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Genetic structure and diversity of dairy cows in commercial herds in Burkina Faso using microsatellite markers

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Abstract

The present study provides knowledge about the genetic diversity and population structure of cows in peri-urban cattle herds that are urgently needed for the planning of systematic selection programs. We considered 21 microsatellite markers to identify genetic clusters for 112 dairy cows from Burkina Faso and a reference dataset of European cattle breeds (n = 179). Unsupervised clustering and a model-based approach were used for identification of latent classes and inference of genetic diversity within classes. Overall, the genetic diversity of cows in commercial dairy herds in Burkina Faso was high. Clustering results suggest four genetic clusters. Almost all cows from Burkina Faso shared the same ancestry and were grouped together in cluster 3. The highest expected heterozygosity ($H_E = 0.74$) and inbreeding coefficient ($F_{IS} = 0.08$) were obtained for this cluster. The other genetic clusters included Original Braunvieh and Tarentaise (cluster 1), Red Holstein (cluster 2) and Fleckvieh (cluster 4). The genetic distances of cluster 3 to the other clusters were large. In conclusion, the poor population structuring, and the low genetic contribution of European cattle breeds underline the need for effective (cross-)breeding strategies for optimal exploitation of heterosis effects and preservation of genetic diversity in dairy cows in Burkina Faso.

Keywords: European cattle crossbred cows, genetic differentiation, West Africa, zebu cattle

1 Introduction

In Burkina Faso, a transformation of peri-/urban livestock production systems has been witnessed, with a shift from traditional extensive cattle production towards a specialised commercial dairy production sector in the outskirts of major cities (Dossa *et al*., 2015; Roessler *et al*., 2016). In Burkina Faso, these peri-urban areas are defined as the surroundings of the contiguous built-up area of Bobo-Dioulasso including its 35 villages (Dossa *et al*., 2015), and the area at an average linear distance of 19-55 km from the geographical city centre of Ouagadougou (Stenchly *et al*., 2018). The transformation of the dairy production sector is accompanied by changes in the breeding management as well as in the breed and trait preferences of livestock owners. On the one hand, specialised, modern dairy producers invest in artificial insemination with semen of various European taurine cattle breeds, namely Holstein Friesian, Montbéliarde, Brown Swiss, Normande, and Tarentaise, or use natural service bulls of regional *Bos indicus* cattle like the Azawak or Gudali to improve local zebu Peul cows to increase milk production per cow (Roessler, 2019). Crossbred cows from European cattle are often preferred because of their higher milk yield and a better growth performance of their offspring compared to pure- and crossbred zebu cows. Accordingly, milk yield and growth performance are the predominant selection criteria used for the selection of insemination bulls (Roessler, 2019). To support their selection decisions, producers keep written animal records, but routine performance testing and structured breeding programs are not available (Roessler, 2019). In Ouagadougou and 10 other sites in the central and Sahel regions of Burkina Faso, a dispersed nucleus scheme was initiated with the aim to upgrade the Fulani Sudanese zebu breed by crossbreeding with Azawak zebu bulls (Ouédraogo *et al*., 2021). However, the genetic potential of imported

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breeds and their crosses is often not fully exploited due to isolated breeding decisions and unsystematic crossbreeding (Roessler *et al*., 2019), as well as poor management of cattle herds (Marshall *et al*., 2016). On the other hand, local cattle herders continue to rely on the local zebu Peul breed. Apart from milk production, this breed fulfils numerous other functions in traditional cattle farming in Burkina Faso. It is preferred for its good adaptation to local production conditions. Selection decisions are not purely based on performance traits, reproduction and behavioural traits also play an important role (Roessler, 2019). The emphasis on adaptation to and survival under harsh and variable environmental conditions instead of more intensive and one-sided selection for increased milk production performance may have resulted in a higher genetic diversity in the Peul breed than in high-performing European cattle breeds (Mwai *et al*., 2015). Indiscriminate crossbreeding resulting in uncontrolled gene flow between breeds and changes in livestock production systems affect the genetic diversity within and between cattle breeds as well as the multiple functions of cattle in traditional production systems. The loss of adaptive traits embedded in the local zebu Peul breed and potential erosion of the breed foundation due to crossbreeding with European breeds might be a relevant risk for the future development of the livestock production sector in Burkina Faso (Leroy *et al*., 2016; Malenje *et al*., 2022). Research on genetic diversity in cattle from Burkina Faso has been very limited in the past and mainly assessed the introgression of zebu genes into native taurine cattle populations (Álvarez *et al*., 2014; Soudré *et al*., 2019). To our knowledge, no prior study has evaluated the genetic diversity in a sample from peri-urban cattle herds in Burkina Faso. The present study therefore aimed at providing knowledge about the genetic diversity levels of cows in peri-urban cattle herds as a basis for systematic selection programs. The specific study objectives were to 1) identify genetic clusters in dairy cows from commercial herds in Burkina Faso and the reference dataset using unsupervised clustering and a model-based approach, 2) compare the original breed assignment based on owners' information and information in the obtained reference dataset to the genetic clusters obtained using clustering, and 3) assess the genetic diversity within the genetic clusters inferred by clustering using different diversity related measures/parameters as described in the practical guide on genomic characterisation of animal genetic resources of the FAO (Ajmone-Marsan *et al*., 2023). Results could help to understand the present and future utility of the local zebu Peul breed for the emerging commercial dairy production sector in the outskirts of larger cities in Burkina Faso.

