investigate diversity among the ram lines and *TMEM154* genotypes. The PCA plot was generated using the "ggplot2" R package (Ginestet, 2011).

Mean observed heterozygosity (Ho) and expected heterozygosity (He) were calculated for the entire breed, each ram line, and different *TMEM154* genotypes using the "hierfstat" package in R (Goudet, 2005). Ho and He were used to determine the Wright inbreeding coefficient as follows (Nei and Chesser, 1983):

$$F_{IS} = 1 - \left(\frac{Ho}{He} \right). \tag{1}$$

The effective population size (Ne) was estimated for 5 (Ne$_5$), 13 (Ne$_{13}$), and 50 (Ne$_{50}$) generations ago on the basis of LD with the "SNeP" package (Barbato et al., 2015; Weir and Hill, 1980). Additionally, Ne was calculated with published data on male (Nm) and female (Nf) population numbers (BLE, Central Documentation on Animal Genetic Resources in Germany (TGRDEU), 2024; VDL, 2023) with the following formula (Birky et al., 1983):

$$Ne = (4 \cdot Nm \cdot Nf)/(Nm + Nf). \tag{2}$$

The expected frequencies and the number of animals per genotype class for the *TMEM154* locus were calculated using Hardy–Weinberg equilibrium (HWE) equation:

$p^2 + 2pq + q^2$ (Mayo, 2008), where p and q represent observed frequencies of K and E alleles, respectively. Moreover, deviation of observed genotype frequencies from HWE for the *TMEM154* locus was assessed with the "HardyWeinberg" package in R using the "HWChisq()" function (Graffelman, 2015).

2.5 Genomic (F_{ROH}) and pedigree-based (F_{PED}) inbreeding coefficient

Prior to runs of homozygosity (ROH) analysis, QC was performed on raw genotype data of unrelated animals using the abovementioned parameters with the exception of excluding SNPs based on minor allele frequency (MAF) as proposed by Meyermans (2020b). Consequently, the dataset for the ROH analysis of the entire population included 185 individuals and 60 409 high-quality SNPs. Likewise, the number of animals per group for the ROH analysis of ram lines (nine groups) and *TMEM154* genotype (three groups) ranged from 11 to 29 and from 36 to 97, respectively. The "–homozyg" function in PLINK was used with the following settings for each run: a minimum ROH length of 1000 kb, a maximum gap between consecutive SNPs of 250 kb, at least one SNP per 100 kb, a scanning window threshold of 0.05, a sliding window of 50 SNPs, one missing SNP, and one heterozygous SNP. The minimum number of SNPs (l) was determined following Eq. (3) of Purfield et al. (2012):

$$l = \frac{\log_e \frac{\alpha}{n_s n_i}}{\log_e (1 - \text{het})}, \tag{3}$$

where n_s is the number of SNPs per individual, n_i is the number of individuals, α is the percentage of false-positive ROH results (0.05), and het is the mean SNP heterozygosity across all SNPs. The value of l was 41 for the entire RPL breed and ranged between 33 (line S) and 40 (genotype EK) in the ram lines and *TMEM154* genotypes. The total ROH number and ROH length (in Mb) were calculated for each sheep, categorized by ram line or *TMEM154* genotype, and three ROH length categories (1–5, > 5–10, and > 10 Mb) for comparison. The individual genomic inbreeding coefficient of ROH (F_{ROH}) was calculated as follows (McQuillan et al., 2008):

$$F_{ROH} = \sum L_{ROH} / L_{AUTO}, \tag{4}$$

where $\sum L_{ROH}$ is the total length of all ROH segments per individual and L_{AUTO} is the length of the autosomal genome covered by SNPs (2.648 Gb). Box plots were constructed to visualize the within-breed distribution of F_{ROH} per ram line and *TMEM154* genotype for F_{ROH} above one Mb.

Furthermore, calculated data of pedigree-based inbreeding coefficients (F_{PED}) using serv.it OVICAP (https://www.vit.de/vit-fuers-tier/vit-fuer-schaf-und-ziege/herdbuchfuehrung-von-schafen-und-ziegen, last access: 16 August 2024), the nationwide database for breeding sheep and goats in Germany (Wilkens, 2021), provided

and maintained by the company vit – "Vereinigte Informationssysteme Tierhaltung w.V." (Verden, Germany), was retrieved from breeders. The calculation was performed by virtual mating of the parents of the analyzed individuals, which was only possible if both parents were still alive, and ewes came from the same flock. Consequently, we obtained only 27 F_{PED} values to compare with the F_{ROH} values using the Pearson rank correlation coefficient (r_p) performed in SAS Studio Version 9.4 (SAS Institute Inc., Cary, NC, USA).

3 Results

3.1 *TMEM154* genotyping

Among the 191 double-genotyped samples, 181 (94.8 %) showed the same *TMEM154* genotypes as determined with the KASP technology, while the remaining 10 (5.2 %) samples had inconclusive results with KASP genotyping technology but clear results in the SNP chip analysis. Details on the distribution of *TMEM154* genotypes per ram lines and sex are given in Table 1.

After QC, the dataset for the genetic diversity analysis included 52 sheep with the genotype (frequency) KK (28 %), 97 with genotype EK (52 %), and 36 with genotype EE (20 %). The putative protective allele K was therefore predominant with 54 %.

Analysis of the expected frequencies for all genotypes revealed values of 29.2 %, 49.7 %, and 21.2 % for KK, EK, and EE, respectively. Likewise, the expected numbers of sheep for each genotype class were as follows: KK = 54, EK = 92, and EE = 39. In addition, a test for deviation from HWE was not significant ($p = 0.51$) for this locus.

3.2 Population structure

The genetic structure of the different ram lines and *TMEM154* genotypes is illustrated in the PCA plots in Fig. 2. The first three principal components explain 4.8 % of the variation within the RPL breed. No distinct clusters were detected in any of the comparisons among the different principal components (PCs). Contrasting PC1 vs. PC3 most clearly showed the admixture of the ram lines (Fig. 2a) and the balanced distribution of the *TMEM154* genotypes (Fig. 2b).

