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Genomic diversity characteristics of sheep populations in the Czech Republic, Slovakia, Serbia and Montenegro

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Abstract: Monitoring the genetic diversity in livestock is a critical component for sustainable management of small and endangered breeds. In this paper we follow up the two most often used metrics of genetic diversity, the average inbreeding coefficients (F) and the effective population (N_e) size in 16 sheep breeds from four countries. The analysis was based on single nucleotide polymorphism (SNP) markers, with about 35 to 49 thousand SNPs and 19 to 98 individuals after quality control. The runs of homozygosity (ROH) method with the cgaTOH software was used to estimate F_{ROH}, for three different time points in the past (3, 6 and 12 generations before present). Three methods were implemented to estimate N_e, using the NeEstimator v2, GONE and CurrentNe software for different time spans in the past. The average F_{ROH} ranged between 0.001 and 0.035 for 3 generations, 0.003 and 0.059 for 6 generations, 0.005 and 0.074 for 12 generations in the past. The wide range of inbreeding coefficients might be a consequence of different population sizes and breed management strategies in the respective countries. The results for N_e ranged from 7 to 352 for NeEstimator, 25 to 303 for GONE, and 15 to 542 for CurrentNe. Overall, the software showed comparable results for 10 out of 16 breeds, and significantly different results for at least one software for at least one of the methods for 6 out of 16 breeds. These differences show a degree of uncertainty in N_e estimations for certain breeds. Overall, we suggest the continued monitoring of sheep breeds, ideally by routine genotyping in all populations. This monitoring is especially important for small breeds with a greater decline in genetic diversity.

Keywords: conservation status; genomic inbreeding; effective population size

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The inbreeding coefficient is one of the most important metrics in assessing livestock diversity. The knowledge of exact inbreeding coefficients on individual and population levels, including the development of inbreeding in subsequent generations, is crucial, as it impacts the fitness, productivity and adaptability to local conditions of populations (Wright 1922). Traditionally, the inbreeding is assessed using written pedigree records. The precision of such estimates relies on the availability, completeness and accuracy of such records (Meszaros et al. 2015).

With the availability of dense SNP microarrays, there are also new opportunities for assessing diversity based on genomics. Unlike the traditional pedigree analysis, genomic inbreeding does not rely on the availability and accuracy of external data, but it is directly evaluated based on the genome of the individual. The so-called runs of homozygosity (ROH) are among the most often used forms of such assessment. These long, continuously homozygous segments denote the parts of the genome originating from a single ancestor. Therefore, these segments are autozygous and form the basis of genomic inbreeding coefficient estimation (F_{ROH}, McQuillan et al. 2008).

Another frequently used metric for assessing the genetic diversity state of a population is the effective population size (N_e). It is a fundamental concept in population genetics, representing the size of the ideal population that would undergo the same extent of genetic drift or inbreeding as the actual population under study (Wright 1931). The assessment of N_e for livestock populations is a crucial part of breeding programs, in particular when both genetic gain and diversity have to be managed (Wang et al. 2016).

The estimation of N_e is closely linked to inbreeding and genetic drift, providing the measure of the rate with which the allele frequencies change due to random sampling. Traditional methods of estimation rely on pedigree and census data, which might be error prone, especially for populations with complex relationship structures (Falconer and Mackay 1996). An alternative of estimation of N_e, similar to genomic inbreeding, is the use of genomic data. A peculiar feature of effective population size is the vast range of predictive equations and estimation methodologies (Wang et al. 2016). The methods can range from simple demographical information (number of breeding males and females, or variance of progeny size), to more complex data, such as evolution of identity by descent probabilities based on coancestry or inbreeding as well as identity by descent rate between two successive generations or individual identity by descent rate (Leroy et al. 2013).

Given the importance of genomic inbreeding coefficients and effective population size, their assessment in populations is of great importance. Despite their importance for assessment of genetic diversity, the exact values are often missing in autochthonous populations. Therefore, the aim of the paper was to get an overview of the genomic inbreeding and effective population size across sheep populations in the Czech Republic, Slovakia, Serbia and Montenegro.

MATERIAL AND METHODS

Data collection and editing

Biological material of 740 animals from 16 sheep populations from the Czech Republic, Slovakia, Serbia and Montenegro was used for extracting DNA and genotyping SNP markers by two different platforms (GGP Ovine 50k and Illumina Ovine 50k) in a commercial lab.