2 Materials and methods

2.1 Samples

All subjects gave their informed verbal consent for inclusion before they participated in the study. The study was conducted in accordance with international and local guidelines ensuring ethically conducted research, and the protocol was approved by the Ethics Committee of the University Joseph Ki-Zerbo in Ouagadougou (CE-UJKZ/2024-01). Individual samples were collected from 39 representative cattle herds in 12 sites in the outskirts of Ouagadougou, capital city of Burkina Faso. They were chosen based on previous field studies that were carried out within the UrbanFood^{Plus} project between 2013-2018. A total of 112 hair samples were collected from 2-3 randomly selected cows from each herd by plucking 20-50 hairs from the tail switch of each cow, ensuring intact follicles. The samples were taken from the local zebu Peul (P; n = 70) (Fig. 1, left), the zebu Gudali (G; n = 4) (Fig. 1, middle) and the zebu Azawak (A; n = 14), as well as from generally indeterminate crosses between the local zebu Peul (as dam) with other cattle breeds (used as sire), namely G x P (n = 4), A x P (n = 3), Holstein Friesian (HF) × P (n = 10) (Fig. 1, right), Brown Swiss (BS) × P (n = 2), Montbéliarde (M) × P (n = 2), Normande (N) × P (n = 2) and Tarentaise (T) × P crossbreds (n = 1). Based on information from the respective owner / responsible farm manager, only unrelated animals were accepted for sampling. All 112 sampled individuals were genotyped for microsatellite markers as described below.

Fig. 1: *Local zebu Peul (left), imported Gudali zebu (middle) and Holstein Friesian × local zebu Peul crossbred cow (right).*

No cattle of pure European origin were present in the studied dairy cattle herds. Hence, the microsatellite data of dairy cows from commercial herds in Burkina Faso were merged with a reference dataset, which included microsatellite data for Fleckvieh (n = 57), Red Holstein (n = 49) and Original Braunvieh (n = 30) from Germany, as well as Tarentaise (n = 43) from France (Medugorac *et al*., 2009). These breeds were included because they represent an ancestry reference for the sampled crossbred cows in commercial herds in Burkina Faso. The final dataset used for the statistical analysis of genetic diversity therefore contained n = 291 individuals (n = 112 samples from Burkina Faso, n = 179 reference samples).

2.2 DNA extraction from hair samples, polymerase chain reaction (PCR) and fragment analysis of microsatellite markers

Genomic DNA was extracted from hair roots using the NucleoSpin Tissue Kit (Macherey Nagel) following the manufacturer's instructions. DNA with a ratio of absorbance at 260 and 280 nm of ~1.8, standing for pure DNA was standardised to 50 ng μl^{-1} using ND-1000 NanoDrop spectrophotometer (NanoDrop Technologies). A total of 30 bovine-specific microsatellite markers (Table 1) from the FAO panel of markers were used to characterize the genetic diversity and population structure of the sampled animals (FAO, 2011). The 179 purebred reference samples of Medugorac *et al*. (2009) had also previously been genotyped for the identical microsatellites. The genotyping results of these samples were used to standardise the evaluation of the microsatellites of the samples from Burkina Faso to obtain direct comparability of the results.