Results of genetic diversity indices for the RPL breed, categorized by ram lines and *TMEM154* genotypes, are given in Tables 2 and 3. The diversity parameters were calculated for groups of sheep with the different *TMEM154* genotypes to determine whether subpopulations of the RPL breed with more favorable or less favorable diversity values would be favored when selecting for MVV resistance. The mean Ho, He, and F_{IS} values of the entire RPL breed were 0.377, 0.379, and 0.005, respectively (Table 2). Genetic diversity was very similar between the *TMEM154* genotypes, with Ho ranging from 0.374 (EK) to 0.378 (EE) (Table 2). In the ram lines, Ho
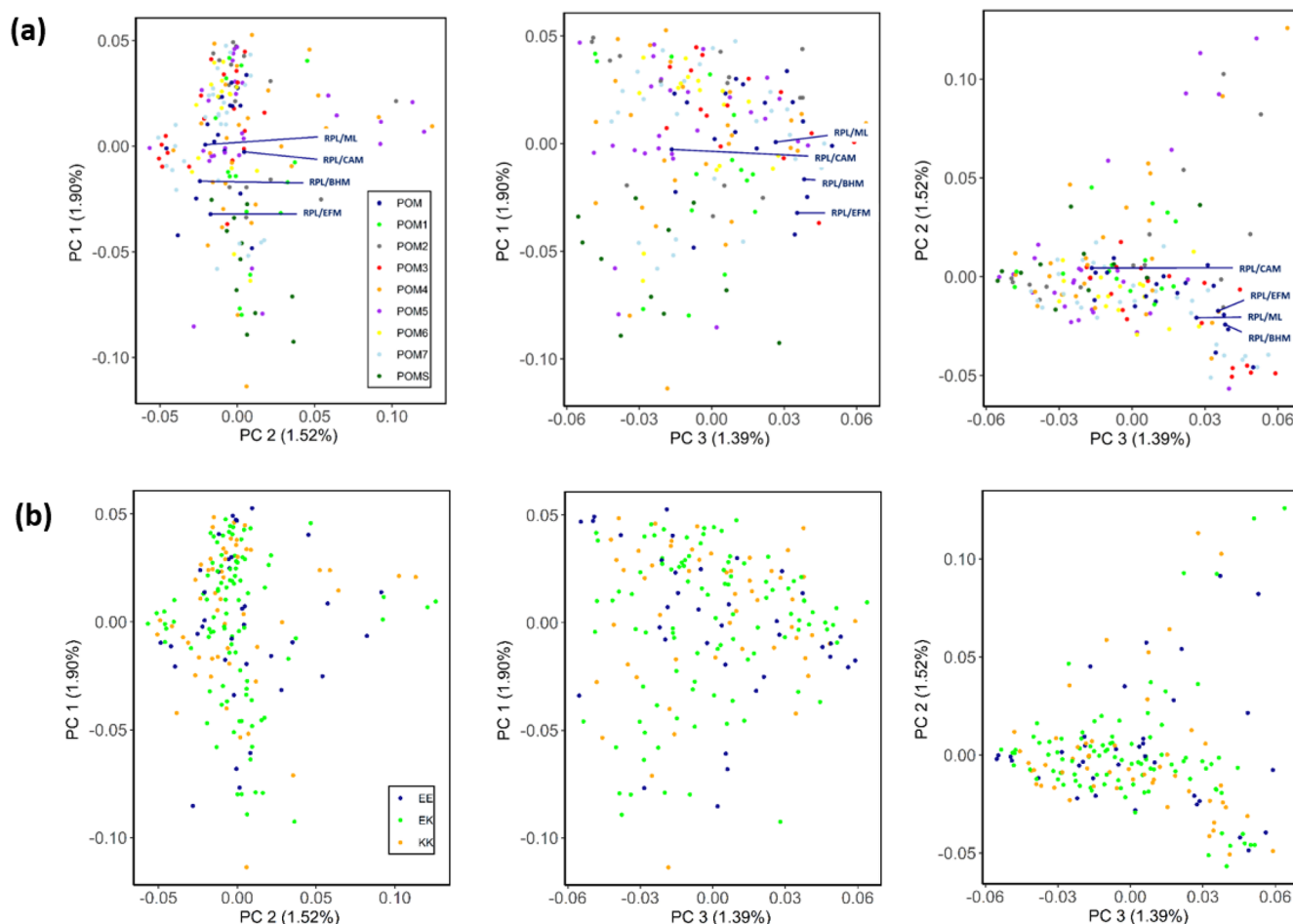
Figure 2. PCA plots for the first (PC1), second (PC2), and third (PC3) component of the RPL breed, categorized by ram lines **(a)** and *TMEM154* genotypes **(b)**. Abbreviations used in the figure are as follows: POM – RPL with unknown ram line; POM1–7/S – ram line 1–7/S; RPL/ML, RPL/CAM, RPL/BHM, and RPL/EFM – crossbreeds between RPL and Merino Land (ML), Cameroon (CAM), Blackheaded Mutton (BHM), and East Friesian Milk (EFM) sheep, respectively; EE, EK, and KK – *TMEM154* genotype EE, EK, and KK at position 35, respectively.

ranged from 0.365 (line 2) to 0.395 (line S), while He ranged from 0.372 (line 2) to 0.385 (unknown line) (Table 3). The F_{IS} values were all close to zero, with three ram lines showing slightly negative results (lines 1, 3, and S).

Effective population size (Ne) was estimated using the QC dataset for the entire breed and for groups of the different *TMEM154* genotypes for 5, 13, and 50 generations ago (Table 2). The Ne for all samples and the combined genotypes KK and EK were the highest, with Ne_5 values of 75 and 72, respectively. The Pearson correlation coefficient (r_p) between these two Ne_5 values was almost 1 ($r_p = 0.99$, $p < 0.0001$). The homozygous genotypes EE and KK had lower Ne values, which can be explained by their limited sample size.

Ne based on the numbers of male and female RPL animals showed substantial differences compared to the genomic Ne ($r_p = 0.03$, $p = 0.93$). This is illustrated in Fig. 3, which shows these differences and the development of Ne over the past 800 generations. All genomic Ne values show

a declining trend, while Ne values based on population numbers have mostly increased in recent generations, with Ne_5 and Ne_{13} reaching 852 and 896, respectively. For the year 2023, Ne was estimated to be 1013.

3.3 Runs of homozygosity

A total of 6690 ROH segments with varying lengths ranging between 1.06 and 38.24 Mb were identified for *TMEM154* genotypes. With one exception, all animals had at least 4 and a maximum of 116 ROH segments (Appendix A). On average, this resulted in 16 ROH segments per individual within the entire RPL breed.

When comparing the different RPL ram lines, animals with unknown line assignment had the highest number of ROH segments, while line 4 had the longest ROH (Appendix B). The majority of ROH segments were in the shortest length class (1–5 Mb), with frequencies between 74.15 %

Table 2. Genetic diversity (Ho, He, and F_{IS}) and effective population size (Ne$_5$, Ne$_{13}$, and Ne$_{50}$) calculated for the total breed and different *TMEM154* genotypes.

TMEM154 E35K genotype	n	Ho	He	F_{IS}	CI95 %	Ne$_5$	Ne$_{13}$	Ne$_{50}$
EE	36	0.378	0.381	0.007	0.006–0.009	43	76	385
EK	97	0.374	0.382	0.020	0.019–0.021	66	107	596
KK	52	0.376	0.380	0.012	0.010–0.014	51	87	459
EK and KK	149	0.375	0.381	0.017	0.016–0.018	72	113	650
All RPL	185	0.377	0.379	0.005	0.003–0.008	75	116	677

Table 3. Genetic diversity (Ho, He, and F_{IS}) calculated for the different ram lines.