The data of all breeds was merged, and a follow-up quality control was performed using PLINK v1.9 (Chang et al. 2015). In the first step, only the SNPs located on the autosomes were kept. Animals and SNPs with more than 10% missingness rate were removed, as well as those not adhering to the Hardy-Weinberg distribution at the level of $P < 0.001$. The exact numbers of SNPs and animals before and after the quality control are shown in Table 1.

This dataset was used to conduct analyses of genomic inbreeding without consideration of the filtering based on minor allele frequencies (MAF). The same quality control limits were used to estimate effective population size, except for the NeEstimator (Do et al. 2014), where SNPs with MAF below 5% were removed internally by the software.

Genomic inbreeding

The genomic inbreeding was estimated based on runs of homozygosity (ROH), long, continu-

Table 1. Description of genotype data for the sheep breeds used for the analyses

Country	Breed name	Samples before QC	SNPs before QC	Samples after QC	SNPs after QC (ROH)
Czechia	Šumava	48	42 994	48	42 518
	Original Valachian	72	43 012	72	42 448
	Improved Valachian	39	42 977	39	42 650
Slovakia	East Friesian	44	49 667	41	48 961
	Original Valachian	94	43 076	94	42 686
	Improved Valachian	71	49 254	68	48 918
	Lacaune	104	49 739	98	48 949
	Tsigai	70	49 229	44	48 678
	Slovak Dairy	36	49 647	36	48 726
	Crossbreed	19	49 599	19	48 813
Serbia	Cigaja	26	48 244	26	47 236
	Vlashko Vitoroga Pramenka	30	50 103	30	48 853
Montenegro	Bardoka	23	47 447	23	45 204
	Pivska Pramenka	24	47 447	24	45 301
	Sora	20	35 469	20	35 227
	Zetska Žuja	20	35 469	20	34 809

QC = quality control; ROH = runs of homozygosit; SNP = single nucleotide polymorphism

ously homozygous segments that are a consequence of mating of related individuals. Three scenarios were explored using the cgaTOH software (Zhang et al. 2013) to estimate the genomic inbreeding coefficient of animals at various points in the past. The three scenarios were distinguished based on the minimum length of ROH segments, which were restricted to 4, 8 and 16 Mb, corresponding to inbreeding due to common ancestors of parents within the past 12, 6 and 3 generations. The quality control of the ROH segments was set via the parameters suggested by Ferencakovic et al. (2013). The minimum number of SNPs within any ROH was set to 15. The maximum physical gap between consecutive homozygous SNPs was set to 1 Mb. The maximum number of missing markers was set to 1, 2 and 4 for ROH with a minimum length of 4, 8 and 16 Mb, respectively. The occurrence of heterozygous markers was not allowed, except for a maximum of one heterozygote in the longest ROH with a minimum of 16 Mb in length. The individual genomic inbreeding coefficients [F_{ROH} (McQuillan et al. 2008; Curik et al. 2014)] were computed as follows:

$$F_{\mathrm{ROH}} = \frac{\sum \mathrm{ROH}_i}{L_{autosome}} \quad (1)$$

where:

$\Sigma \mathrm{ROH}_i$ – the length of all ROH in the genome of the individual;

$L_{autosome}$ – the specific length of the autosomal genome.

The length of the genome ($L_{autosome}$) covered by SNPs was 2 647 660 kb, determined using an in-house script based on the PLINK map files after quality control.

Effective population size

Contemporary and historical effective population sizes were estimated for the sheep breeds. Three different approaches were used to determine the current effective population size. The first approach was based on the method implemented in NeEstimator v2 (Do et al. 2014), which used methodological approaches described by Waples and Do (2008) and is based on gamete disequilibrium. The second estimation of the current effective population size was based on artificial neural networks implemented in the software CurrentNe (Santiago et al. 2024). The third approach was realised with the software GONE (Santiago et al. 2020), which estimates the effective population size using a complex modelling approach based on the functional relationship between gamete and linkage disequilibrium and effective population size (Hill 1981). The algorithm in the GONE software was also used to determine the historical effective population size. The development of historical effective population size was estimated for 40 generations back, corresponding to up to 160 years, accounting for an estimated generation interval of sheep of about four years (Machova et al. 2021).