PCR reactions were performed using 12.5 μL Quiagen® PCR Master Mix (Qiagen), 10 pM of each primer, and 50 ng bovine genomic DNA, and filled up to a final volume of 25 μl with H_2O. The reverse primer was labelled with a fluorescent dye at the 5' end. Microsatellite genotype analysis was performed on an Applied Biosystems 3130 Genetic Analyser (Applied Biosystems) using the Gene MapperTM software version 4.0 (Applied Biosystems).

2.3 Statistical analyses

Microsatellite markers

The presence of null alleles was tested using the *adegenet* package (Jombart, 2008; Jombart & Ahmed, 2011) in R version 4.0.2 (R Core Team, 2020). Loci with estimated frequencies of null alleles of $r \geq 0.2$ were removed from the statistical analyses (Berthouly-Salazar *et al*., 2012). Out of the 30 microsatellite markers, nine (*BM1824, ETH185, HEL5, HEL13, INRA005, MM12, SPS115, TGLA122, TGLA227*) exceeded this threshold value and were excluded from further analysis. For the remaining 21 microsatellite markers, the total and the mean number of alleles per locus (N_A), the observed (H_O) heterozygosity, and the expected unbiased heterozygosity (H_E) were calculated for each micro-satellite marker (locus). We used the *adegenet* package to obtain these estimates. Deviations from the Hardy-Weinberg equilibrium (HWE) were tested with the *hw.test* function from the *pegas* package (Paradis, 2010). The F-statistics (F_{IS}, F_{ST}, F_{IT}) were estimated using the *hierfstat* package (Goudet & Jombart, 2015).

Table 1: *Microsatellite markers used to assess the genetic structure and diversity of commercial dairy cows in Burkina Faso and European dairy/dairy-beef cattle populations.*

Marker	*Chromosome*	*Primer sequence (5'-3') Forward / Reverse*
BM1818	23	AGCTGGGAATATAACCAAAGG AGTGCTTTCAAGGTCCATGC
BM1824	1	GAGCAAGGTGTTTTTCCAATC CATTCTCCAACTGCTTCCTTG
BM2113	2	GCTGCCTTCTACCAAATACCC CTTAGACAACAGGGGTTTGG
CSRM60	10	AAGATGTGATCCAAGAGAGAGGCA AGGACCAGATCGTGAAAGGCATAG
CSSM66	14	ACACAAATCCTTTCTGCCAGCTGA AATTTAATGCACTGAGGAGCTTGG
ETH3	19	GAACCTGCCTCTCCTGCATTGG ACTCTGCCTGTGGCCAAGTAGG
ETH10	5	GTTCAGGACTGGCCCTGCTAACA CCTCCAGCCCACTTTCTCTTCTC
ETH152	5	TACTCGTAGGGCAGGCTGCCTG GAGACCTCAGGGTTGGTGATCAG
ETH185	17	TGCATGGACAGAGCAGCCTGGC GCACCCCAACGAAAGCTCCCAG
ETH225	9	GATCACCTTCGGACTATTTCCT ACATGACAGCCAGCTGCTACT
HAUT24	22	CTCTCTGCCTTTGTCCCTGT AATACACTTTAGGAGAAAAATA
HAUT27	26	TTTTATGTTCATTTTTTGACTGG AACTGCTGAAATCTCCATCTTA
HEL1	15	CAACAGCTATTTAACAAGGA AGGCTACAGTCCATGGGATT
HEL5	21	GCAGGATCACTTGTTAGGGA AGACGTTAGTGTACATTAAC
HEL9	8	CCCATTCAGTCTTCAGAGGT CACATCCATGTTCTCACCAC
HEL13	11	TAAGGACTTGAGATAAGGAG CCATCTACCTCCATCTTAAC
ILSTS005	10	GGAAGCAATGAAATCTATAGCC TGTTCTGTGAGTTTGTAAGC
ILSTS006	7	TGTCTGTATTTCTGCTGTGG ACACGGAAGCGATCTAAACG
INRA005	12	CAATCTGCATGAAGTATAAATAT CTTCAGGCATACCCTACACC
INRA023	3	GAGTAGAGCTACAAGATAAACTTC TAACTACAGGGTGTTAGATGAACTCA
INRA032	11	AAACTGTATTCTCTAATAGCAC GCAAGACATATCTCCATTCCTTT
INRA035	16	ATCCTTTGCAGCCTCCACATTG TTGTGCTTTATGACACTATCCG
INRA037	10	GATCCTGCTTATATTTAACCAC AAAATTCCATGGAGAGAGAAAC
INRA063	18	ATTTGCACAAGCTAAATCTAACC AAACCACAGAAATGCTTGGAAG
MM12	9	CAAGACAGGTGTTTCAATCT ATCGACTCTGGGGATGATGT
SPS115	15	AAAGTGACACAACAGCTTCTCCAG AACGAGTGTCCTAGTTTGGCTGTG
TGLA53	16	GCTTTCAGAAATAGTTTGCATTCA ATCTTCACATGATATTACAGCAGA
TGLA122	21	CCCTCCTCCAGGTAAATCAGC AATCACATGGCAAATAAGTACATAC
TGLA126	20	CTAATTTAGAATGAGAGAGGCTTCT TTGGTCTCTATTCTCTGAATATTCC
TGLA227	18	CGAATTCCAAATCTGTTAATTTGCT ACAGACAGAAACTCAATGAAAGCA