Ram line	n	Ho	He	F_{IS}	CI95 %
Line 1	15	0.381	0.380	−0.001	−0.004–0.001
Line 2	17	0.365	0.372	0.019	0.017–0.022
Line 3	19	0.380	0.378	−0.004	−0.006 to −0.002
Line 4	28	0.373	0.379	0.015	0.014–0.018
Line 5	28	0.373	0.377	0.011	0.009–0.013
Line 6	17	0.374	0.375	0.002	−0.000–0.004
Line 7	29	0.374	0.379	0.013	0.010–0.015
Line S	11	0.395	0.382	−0.035	−0.039 to −0.032
Unknown line	21	0.375	0.385	0.028	0.026–0.030

(unknown line) and 78.18 % (line S), followed by the intermediate class (> 5–10 Mb), ranging from 17.46 % (line S) to 20.17 % (line 1). Only 4.37 % (line S) to 7.45 % (unknown line) of the ROH segments were longer than 10 Mb (Fig. 4). The distributions of the frequencies of ROH segments in different length classes (1–5, > 5–10, and > 10 Mb) and the ram lines are shown in Fig. 4.

Based on ROH analysis, genomic inbreeding (F_{ROH}) was estimated for the entire breed, for *TMEM154* genotypes (Appendix A), and separately for the different ram lines (Appendix B). In the RPL breed, F_{ROH} values ranged from 0 to 0.277, with a mean of 0.062. The within-breed distribution of F_{ROH} is visualized in Fig. 5, where the bottom of the box represents the third quartile (Q3), followed by the median and the first quartile (Q1).

The highest mean F_{ROH} was found in genotype EK (0.065), while genotype EE had the lowest (0.058) (Appendix A). Otherwise, the highest median was presented in genotype KK (Fig. 5c). The Kruskal–Wallis test indicated no significant differences between the mean F_{ROH} of the *TMEM154* genotypes ($p = 0.836$).

A significant difference was observed between the F_{ROH} of the eight ram lines ($p = 0.0002$) (Appendix C). Only the F_{ROH} comparisons between line S and six other lines, with the exception of line 3, were significant. The highest median and mean value were observed in line 2, whereas the lowest values were observed in line S (Appendix B, Fig. 5b).

In 27 individuals for which a pedigree-based inbreeding coefficient (F_{PED}) could be calculated, the F_{ROH} and F_{PED}

values were compared (Appendix D). The F_{ROH} values of these animals ranged between 1.12 % and 12.90 % (average of 5.46 %), whereas the F_{PED} values were consistently lower, ranging from 0 % to 1.56 % (average of 0.44 %). A value of 0 % indicates no inbreeding, either genomic (F_{ROH}) or pedigree-based (F_{PED}). The Pearson correlation coefficient (r_p) between F_{ROH} and F_{PED} was positive and moderately significant, with a result of 0.42 ($p = 0.02$).

4 Discussion

4.1 Genetic diversity in the RPL breed

This study presents the first comprehensive analysis of genetic diversity in the German RPL sheep breed. Faced with the danger of extinction, efforts to conserve the breed began almost 40 years ago with seven rams from the eastern federal state Mecklenburg–Western Pomerania and one ram from southwestern Germany (IGRPL, 2024). Today, these eight founding ram lines are distributed across the whole country (VDL, 2023). The PCA plot (Fig. 2a) indicates an equal genetic distribution with no distinct clustering among the ram lines. A genetic separation of individuals from different geographical regions in PCA plots, as reported in previous studies of different breeds (Eydivandi et al., 2021; Kijas et al., 2009; Kijas et al., 2012), could not be observed in the present study. Line S, originating from southern Germany, showed no distinct separation from the seven northern lines, despite its different geographical origin. This out-
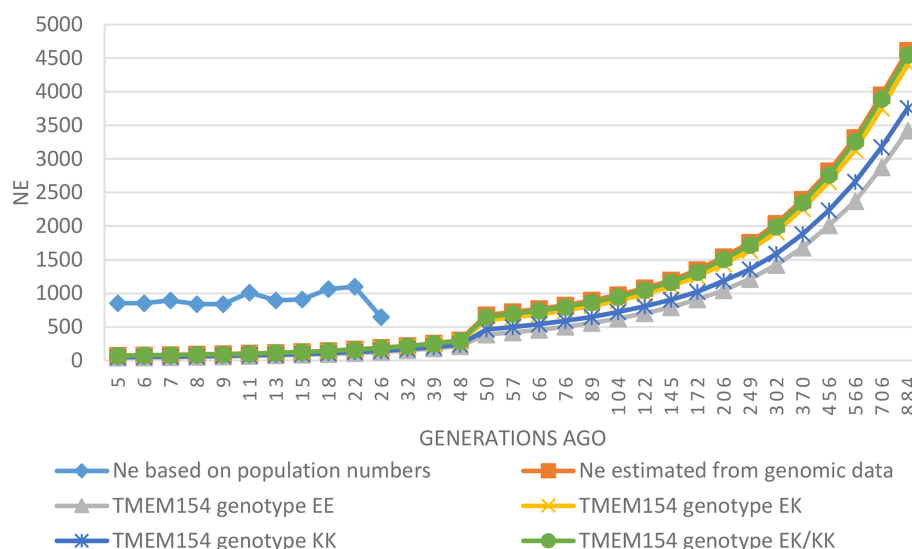
Figure 3. Ne based on population numbers across 26 generations and estimated genomic Ne across 884 generations for the total breed and the different *TMEM154* genotypes.
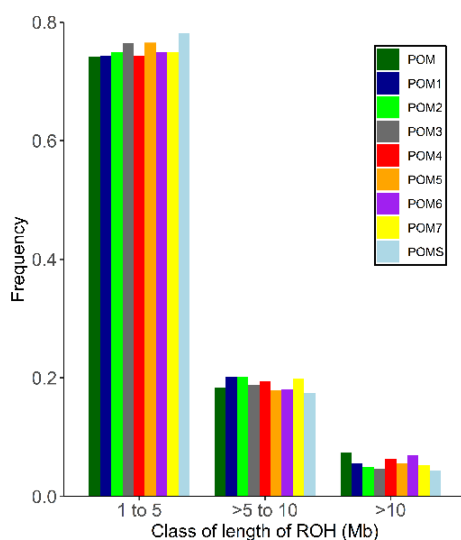

Figure 4. Frequency distribution of the number of ROH in different length classes and for the RPL breed, categorized by ram lines. Abbreviations used in the figure are as follows: POM – RPL with unknown ram line; POM1–7/S – ram line 1–7/S.

come speaks for a successful implementation of the line-rotation method by the RPL breeders. Normally, the genetic distance among animals from the same breed is smaller than the distance between animals of divergent breeds (Lenstra et al., 2012). However, the four crossbred RPL sheep (resulting from crosses with Cameroon, Blackheaded Mutton, Merino Land, and East Friesian Milk sheep) exhibited no clearly visible genetic distance from the purebred individuals in the PCA plot. For identification of crossbred animals with this method, it may be necessary to include SNP data from

sheep of the other breeds. In fact, the genetic proportion of the crossed-in breed also depends on how many generations ago the cross was made. Unfortunately, we do not have this information for the crossbred animals included in this study.