RESULTS AND DISCUSSION

Genomic inbreeding

The results for average genomic inbreeding coefficients for each breed are shown in Table 2. Based on the distance to the common ancestors, the averages ranged between 0.001 and 0.035 for 3 generations, 0.003 and 0.059 for 6 generations, 0.005 and 0.074 for 12 generations in the past. As expected, the overall inbreeding coefficient increases with the increasing number of generations being considered. The reason for this is a possibility of the occurrence of animals as common ancestors in the unobserved pedigrees of individual animals. This feature of the genomic inbreeding coefficients is a great advantage for a more precise estimation of genetic diversity, as it does not rely on the availability or accessibility of written pedigree records (Rodriguez-Ramilo et al. 2019; Antonios et al. 2021; Nishio et al. 2023). This can be confirmed, for example, with the two Czech breeds Sumava and Original Wallachian sheep when estimates of the inbreeding coefficient for these two breeds based on the full pedigree were found to be lower than for genomic inbreeding for 12 generations (Machova et al. 2021; F_X = 0.03 and 0.05).

In several studies (e.g. Amandykova 2023; Smaragdov 2023), more distant ancestors were also considered via setting the minimum length of detected ROH segments to 2 and 1 Mb, accounting for 25 and 50 generations in the past. In our case, we focused on a relatively shorter time period. The reason for this approach was to get an overview of the recent management of genetic diversity within the populations in a more realistic time frame. Counting with a generation interval of 3 years, on average, the 50-generation interval would mean 150 years in the past, pointing to selection decisions made in the 19th century. While the evaluation of ancestral inbreeding is a relevant topic (see Curik et al. 2014; Schaler et al. 2020), in our case, we preferred to examine the decisions made within the current socio-economic landscape.

Table 2. Means and standard deviations of genomic inbreeding coefficients (F_{ROH}) for 3 (F_{ROH} 3 gen.), 6 (F_{ROH} 6 gen.) and 12 (F_{ROH} 12 gen.) generations in the past

Country	Breed	F_{ROH} 3 gen. mean (SD)	F_{ROH} 6 gen. mean (SD)	F_{ROH} 12 gen. mean (SD)
Czechia	Šumava	0.014 (0.021)	0.026 (0.028)	0.039 (0.031)
	Original Valachian	0.035 (0.033)	0.059 (0.044)	0.083 (0.054)
	Improved Valachian	0.002 (0.005)	0.003 (0.008)	0.006 (0.009)
Slovakia	East Friesian	0.010 (0.021)	0.021 (0.030)	0.036 (0.038)
	Original Valachian	0.020 (0.005)	0.038 (0.040)	0.058 (0.052)
	Improved Valachian	0.001 (0.005)	0.003 (0.007)	0.005 (0.010)
	Lacaune	0.002 (0.005)	0.006 (0.007)	0.012 (0.010)
	Tsigai	0.004 (0.007)	0.007 (0.010)	0.012 (0.013)
	Slovak Dairy	0.003 (0.009)	0.005 (0.014)	0.007 (0.018)
Serbia	Cigaja	0.023 (0.016)	0.045 (0.020)	0.073 (0.026)
	Vlashko Vitoroga Pramenka	0.005 (0.009)	0.013 (0.019)	0.020 (0.023)
Montenegro	Bardoka	0.030 (0.046)	0.044 (0.058)	0.059 (0.074)
	Pivska Pramenka	0.024 (0.033)	0.037 (0.045)	0.046 (0.051)
	Sora	0.027 (0.027)	0.041 (0.038)	0.055 (0.046)
	Zetska Žuja	0.031 (0.025)	0.052 (0.037)	0.068 (0.048)

Also, for the evaluation of very short ROH segments (with a minimum length of 2, and especially 1 Mb), denser SNP chip data is preferable. If these short segments are determined using 50K SNP chips, there is a chance of frequent false positive results (Curik et al. 2014).

In our results, the breed history seems to have a great effect on the overall genomic inbreeding levels. The breeds that have undergone improvement in recent decades seem to have a much lower genomic inbreeding coefficient overall. Good examples are the Improved Wallachian breed from both the Czech Republic and Slovakia or the Slovak Dairy breed from Slovakia. No ROH segments with a minimum length of 4 Mb were found in the crossbred population from Slovakia. Of course, there were examples of animals with a relatively high inbreeding coefficient in all breeds. The maximum value for the Improved Wallachian population from the Czech Republic was 0.043, for the Improved Wallachian from Slovakia it was 0.062, and for the Slovak Dairy from Slovakia it was 0.087. The results were quite interesting, as one would expect substantial inbreeding coefficients in any breed with very recent common ancestors. It seems, however, that the mating of closely related animals was avoided in these breeds. The reason could be the relatively higher population size within the country; therefore, there is a better possibility of avoiding close relatives.