Identification of genetic clusters using unsupervised K-means clustering and DAPC

Genetic clusters were initially inferred using the *K*-means clustering algorithm (find.clusters function within the *adegenet* package). The maximum number of clusters was set to 20, and 250 principal components (PC) were retained. The final choice of the optimal number of clusters was based on the lowest associated Bayesian information criterion (BIC) value (597.5) that was obtained for $K = 4$ (Fig. 2). Then, principal component analysis (PCA) and discriminant analysis of principal components (DAPC) were performed. Cross-validation of DAPC was carried out with the function xvalDapc to determine the optimum number of PCs to be retained. The first 40 PCs were retained based on the highest mean successful assignment (40.4 %) and lowest root mean squared error (0.60). They cumulatively explained 72.5 % of the total variance of the data. The reports of the allele frequencies (loadings) in the merged dataset allowed determination of the contribution of alleles to the distribution of original breeds in the DAPC scatterplot.

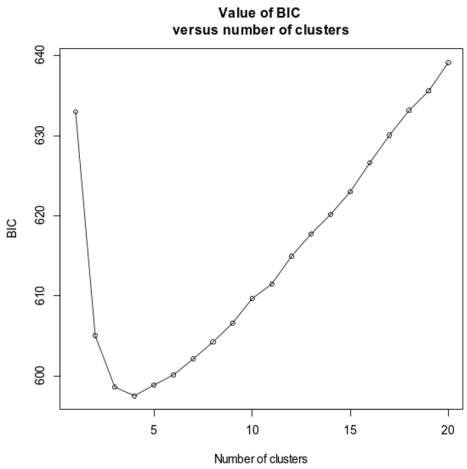

Fig. 2: *Bayesian information criterion (BIC) showing the most likely number of clusters using unsupervised clustering.*

Subsequently, inferred genetic clusters were compared to the original breed assignments according to the owner's information and prior knowledge in the reference dataset. Since no traceable valid pedigree records were available for the cows in the sample, the breed proportions of the crossbred cows were unknown. In addition, the phenotypical appearance was used to confirm the owners' classification. For the reference dataset of the European cattle breeds, information on the original breed was available for each individual. The accordance of inferred cluster assignments with breed assignment information for each individual was also compared visually using results from the PCA.

Identification of genetic clusters using a model-based approach

Genetic structure analysis was performed using the STRUCTURE 2.3.4 software (Pritchard *et al*., 2000) with the parameter values set as follows: length of burnin period: 200,000; number of Markov Chain Monte Carlo (MCMC) repetitions after burnin: 500,000; use admixture model with correlated allele frequencies (Falush *et al*., 2003); allele frequencies are correlated among populations; 20 iterations; and $K = 1$–10. The most likely number of *K* was determined according to the ΔK method implemented in the R package *pophelper* (Francis, 2017) by identifying *K* with the highest value of ΔK and the lowest value of the mean posterior probability of the data (Lnp[D]) (Fig. 3). As the inferred number of *K* diverged between *K*-means clustering, DAPC and the model-based approach, barplots for $K = 2$– 4 are presented for discussion. Microsoft Excel was used for calculation and graphical representation of the results obtained by STRUCTURE 2.3.4.