Numbers of breeding males and females have traditionally been used to estimate Ne in livestock (Birky et al., 1983). However, these estimates have limitations, such as assumptions of perfect random mating, including self-fertilization, or an equal number of offspring per parent. Ne based on genomic data serves as a more accurate indicator of the genetic variation within a population and is usually much smaller than Ne based on population numbers (Lenstra et al., 2012). When using the SNeP software for Ne analysis, the authors caution that Ne values based on genome data are unreliable when calculated for less than 10 generations (Corbin et al., 2012). Therefore, genome-based Ne values lower than 10 generations ago found in this study are not comparable to results from population numbers.

The present study supports the latter finding, e.g., with Ne_{13} values of 116 (genomic) and 896 (population numbers) for all analyzed samples. Both values are over the threshold recommended guideline value of at least 50 from the Food and Agriculture Organization of the United Nations (Bradley et al., 1998), indicating that the RPL breed is not currently at risk of extinction or inbreeding depression. The genomic Ne of the RPL breed is higher than those reported for many other sheep breeds (Adeniyi et al., 2022; Meyermans et al., 2020a; Purfield et al., 2017). Comparable or even higher values have been reported in some Swiss sheep breeds (Signer-Hasler et al., 2019). Overall, the genomic Ne of the RPL breed shows a decreasing trend over the last 800 generations (Fig. 3). This decline aligns with population subdivision and selection (Ki-
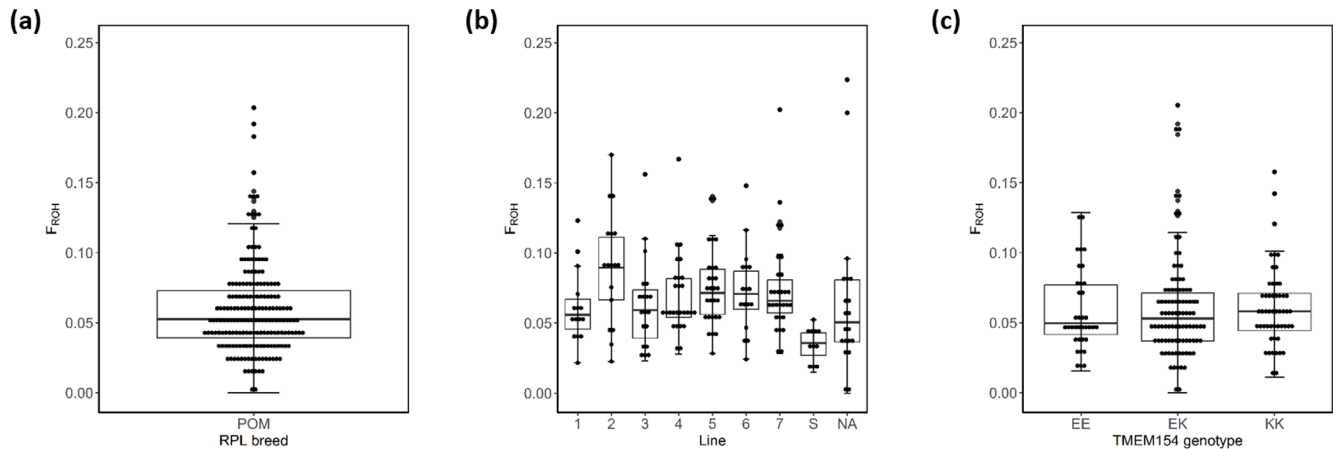
Figure 5. Box plots of within-breed F_{ROH} for the entire RPL breed **(a)**, the ram lines **(b)**, and *TMEM154* genotypes **(c)**. Abbreviations used in the figure are as follows: POM – all 185 RPL; 1–7 – ram line 1–7; NA – line data not available; EE, EK, and KK – *TMEM154* genotype EE, EK, and KK at position 35, respectively.

jas et al., 2012), and such a decline is to be expected for breeding in a closed population.

The still acceptable effective population size of the RPL breed is consistent with the results for other parameters of genetic diversity. A higher level of heterozygosity indicates greater genetic variability, while a lower level suggests both lower genetic variability and a lower Ne (Lenstra et al., 2012). The mean observed heterozygosity (Ho) of the RPL breed is higher than that of 10 northern European sheep breeds (Meyermans et al., 2020a) and nearly matches the Ho value of 0.38 in Australian Merino sheep, which have been described as the most diverse sheep population among a selection of Australian breeds (Al-Mamun et al., 2015). Other European sheep breeds exhibited both lower and higher values (of up to 0.41) (Adeniyi et al., 2022; Signer-Hasler et al., 2019; Sveistiene and Tapio, 2021). Within RPL sheep, the S-line had the highest heterozygosity (0.40), comparable to that of the German Texel breed (Sveistiene and Tapio, 2021). A German diversity study from 1999 using microsatellites estimated a heterozygosity of 0.77 for the RPL breed (Falge et al., 1999). The phenomenon that microsatellite data lead to higher estimates of heterozygosity than SNP chip genotypes has already been described (Handley et al., 2007). Microsatellite analyses show higher heterozygosity because most of these markers represent highly polymorphic sites with more than two alleles, in contrast to SNPs that usually represent sites with two alleles. However, SNP chip genotypes are more accurate than microsatellites due to the higher number of markers and their more even distribution across the genome. Therefore, they are able to detect even weak relationships, and they result in smaller confidence intervals (Laoun et al., 2020). The inbreeding coefficient F_{IS} showed both positive and negative results across the different ram lines, although all were close to 0. Other German breeds, such as Blackheaded Mutton, East Friesian Brown, or

Texel sheep, showed negative results ranging from -0.02 to -0.03 based on SNP chip data (Sveistiene and Tapio, 2021). The mean F_{IS} value for the RPL breed was slightly positive, which indicates a slight tendency towards inbreeding.