However, in small autochthonous and indigenous breeds with lower population size, we have found individuals with higher genomic inbreeding coefficients more often. An additional reason for the small population size could be that the breeders want to keep these populations pure, and the populations are closed to matings from outside. This limited pool of possibilities then causes the rise in genomic inbreeding coefficients.

While the strategy of closed populations is common, it also highlights the increased need for diversity management in these breeds. The choice of mate pairs should be done in a planned manner, considering the relatedness between the potential mate pairs. This relatedness is ideally computed using SNP genotypes, or at least conventional pedigree relatedness, if genotypes are not readily available. The importance of genetic management of breeds was also highlighted by Akdemir and Sanchez (2016), Sedighi et al. (2019) or Zhang et al. (2022).

Effective population size

The results for the contemporary estimates of effective population size are presented in Table 3. The estimation of effective population size obtained with NeEstimator was lower in 15 out of 16 cases than the estimation from GONE and CurrentNe. These lower estimates were found in 6 out of 16 breeds using GONE and 2 out of 16 breeds using CurrentNe. The significance of differences between the estimates was assessed by the absence of overlap between confidence intervals from the three software tools. Similar conclusions were reached in other studies by Vostry et al. (2023) and Vostry et al. (2024). The existence of overlapping generations introduces additional noise to the N_{eLD} estimates because of potential inaccuracies, as described by Waples et al. (2014). According to simulations performed in several studies (Santiago et al. 2020; Novo et al. 2023), the N_{eLD} estimates obtained by GONE are generally considered to be more accurate. Also, the effective population size estimated by CurrentNe showed lower estimates in most cases than those obtained from GONE. These differences between CurrentNe and GONE were significant in 2 out of 16 breeds. When comparing these results and considering the farming conditions for the respective breeds analysed, GONE showed more realistic estimates. The relatively low estimates of effective population size correspond to the historical development of the analysed breeds. The relatively wide confidence intervals of effective population size, which provide less informative estimates, were caused by the lower number of analysed individuals, for example, in the Tsigai breed.

Interestingly, the N_e estimates for 13 out of 16 populations were higher than the critical value of 50 effective animals recommended by FAO (1998), despite the closed nature of the autochthonous sheep populations. Our estimates were in the same range as those obtained in other small ruminant populations (Drzaic et al. 2024; Vostry et al. 2024). The estimates of N_e for two Czech breeds – Sumava and Original Wallachian – were very similar in the context of confidence intervals to estimates based on pedigree analysis (Machova et al. 2021; N_e = 99 and 51). On the other hand, the N_e estimates based on SNP data obtained by Machova et al. (2023) were significantly lower compared to the current analysis. The difference could be due to the use of the SNeP software (Barbato et al. 2015) in Machova

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Table 3. Genomic contemporary Ne_{LD} estimates with 95% confidence intervals in parenthesis for 16 sheep breeds in Danube regions estimated using three different approaches

Country	Breed	*n*	NeEstimator v.2	GONE	CurrentNe
Czechia	Šumava	48	52 (37–78)	73 (58–92)	98 (78–123)
	Original Valachian	72	40 (30–55)	65 (55–77)	80 (76–104)*
	Improved Valachian	39	352 (217–873)	303 (211–435)	542 (317–927)
Slovakia	East Friesian	44	30 (21–48)	67 (53–84)*	52 (43–64)
	Original Valachian	94	34 (29–40)	75 (64–85)*	75 (67–84)
	Improved Valachian	71	106 (73–177)	265 (210–331)*	169 (138–208)†
	Lacaune	104	81 (63–109)	121 (105–140)	111 (98–126)
	Tsigai	70	97 (58–233)	197 (421–725)*	39 (33–45)*†
	Slovak Dairy	36	46 (30–82)	94 (70–123)	78 (60–103)
	Crossbreed	19	13 (4–77)	57 (41–80)	28 (20–38)†
Serbia	Cigaja	26	13 (8–22)	44 (33–59)*	32 (25–41)*
	Vlashko Vitoroga Pramenka	30	95 (70–142)	119 (84–165)	148 (99–222)
Montenegro	Bardoka	23	33 (22–58)	70 (50–99)	40 (29–54)
	Pivska Pramenka	24	27 (18–46)	67 (48–93)*	37 (28–50)
	Sora	29	7 (3–16)	25 (12–30)	15 (14–20)
	Zetska Žuja	29	28 (20–44)	35 (26–44)	45 (35–59)

*Significantly different estimates – GONE or CurrentNe versus NeEstimator 2v; †Significantly different estimates – GONE versus CurrentNe

et al. (2023), which tends to underestimate the N_e estimates compared to GONE.