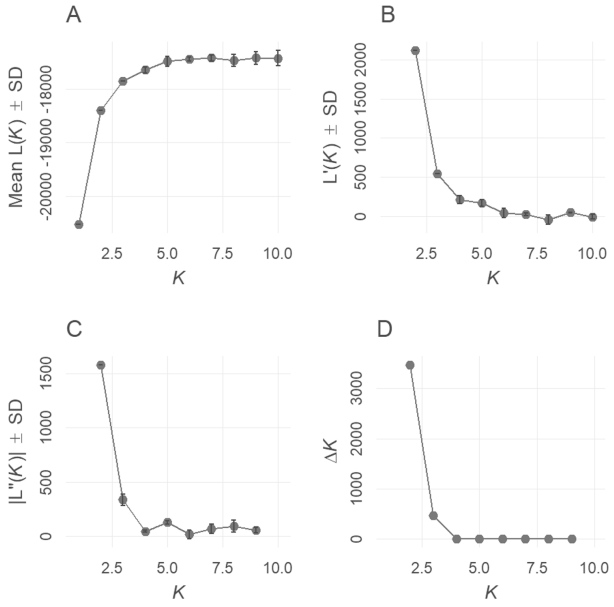

Fig. 3: *Plot of mean likelihood L(K) and standard deviation (SD) per K value (A) and Evanno plots (Evanno et al., 2005) for detecting the number of clusters (K) that best fit the data.*

Genetic diversity within and between genetic clusters identified through unsupervised clustering

The merged dataset was used to calculate the F-statistics (Wright, 1965) using the *hierfstat* package. Observed heterozygosity (H_O), expected heterozygosity (H_E), and Wright's inbreeding coefficient (F_{IS}) were calculated to evaluate the levels of genetic diversity within genetic clusters

inferred by unsupervised clustering (Nei, 1987). The boot.ppfis function in the same package was used to estimate 99 % confidence intervals for F_{IS} values. Pairwise fixation index (F_{ST}) was estimated using the method of Weir & Cockerham (1984) and the method of Nei (1986) to evaluate the level of genetic differentiation between and within genetic clusters identified through unsupervised clustering.

3 Results

3.1 Microsatellite markers

In total, 204 alleles were detected at the 21 loci in the 112 samples of dairy cows in Burkina Faso, implying a mean number of 9.7 (± 2.45 SD) alleles per locus (Table 2). The most polymorphic locus was *TGLA53* ($N_A = 16$ alleles), while the locus with the lowest number of alleles was *ILSTS005* ($N_A = 5$). Across the studied loci, H_O was generally lower than H_E, except for *BM2113, CSSM66, HAUT24* and *HAUT27*. Overall, H_O and H_E averaged 0.681 and 0.743 ($p < 0.01$). H_O was lowest for *INRA35* (0.437) and highest for *BM2113* (0.867), while the H_E values ranged between 0.456 (*INRA35*) and 0.845 (*BM1818*). Over half of the studied loci (57 %) were not in HWE. The global deficit of heterozygotes (F_{IT}) was estimated at 0.10. The deficiency of heterozygotes was mostly due to within-group inbreeding ($F_{IS} = 0.076$), while the contribution of genetic drift among the pre-defined group to the overall reduction in heterozygosity was small ($F_{ST} = 0.025$). The F_{IS} value was positive for 81 % of the studied microsatellite markers, and only 19 % showed negative values, with the lowest and highest value being observed for *BM2113* and *TGLA53*, respectively. Except locus *BM2113*, all of the loci which deviated from HWE were related to a positive F_{IS}, indicating HWE deviation in the direction of heterozygote deficits. The F_{IT} estimates ranged between −0.197 (*BM2213*) and 0.53 (*TGLA53*), while the F_{ST} estimates of individual loci ranged from −0.002 (*CSMM66*) to 0.09 (*ETH152*) (Table 2).

3.2 Identification of genetic clusters using K-means clustering and DAPC

In total, $K = 4$ genetic clusters were identified by unsupervised clustering (BIC = 597.5). Cluster sizes were n = 59 (genetic cluster 1), n = 55 (genetic cluster 2), n = 105 (genetic cluster 3) and n = 72 (genetic cluster 4). Inferred genetic clusters were in general concordance with the original

Table 2: *Genetic statistics for 21 microsatellite loci analysed in 112 cows in Burkina Faso.*