The majority of the ROH segments across all ram lines belonged to the shortest length class (Fig. 4), which indicates older inbreeding events, such as bottlenecks during breed formation due to the small initial population (Curik et al., 2014; Peripolli et al., 2017). Only a small proportion of long ROH segments were detected, suggesting low recent inbreeding (Curik et al., 2014). This recent inbreeding could be attributed to selective breeding and non-random mating, as usually only a small number of rams are used. The genomic inbreeding coefficient F_{ROH} aligns with the F_{IS} values, with the highest F_{ROH} average found in line 2 (0.090) and the lowest in line S (0.035) (Appendix A). The overall breed value was 0.062, which is far below the average of 0.134 for European breeds (Eydivandi et al., 2021) and other endangered sheep breeds (Adeniyi et al., 2022; Meyermans et al., 2020a).

When comparing the genomic inbreeding coefficient (F_{ROH}) with the pedigree-based inbreeding coefficient (F_{PED}), the F_{ROH} values were consistently higher than the F_{PED} values, with a correlation of only 0.42. Moderate to weak correlations were also detected in the Vendéen breed (value of 0.15) (Purfield et al., 2017) and some Swiss sheep and goat breeds (Burren et al., 2016; Signer-Hasler et al., 2019). In contrast, other studies on sheep, pigs, and cattle have reported higher correlations (Gorssen et al., 2020; Meyermans et al., 2020a; Signer-Hasler et al., 2017), while dogs showed the highest at 0.78 (Wiener et al., 2017). The discrepancy could be explained by a higher degree of incompleteness and lower depth of pedigrees of small ruminants (Purfield et al., 2017). In comparison, pets generally have a better-documented pedigree due to easier control of mating and birth. Regarding birth, sheep and goats often lamb

in groups and at night. An overlooked adoption of foreign lambs by ewes can lead to errors in the pedigree. Control of mating is also an advantage of artificial insemination, which (at least in Europe) is more common in cattle and pigs than in sheep and goats. Moreover, F_{PED} is based on theoretical inbreeding and does not consider the stochastic effect of Mendelian sampling (Curik et al., 2014). Another possible explanation for lower correlations is the assumption that the founder population is unrelated, which is unlikely. Due to these limitations, F_{PED} often underestimates inbreeding. Consequently, F_{ROH} is more accurate because it is independent of ancestry information and reflects both past and recent relatedness (Curik et al., 2014; Peripolli et al., 2017).

4.2 Breeding for maedi-visna resistance

Based on the diversity parameters calculated in the present study, the genetic diversity of the RPL breed is not at risk. Due to the high frequency of the *TMEM154* allele K in this study (54 %) and a previous study (53 %) (Frölich et al., 2024), breeding for MVV resistance could be possible. The PCA results showed no genetic separation between sheep with the three different *TMEM154* genotypes. This implies that no genetically distinct subgroup will be excluded from breeding when selecting for the K allele. However, a strong preference in breeding for the putative protective allele K might jeopardize the genetic variability in this breed and increase inbreeding rates by reducing the effective population size (Peripolli et al., 2017; Williams, 2005). The estimated Ne for the subpopulation of sheep with the *TMEM154* genotype KK was slightly lower than that of the entire breed, whereas the Ne for sheep with genotypes KK and EK was similar (Fig. 3). Implementing mating strategies that include both genotypes (KK and EK) would not substantially reduce Ne and, consequently, help maintain allelic variation (Peripolli et al., 2017). Moreover, the observed heterozygosity (Ho) remained the same, whereas the expected heterozygosity (He) was higher for *TMEM154* genotypes KK and EK (Table 2), resulting in a slightly higher but still near-zero F_{IS} value. On the other hand, the mean F_{ROH} value of 0.063 for both genotypes was comparable to that of the whole breed. Although the *TMEM154* genotype EE exhibited the lowest F_{IS} and F_{ROH} results, a selection against this genotype is not problematic due to its reactively low frequency in the RPL population (20 %). To reduce genotyping costs, sire-only genotyping and selection should be considered. While this approach would slow the selection for the K allele, it would avoid high costs and limit the reduction in the population size (White and Knowles, 2013).

However, the effectiveness of selection for the *TMEM154* allele K with respect to reducing MVV susceptibility in the RPL breed needs further validation through studies involving a larger number of MVV-positive sheep, as the effect showed only a trend towards significance (Frölich et al., 2024). Nonetheless, it has the potential to complement MVV eradication measures in infected flocks, such as regular serological monitoring of the flock and culling of seropositive sheep and/or motherless rearing of lambs (Reina et al., 2009). In the light of the high frequency of the K allele in the RPL breed, a prioritization of breeding rams with the genotypes KK or EK in MVV-infected flock is a relatively simple way to increase the chances of reducing the infection pressure within the flock.

5 Conclusion

This study describes, for the first time, the genomic diversity of the German RPL sheep breed. The estimated genetic diversity parameters suggest that its diversity is not at risk, indicating successful breeding practices in recent years. Nevertheless, it is important to maintain genetic diversity and further reduce the level of inbreeding in the future. For this purpose, the genomic inbreeding coefficient should be used, as the pedigree-based method consistently underestimated the inbreeding level. However, to enable this, it would be necessary to establish genome analysis as a routine procedure in German sheep breeding.

Furthermore, the present study showed that breeding for MVV resistance would be possible without a major loss of genetic diversity. However, selecting the entire breed for the *TMEM154* allele K is not recommended at this time, as the effect on MVV susceptibility was not statistically significant in a previous study. An exception are MVV-affected flocks, in which rams with the genotypes KK or EK could be prioritized. Further research with a larger number of MVV-positive RPL sheep is required in order to validate a protective effect of the genotype KK against MVV in the RPL breed.

Appendix A

Table A1. Descriptive statistics for the ROH analysis and F_{ROH} of the total breed and the *TMEM154* genotypes.

TMEM154 E35K genotype	n	ROH length (Mb) Mean (SD)	Range	ROH number Mean (SD)	Range	F_{ROH} Mean	Range
EE	36	4.28 (2.78)	1.06–33.77	36.17 (15.29)	12–69	0.058	0.015–0.129
EK	97	4.55 (3.14)	1.27–38.24	37.52 (20.24)	0–118	0.065	0–0.261
KK	52	4.38 (2.74)	1.10–25.70	36.77 (14.65)	9–79	0.061	0.011–0.158
EK and KK	149	4.52 (3.01)	1.10–38.24	36.92 (18.28)	0–118	0.063	0–0.261
Total	185	4.52 (2.98)	1.06–38.24	36.16 (17.50)	0–116	0.062	0–0.259

Appendix B

Table B1. Descriptive statistics for the ROH analysis and F_{ROH} of the eight different ram lines.