Figure 1 represents a trend of the historical effective population size over the last 40 generations obtained from GONE. The analysed populations were split into two parts. The first part of populations (Czech Improved Wallachian, Czech Sumava, Serbian Tsigai, East Friesian, Lacaune) (Figure 1A) presents a gradually decreasing effective population size over the analysed period. The decrease in the effective size of the population in these breeds is related to the decreasing interest and overall importance of these breeds. In the second group (Figure 2B) of the analysed populations (Czech and Slovak Original Wallachian, Slovak Improved Wallachian, Pivska Pramenka, Sora, Zetska Zuja, Vlashko Vitoroga Pramenka, Slovak Dairy, Tsigai, crossbreds) there is a significant decrease in N_e between the second and the eighth generation. According to Novo et al. (2023) this drastic reduction in effective population size is most likely influenced by admixture. This statement may be supported by the fact that this second group of populations has the same trend of historic N_e as the crossbreds and Slovak Dairy.

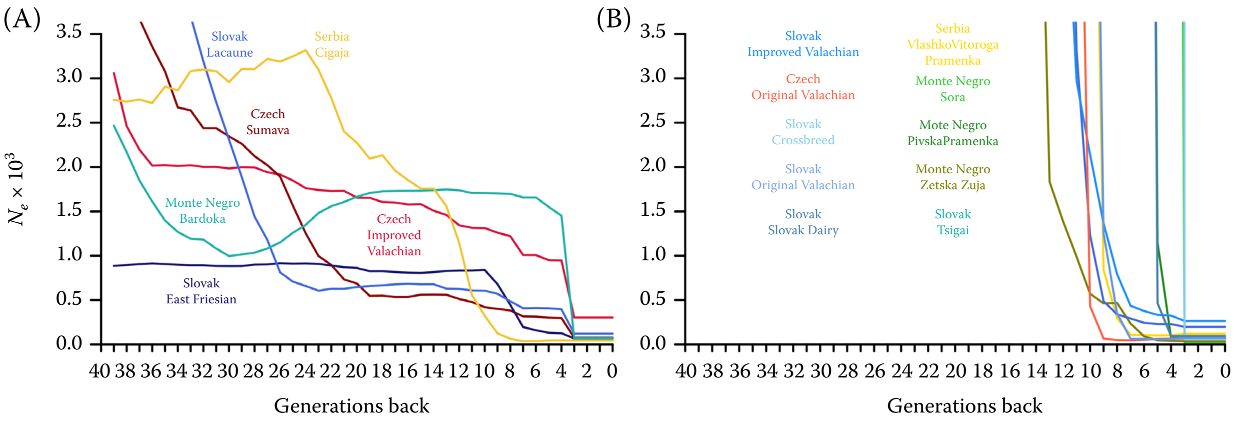

Figure 1. Historical gametic/linkage effective population size (N_{eLD}) of autochthonous sheep breeds

The Improved Wallachian, the Slovak Dairy and the group of crossbreds are examples of breeds with intentional crossbreeding and efforts to create synthetic lines during their development, where a high degree of admixture was present. These efforts are also reflected in the higher effective population sizes of potentially more admixed breeds. This is also supported by Waples and England (2011) and Novo et al. (2023), who stated that the estimates of current N_e based on LD are not significantly affected by admixture.

CONCLUSION

The availability of genomic information provides opportunities to estimate genomic inbreeding and effective population size in sheep breeds, even without the availability of conventional pedigree records. In general, the findings in this paper underline the importance of the management of genetic diversity, especially for autochthonous and small breeds. In the present paper two of the most frequently used metrics of genetic diversity assessment were explored. The ROH metric was used to assess the genomic inbreeding coefficient within breeds. Breeds with the recent history of improvement, sometimes using crossbreeding techniques, had a much lower average inbreeding compared to autochthonous breeds with smaller, closed populations. The effective population size was estimated using three different methodological approaches based on linkage disequilibrium, also to address the uncertainty within any one approach. The results were mostly consistent, although we observed significantly different estimates between software tools for some of the breeds. In general, the effective population size for most of the breeds was above 50, which is considered as a limit of the endangerment status. We suggest the continued monitoring of sheep breeds, ideally by routine genotyping in all populations. This monitoring is especially important for small breeds with a greater decline in genetic diversity.

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Conflict of interest

The authors declare no conflict of interest.

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