Locus	N_A	H_E	H_O	*HWE* (X^2)	F_{IS}	F_{IT}	F_{ST}
BM1818	9	0.845	0.771	64.8*	0.086	0.098	0.013
BM2113	13	0.717	0.867	158.4**	−0.214	−0.197	0.014
CSRM60	9	0.619	0.582	26.9n.s.	0.045	0.081	0.038
CSSM66	14	0.832	0.840	148.0n.s.	−0.003	−0.005	−0.002
ETH3	7	0.657	0.514	54.4**	0.203	0.236	0.041
ETH10	10	0.792	0.682	151.3*	0.129	0.154	0.029
ETH152	9	0.619	0.480	67.1**	0.188	0.260	0.090
ETH225	12	0.670	0.624	181.4*	0.031	0.106	0.077
HAUT24	11	0.830	0.832	161.6n.s.	−0.007	0.012	0.019
HAUT27	9	0.754	0.773	24.1n.s.	−0.029	−0.013	0.015
HEL1	8	0.786	0.728	42.4n.s.	0.063	0.092	0.031
HEL9	9	0.842	0.818	23.9n.s.	0.029	0.036	0.007
ILSTS005	5	0.673	0.565	17.6*	0.151	0.178	0.032
ILSTS006	9	0.766	0.692	54.2*	0.093	0.108	0.017
INRA023	12	0.792	0.742	126.8***	0.061	0.074	0.014
INRA032	9	0.852	0.724	54.9***	0.143	0.164	0.024
INRA035	8	0.456	0.437	18.2n.s.	0.048	0.047	−0.001
INRA037	8	0.818	0.808	22.8n.s.	0.002	0.030	0.028
INRA063	9	0.746	0.588	188.3***	0.210	0.223	0.017
TGLA53	16	0.796	0.521	346.9***	0.347	0.352	0.007
TGLA126	8	0.745	0.704	20.2n.s.	0.043	0.075	0.034
Mean	9.7	0.743	0.681		0.077	0.101	0.026
SD	2.45	0.096	0.126		0.110	0.113	0.022

breed classification by the cattle owners/ herders (Table 3). Almost all pure- and crossbred zebu cows from commercial herds in Burkina Faso were grouped in genetic cluster 3, except for HF × P crosses that were also partly assigned to genetic cluster 2. European cattle breeds (reference dataset) were assigned to genetic cluster 1 (Original Braunvieh and Tarentaise), genetic cluster 2 (Red Holstein) or genetic cluster 4 (Fleckvieh).

Table 3: *Comparison of inferred genetic clusters by DAPC and original breed classification of commercial dairy cows in Burkina Faso and European cattle populations.*

	Inferred genetic cluster (number of individuals)			
*Original classification**	*1*	*2*	*3*	*4*
Burkina Faso				
Local zebu Peul (P)	0	0	70	0
Azawak zebu (A)	0	0	14	0
Gudali zebu (G)	0	0	4	0
A × P cross	0	0	3	0
G × P cross	0	0	4	0
Holstein Friesian × P	1	4	4	1
Montbéliarde × P	0	0	2	0
Brown Swiss × P	0	0	1	1
Normande × P	0	0	2	0
Tarentaise × P	0	0	1	0
Europe				
Fleckvieh	1	2	0	54
Red Holstein	0	49	0	0
Original Braunvieh	28	0	0	2
Tarentaise	29	0	0	14
Cluster size (total n)	59	55	105	72

*breed.

The first principal component (PC) clearly separated genetic cluster 3 from genetic clusters 1, 2 and 4. The second PC further separated genetic cluster 2 from genetic clusters 1 and 4. There is considerable overlap between genetic clusters 1 and 4 (Fig. 4). The distribution of allele frequencies for the most informative loci across genetic clusters showed that allele *ETH225-158* bp was not found in European cattle breeds in the reference dataset, contributing most to the genetic difference between cows from commercial herds in Burkina Faso and the European cattle breeds in the reference dataset (results not shown).