Ram line	n	ROH length (Mb) Mean (SD)	Range	ROH number Mean (SD)	Range	F_{ROH} Mean	Range
Line 1	15	4.21 (3.24)	1.05–36.16	38.67 (14.12)	15–67	0.061	0.022–0.123
Line 2	17	4.25 (3.09)	1.01–38.39	56.12 (20.46)	15–86	0.090	0.023–0.170
Line 3	19	4.09 (2.87)	1.07–25.37	41.47 (15.59)	19–82	0.064	0.023–0.156
Line 4	28	4.42 (3.80)	1.10–64.46	46.14 (19.16)	20–108	0.077	0.028–0.280
Line 5	28	4.12 (2.83)	1.02–28.21	48.54 (14.21)	19–81	0.075	0.028–0.140
Line 6	17	4.35 (3.42)	1.02–35.70	44.59 (14.50)	17–79	0.073	0.024–0.148
Line 7	29	4.25 (3.17)	1.05–36.25	46.83 (15.32)	20–88	0.075	0.028–0.202
Line S	11	3.99 (2.75)	1.07–21.24	22.91 (8.14)	11–34	0.035	0.015–0.052
Unknown line	21	4.60 (3.89)	1.08–31.04	43.48 (29.51)	0–121	0.076	0–0.272

Appendix C

Table C1. Results of the Kruskal–Wallis test comparing the eight ram lines.

Line comparison	p value
6 vs. 5	1.000
6 vs. 4	1.000
6 vs. 2	0.902
6 vs. 3	0.959
6 vs. 1	0.924
6 vs. 7	1.000
6 vs. S	0.012
5 vs. 4	0.997
5 vs. 2	0.755
5 vs. 3	0.822
5 vs. 1	0.666
5 vs. 7	1.000
5 vs. S	0.001
4 vs. 2	0.769
4 vs. 3	0.975
4 vs. 1	0.940
4 vs. 7	0.999
4 vs. S	0.001
2 vs. 3	0.390
2 vs. 1	0.393
2 vs. 7	0.775
2 vs. S	0.009
3 vs. 1	1.000
3 vs. 7	0.956
3 vs. S	0.154
1 vs. 7	0.835
1 vs. S	0.036
7 vs. S	0.001

Appendix D

Table D1. Comparison of the genomic (F_{ROH}) and pedigree-based (F_{PED}) inbreeding coefficients for 27 pedigreed RPL individuals.

Pedigreed individual	F_{ROH} (%)	F_{PED} (%)
1	4.04	0.00
2	6.37	1.56
3	2.41	0.00
4	3.56	0.00
5	5.38	0.78
6	2.74	0.00
7	7.20	1.17
8	3.57	0.98
9	3.19	0.39
10	6.07	0.00
11	7.60	0.98
12	10.12	0.20
13	6.99	0.39
14	2.01	0.00
15	8.19	1.56
16	5.33	0.00
17	4.80	0.98
18	6.87	0.00
19	4.40	0.00
20	8.62	0.39
21	12.90	0.52
22	8.87	1.17
23	4.33	0.78
24	1.95	0.00
25	1.12	0.00
26	4.16	0.00
27	4.68	0.00

Ethical statement. All animal procedures were reviewed and approved by the respective state veterinary offices of the nine different German states. The approval numbers are as follows: Baden-Württemberg, 35-9185.82/A-11/23 (8 August 2023); Brandenburg, LAVG-V6-2347-19-2023- 23-E (7 August 2023); Hesse, V 54 19 c 20 15 h 01 Nr. V 3/2023 (21 August 2023); Lower Saxony, 33.19-42502-04-23-00387 (4 August 2023); Mecklenburg–Western Pomerania, 7221.3-2-012/23 (5 September 2023); North Rhine-Westphalia, 81-02.04.40.2023.VG036 (11 August 2023); Saxony, 25-5131/564/17 (9 October 2023); Saxony-Anhalt, 203.m-42502-6-011_TiHo_G (25 September 2023); Schleswig-Holstein, IX 552 – 117467/2023 (56-9/23V) (25 September 2023). The handling and sampling of the sheep followed the European Union guidelines for animal care and handling and the Guidelines of Good Veterinary Practices.

References

Adeniyi, O. O., Simon, R., Bytyqi, H., Kugler, W., Mehmeti, H., Berisha, K., Simcic, M., Magdy, M., and Lühken, G.: Capturing Genetic Diversity and Selection Signatures of the Endangered Kosovar Balusha Sheep Breed, Genes-Basel, 13, 866, https://doi.org/10.3390/genes13050866, 2022.

Al-Mamun, H. A., Clark, S. A., Kwan, P., and Gondro, C.: Genome-wide linkage disequilibrium and genetic diversity in five populations of Australian domestic sheep, Genet. Sel. Evol., 47, 90, https://doi.org/10.1186/s12711-015-0169-6, 2015.

Barbato, M., Orozco-TerWengel, P., Tapio, M., and Bruford, M. W.: SNeP: a tool to estimate trends in recent effective population size trajectories using genome-wide SNP data, Front. Genet., 6, 109, https://doi.org/10.3389/fgene.2015.00109, 2015.

Birky, C. W., Maruyama, T., and Fuerst, P.: An Approach to Population and Evolutionary Genetic Theory for Genes in Mitochondria and Chloroplasts, and Some Results, Genetics, 103, 513–527, 1983.

BLE, Central Documentation on Animal Genetic Resources in Germany (TGRDEU): Livestock animals: Sheep: Rauhwolliges Pommersches Landschaf, https://tgrdeu.genres.de/en/livestock-animals/search-for-animal-species, last access: 30 October 2024.

Bradley, D., Fries, R., Bumstead, N., Nicholas, F., Cothran, E., Ollivier, L., and Crawford, A.: Secondary guidelines for development of national farm animal genetic resources management plans: Management of small populations at risk, FAO, https://openknowledge.fao.org/items/498e808d-088a-4ad4-9215-6dc8f3a5ff39 (last access: 8 August 2024)1998.

Burren, A., Neuditschko, M., Signer-Hasler, H., Frischknecht, M., Reber, I., Menzi, F., Drögemüller, C., and Flury, C.: Genetic diversity analyses reveal first insights into breed-specific selection signatures within Swiss goat breeds, Anim. Genet., 47, 727–739, https://doi.org/10.1111/age.12476, 2016.

Chang, C. C., Chow, C. C., Tellier, L. C., Vattikuti, S., Purcell, S. M., and Lee, J. J.: Second-generation PLINK: rising to the challenge of larger and richer datasets, Gigascience, 4, 7, https://doi.org/10.1186/s13742-015-0047-8, 2015.

Chen, W.: KING: Kinship-based Inference for Gwas, https://www.kingrelatedness.com/manual.shtml, last access: 8 September 2024.

Corbin, L. J., Liu, A. Y., Bishop, S. C., and Woolliams, J. A.: Estimation of historical effective population size using linkage disequilibria with marker data, J. Anim. Breed. Genet., 129, 257–270, https://doi.org/10.1111/j.1439-0388.2012.01003.x, 2012.