3.3 Identification of genetic clusters using a model-based approach

While the *K*-means clustering based on PCA and DAPC suggested a subdivision of the global sample into three to four clusters, the Bayesian procedure performed in STRUCTURE 2.3.4 revealed a subdivision into two ($\Delta K = 3472$) or three clusters ($\Delta K = 461$) (Fig. 5). A comparison of the STRUCTURE results for $K = 2$ to $K = 4$ shows that two clusters are generally sufficient to identify distinct genetic clusters in the dataset. Two clusters clearly separated all the cows sampled in Burkina Faso from the purebred European cattle populations of the reference dataset (Fig. 5; upper plot). For $K = 2$, the average individual membership proportion of the cows from Burkina Faso for cluster 1 was estimated at 0.996, compared to 0.006 in European cattle breeds of the reference dataset. The average membership proportion for cluster 1 was generally higher in cows of pure zebuine origin (P: 0.993, A: 0.974, G: 0.997, A × P: 0.952, A × P: 0.980) than in crossbred cows with genetic influence of European cattle breeds which were a mixture of both clusters (average individual membership proportions: 0.575 and 0.425 for cluster 1 and 2, respectively). $K = 3$ and $K = 4$ further subdivided the European cattle breeds of the reference dataset and the crossbred cows with European cattle influence in dairy herds in Burkina Faso (Fig. 5; middle and lower plot). In more detail, for $K = 3$, pure Red Holstein cattle formed a separate homogenous genetic group (average estimated individual membership proportion for cluster 3: 0.973). Furthermore, crossbred Holstein Friesian × zebu cows showed noticeable ancestry contribution of this cluster (0.335), which was higher than that of crosses with other European cattle breeds, namely Brown Swiss (0.147), Normande (0.064), Montbéliarde (0.023), and Tarentaise (0.004).

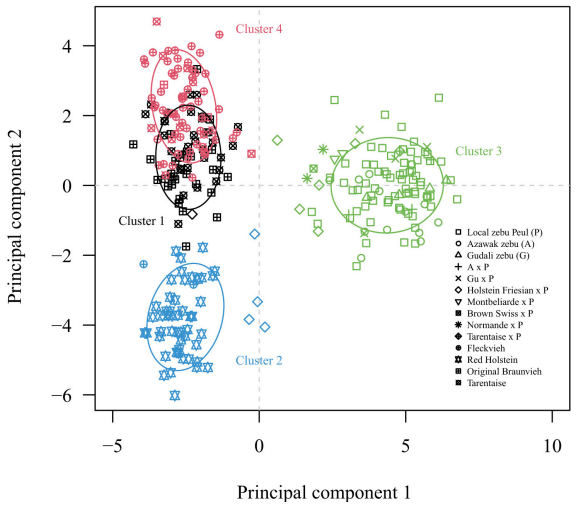

Fig. 4: *Scatterplot for the first two principal components (total number of PCs retained = 40) estimated from DAPC analysis. The shapes are based on the original classification (n = 14) of each individual. Inferred genetic groups (*K *= 4) are visualised using ellipses and different colours.*

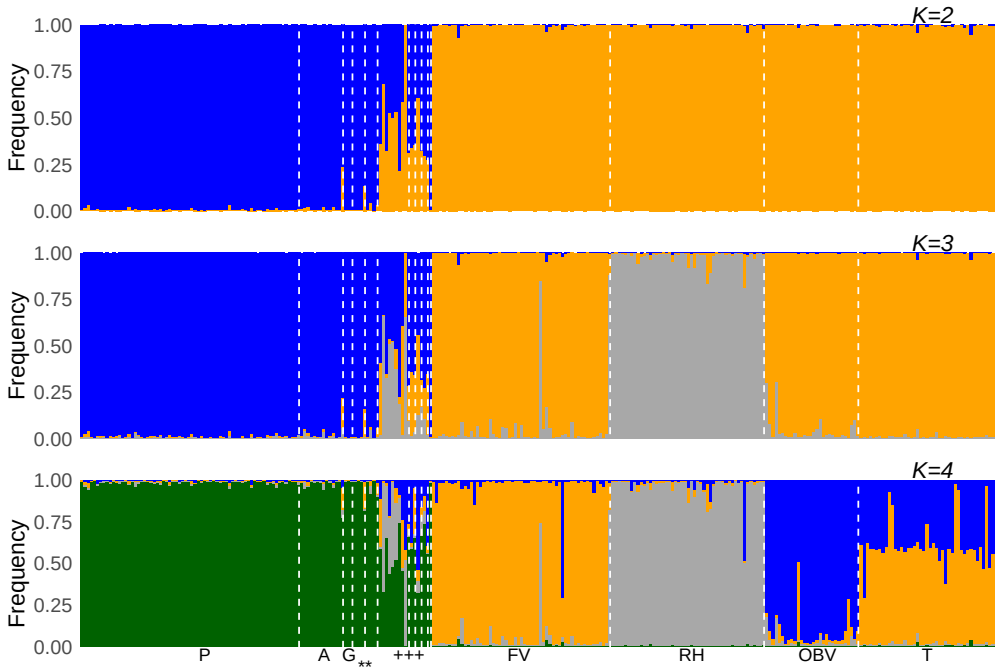

Fig. 5: *Bayesian inference of the most likely number of clusters (*K = *2–4). Each cow is represented by a single vertical bar. Colours reflect the likelihood of individual cows to belong to one of the* K = *2 or* K = *4 clusters. Original breeds are separated by white dashed lines; from left to right: Local zebu Peul (P), Azawak zebu (A), Gudali zebu (G), A × P cross and G × P cross (**); Holstein Friesian × P cross, Brown Swiss × P cross, Montbéliarde × P cross, Normande × P cross, Tarentaise × P cross (+++); Fleckvieh (FV), Red Holstein (RH), Original Braunvieh (OBV) and Tarentaise (T).*