Curik, I., Ferencakovic, M., and Sölkner, J.: Inbreeding and runs of homozygosity: A possible solution to an old problem, Livest. Sci., 166, 26–34, https://doi.org/10.1016/j.livsci.2014.05.034, 2014.

Drögemüller, C., De Vries, F., Hamann, H., Leeb, T., and Distl, O.: Breeding German sheep for resistance to scrapie, Vet. Rec., 154, 257–260, https://doi.org/10.1136/vr.154.9.257, 2004.

Eydivandi, S., Roudbar, M. A., Ardestani, S. S., Momen, M., and Sahana, G.: A selection signatures study among Middle Eastern and European sheep breeds, J. Anim. Breed. Genet., 138, 574–588, https://doi.org/10.1111/jbg.12536, 2021.

FAO: European Farm Animal Biodiversity Information System (EFABIS), https://www.fao.org/dad-is/regional-national-nodes/efabis/en/, last access: 5 August 2024.

Falge, R., Terletski, V., Mendel, C., Grumbach, S., Gerdes, K., Carnwath, J., and Niemann, H.: Schätzung des mittleren Heterozygotiegrades aus DNA-Fingerprints bei einheimischen Landschafrassen des norddeutschen und süddeutschen Raumes, Züchtungskunde, 71, 147–157, 1999.

Frölich, C., Lühken, G., and Ganter, M.: Maedi-visna in Pomeranian Coarsewool sheep in Germany: Seroprevalence, environmental and genetic risk factors, Research Square [preprint], https://doi.org/10.21203/rs.3.rs-4678425/v1, 2024.

Gaede, U.: Das Pommersche grauwollige Landschaf, University of Jena, https://ig-pommernschafe.de/service/downloads.html (last access: 30 July 2024), 1926.

GEH: Die Rote Liste: https://www.g-e-h.de/rote-liste-menu/rote-liste, last access: 5 August 2024.

Ginestet, C.: ggplot2: Elegant Graphics for Data Analysis, J. R. Stat. Soc. A, 174, 245–245, https://doi.org/10.1111/j.1467-985X.2010.00676_9.x, 2011.

Gorssen, W., Meyermans, R., Buys, N., and Janssens, S.: SNP genotypes reveal breed substructure, selection signatures and highly inbred regions in Pietrain pigs, Anim. Genet., 51, 32–42, https://doi.org/10.1111/age.12888, 2020.

Goudet, J.: HIERFSTAT, a package for R to compute and test hierarchical F-statistics, Mol. Ecol. Notes, 5, 184–186, https://doi.org/10.1111/j.1471-8286.2004.00828.x, 2005.

Graffelman, J.: Exploring Diallelic Genetic Markers: The HardyWeinberg Package, J. Stat. Softw., 64, 3, https://doi.org/10.18637/jss.v064.i03, 2015.

Grumbach, S.: Rauhwollige Pommersche Landschafe 1982 bis 2002 20 Jahre erfolgreiche Erhaltungszucht, https://ig-pommernschafe.de/service/downloads.html (last access: 30 July 2024), 2002.

Grumbach, S. and Zupp, W.: Rauhwolliges Pommersches Landschaf wieder im Aufwind, Deutsche Schafzucht, 22, 512–514, 1992.

Grumbach, S. and Zupp, W.: Online-Broschüre Schwerpunkt Schafe, Ziegen Gebrauchshunde, https://www.g-e-h.de/images/stories/rassebeschreib/schaf/DasRauhwolligePommersche.pdf (last access: 10 August 2024), 2008.

Handley, L. J. L., Byrne, K., Santucci, F., Townsend, S., Taylor, M., Bruford, M. W., and Hewitt, G. M.: Genetic structure of European sheep breeds, Heredity, 99, 620–631, https://doi.org/10.1038/sj.hdy.6801039, 2007.

Heaton, M. P., Clawson, M. L., Chitko-Mckown, C. G., Leymaster, K. A., Smith, T. P., Harhay, G. P., White, S. N., Herrmann-Hoesing, L. M., Mousel, M. R., Lewis, G. S., Kalbfleisch, T. S., Keen, J. E., and Laegreid, W. W.: Reduced lentivirus susceptibility in sheep with TMEM154 mutations, PLoS Genet., 8, e1002467, https://doi.org/10.1371/journal.pgen.1002467, 2012.

IGRPL: 20 Jahre erfolgreiche Erhaltungszucht 1982–2002, https://www.ig-pommernschafe.de/historisches/historie-1982-2002.html, last access: 5 October 2024.

Keller, L. F. and Waller, D. M.: Inbreeding effects in wild populations, Trends Ecol. Evol., 17, 230–241, https://doi.org/10.1016/S0169-5347(02)02489-8, 2002.

Kijas, J. W., Townley, D., Dalrymple, B. P., Heaton, M. P., Maddox, J. F., McGrath, A., Wilson, P., Ingersoll, R. G., McCulloch, R., McWilliam, S., Tang, D., McEwan, J., Cockett, N., Oddy, V. H., Nicholas, F. W., Raadsma, H., and Conso, I. S. G.: A Genome Wide Survey of SNP Variation Reveals the Genetic Structure of Sheep Breeds, Plos One, 4, e4668, https://doi.org/10.1371/journal.pone.0004668, 2009.

Kijas, J. W., Lenstra, J. A., Hayes, B., Boitard, S., Neto, L. R. P., San Cristobal, M., Servin, B., McCulloch, R., Whan, V., Gietzen, K., Paiva, S., Barendse, W., Ciani, E., Raadsma, H., McEwan, J., Dalrymple, B., and Consortium, I. S. G.: Genome-Wide Analysis of the World's Sheep Breeds Reveals High Levels of Historic Mixture and Strong Recent Selection, Plos Biol., 10, 2, https://doi.org/10.1371/journal.pbio.1001258, 2012.

Laoun, A., Harkat, S., Lafri, M., Gaouar, S. B. S., Belabdi, I., Ciani, E., De Groot, M., Blanquet, V., Leroy, G., Rognon, X., and Da Silva, A.: Inference of Breed Structure in Farm Animals: Empirical Comparison between SNP and Microsatellite Performance, Genes-Basel, 11, 57, https://doi.org/10.3390/genes11010057, 2020.

Lenstra, J. A., Groeneveld, L. F., Eding, H., Kantanen, J., Williams, J. L., Taberlet, P., Nicolazzi, E. L., Sölkner, J., Simianer, H., Ciani, E., Garcia, J. F., Bruford, M. W., Ajmone-Marsan, P., and Weigend, S.: Molecular tools and analytical approaches for the characterization of farm animal genetic diversity, Anim. Genet., 43, 483–502, https://doi.org/10.1111/j.1365-2052.2011.02309.x, 2012.

Mayo, O.: A century of Hardy-Weinberg equilibrium, Twin Res. Hum. Genet., 11, 3, https://doi.org/10.1375/twin.11.3.249, 2008.

McQuillan, R., Leutenegger, A. L., Abdel-Rahman, R., Franklin, C. S., Pericic, M., Barac-Lauc, L., Smolej-Narancic, N., Janicijevic, B., Polasek, O., Tenesa, A., MacLeod, A. K., Farrington, S. M., Rudan, P., Hayward, C., Vitart, V., Rudan, I., Wild, S. H., Dunlop, M. G., Wright, A. F., Campbell, H., and Wilson, J. F.: Runs of homozygosity in European populations, Am. J. Hum. Genet., 83, 359–372, https://doi.org/10.1016/j.ajhg.2008.08.007, 2008.

Mendelsohn, R.: The challenge of conserving indigenous domesticated animals, Ecol. Econ., 45, 501–510, https://doi.org/10.1016/S0921-8009(03)00100-9, 2003.

Meyermans, R., Gorssen, W., Wijnrocx, K., Lenstra, J. A., Vellema, P., Buys, N., and Janssens, S.: Unraveling the genetic diversity of Belgian Milk Sheep using medium-density SNP genotypes, Anim. Genet., 51, 258–265, https://doi.org/10.1111/age.12891, 2020a.

Meyermans, R., Gorssen, W., Buys, N., Janssens, S.: How to study runs of homozygosity using PLINK? A guide for analyzing medium density SNP data in livestock and pet species, BMC Genomics, 21, 1–14, https://doi.org/10.1186/s12864-020-6463-x, 2020b.

Molaee, V., Eltanany, M., and Luhken, G.: First survey on association of TMEM154 and CCR5 variants with serological maedi-visna status of sheep in German flocks, Vet. Res., 49, 36, https://doi.org/10.1186/s13567-018-0533-y, 2018.

Nei, M. and Chesser, R. K.: Estimation of Fixation Indexes and Gene Diversities, Ann. Hum. Genet., 47, 253–259, https://doi.org/10.1111/j.1469-1809.1983.tb00993.x, 1983.

Peripolli, E., Munari, D. P., Silva, M. V. G. B., Lima, A. L. F., Irgang, R., and Baldi, F.: Runs of homozygosity: current knowledge and applications in livestock, Anim. Genet., 48, 255–271, https://doi.org/10.1111/age.12526, 2017.

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

Purfield, D. C., McParland, S., Wall, E., and Berry, D. P.: The distribution of runs of homozygosity and selection signatures in six commercial meat sheep breeds, Plos One, 12, e0176780, https://doi.org/10.1371/journal.pone.0176780, 2017.

Rege, J. E. O. and Gibson, J. P.: Animal genetic resources and economic development: issues in relation to economic valuation, Ecol. Econ., 45, 319–330, https://doi.org/10.1016/S0921-8009(03)00087-9, 2003.

Reina, R., Berriatua, E., Luján, L., Juste, R., Sánchez, A., de Andrés, D., and Amorena, B.: Prevention strategies against small ruminant lentiviruses: An update, Vet. J., 182, 31–37, https://doi.org/10.1016/j.tvjl.2008.05.008, 2009.

Rischkowsky, B. and Pilling, D.: The state of the world's animal genetic resources for food and agriculture, FAO, https://www.fao.org/4/a1250e/a1250e00.htm (last access: 8 August 2024), 2007.

Scherf, B.: Worldwatch list, FAO, https://www.fao.org/4/x8750e/x8750e00.htm (last access: 8 August 2024), 2000.

Scherf, B. D. and Pilling, D.: The second report on the state of the world's animal genetic resources for food and agriculture, FAO, https://www.fao.org/4/i4787e/i4787e00.htm (last access: 8 August 2024), 2015.

Signer-Hasler, H., Burren, A., Neuditschko, M., Frischknecht, M., Garrick, D., Stricker, C., Gredler, B., Bapst, B., and Flury, C.: Population structure and genomic inbreeding in nine Swiss dairy cattle populations, Genet. Sel. Evol., 49, 83, https://doi.org/10.1186/s12711-017-0358-6, 2017.

Signer-Hasler, H., Burren, A., Ammann, P., Drgemller, C., and Flury, C.: Runs of homozygosity and signatures of selection: a comparison among eight local Swiss sheep breeds, Anim. Genet., 50, 512–525, https://doi.org/10.1111/age.12828, 2019.

Sveistiene, R. and Tapio, M.: SNPs in Sheep: Characterization of Lithuanian Sheep Populations, Animals-Basel, 11, 2651, https://doi.org/10.3390/ani11092651, 2021.

Tisdell, C.: Socioeconomic causes of loss of animal genetic diversity: analysis and assessment, Ecol. Econ., 45, 365–376, https://doi.org/10.1016/S0921-8009(03)00091-0, 2003.

VDL: VDL-Statistik 2023 Entwicklung und Leistungen der Herdbuchzucht 2023, https://lsv-st.de/landesschafzuchtverband/userfiles/downloads/Termine_2024/vdl_bericht_herdbuchzucht_schaf_2023.pdf (last access: 15 October 2024), 2023.

Weir, B. S. and Hill, W. G.: Effect of Mating Structure on Variation in Linkage Disequilibrium, Genetics, 95, 477–488, 1980.

White, S. N. and Knowles, D. P.: Expanding Possibilities for Intervention against Small Ruminant Lentiviruses through Genetic Marker-Assisted Selective Breeding, Viruses-Basel, 5, 1466–1499, https://doi.org/10.3390/v5061466, 2013.

Wiener, P., Sánchez-Molano, E., Clements, D. N., Woolliams, J. A., Haskell, M. J., and Blott, S. C.: Genomic data illuminates demography, genetic structure and selection of a popular dog breed, BMC Genomics, 18, 609, https://doi.org/10.1186/s12864-017-3933-x, 2017.

Wilkens, J.: Central information processing in German sheep and goat breeding, Genetic Resources, 2, 11, https://doi.org/10.46265/genresj.QULD1720, 2021.

Williams, J. L.: The use of marker-assisted selection in animal breeding and biotechnology, Revue Scientifique Et Technique-Office International Des Epizooties, 24, 379–391, https://doi.org/10.20506/rst.24.1.1571, 2005.

Yang, J., Li, W.-R., Lv, F.-H., He, S.-G., Tian, S.-L., Peng, W.-F., Sun, Y.-W., Zhao, Y.-X., Tu, X.-L., and Zhang, M.: Whole-genome sequencing of native sheep provides insights into rapid adaptations to extreme environments, Mol. Biol. Evol., 33, 2576–2592, https://doi.org/10.1093/molbev/msw129, 2016.