For $K = 4$, Original Braunvieh, Fleckvieh and Red Holstein of the reference dataset, as well as the cows with pure zebuine origin managed in dairy herds in Burkina Faso, built separate homogenous genetic clusters, with most animals being assigned to cluster 1, 2, 3 or 4, respectively (average estimated individual membership proportions: 0.917, 0.914, 0.953, 0.976). The other cattle genotypes showed mixed ancestry contributions with $K = 4$ (Fig. 5; lower plot).

3.4 Genetic diversity within and between genetic clusters derived by K-means clustering and DAPC

H_O of genetic cluster 3 which included most cows with pure zebuine origin from commercial herds in Burkina Faso, was similar to the other clusters which comprised European cattle breeds from the reference dataset. The highest H_E was calculated for this cluster, indicating a high genetic diversity of cows in commercial dairy herds in Burkina Faso. H_E was significantly different from H_O in this cluster, while no differences between H_E and H_O could be detected for the other clusters. Mean F_{IS} values indicated low inbreeding within each cluster. The highest value was calculated for individuals in genetic cluster 3; however, it is still close to zero. The 99 % confidence intervals for the group-wise F_{IS} values only indicated a moderate heterozygosity deficit of individuals in genetic cluster 1 which contained mostly Original Braunvieh and Tarentaise cattle (Table 4).

Pairwise F_{ST} values according to Weir & Cockerham (1984) and according to Nei (1987) point to the strongest

Table 4: *Observed heterozygosity (H_O), expected heterozygosity (H_E) and Wright's inbreeding coefficient (F_{IS}) with 99 % confidence intervals (CI) of each genetic cluster inferred by unsupervised clustering.*

		F-statistics (mean ± standard deviation)			*99 % CI*
Inferred genetic cluster	*n*	H_O	H_E	F_{IS}	F_{IS}
Genetic cluster 1	59	$0.62^a \pm 0.161$	$0.65^a \pm 0.148$	0.04 ± 0.107	0.02–0.13
Genetic cluster 2	55	$0.69^a \pm 0.117$	$0.68^a \pm 0.103$	-0.00 ± 0.084	−0.04–0.04
Genetic cluster 3	105	$0.68^a \pm 0.132$	$0.74^b \pm 0.099$	0.08 ± 0.121	−0.02–0.06
Genetic cluster 4	72	$0.64^a \pm 0.122$	$0.66^a \pm 0.120$	0.02 ± 0.080	−0.00–0.10

genetic differentiation between genetic cluster 3 (zebuine cows in commercial herds in Burkina Faso) and the other three clusters (taurine European cattle breeds). The lowest F_{ST} values were observed between genetic cluster 1 and 4 for both approaches (Table 5).

Table 5: *Pairwise F_{ST} values according to Weir & Cockerham (1984) (above diagonal) and according to Nei (1987) (below diagonal).*

Inferred genetic cl.	*Inferred genetic cluster*			
	1	*2*	*3*	*4*
1	–	0.09	0.15	0.05
2	0.22	–	0.15	0.08
3	0.53	0.59	–	0.15
4	0.11	0.22	0.52	–

4 Discussion

4.1 Genetic diversity of microsatellite markers

The studied microsatellite markers showed a high degree of polymorphism, indicating that they were suitable for genetic diversity studies of cows in peri-urban cattle herds in Burkina Faso. Although microsatellite markers have been gradually replaced by single-nucleotide-polymorphism (SNP) marker genotyping in the last decade (Olschewsky & Hinrichs, 2021), they can still be useful, particularly if financial or technical capacity to analyse SNP data are limited (Álvarez *et al*., 2021), as often is the case in developing countries (Yaro *et al*., 2017).

In the present study, all microsatellite markers exceeded the recommended threshold value for N_A, which equals 5 (FAO, 2011). The most informative markers were *TGLA53* (NA = 16) and *CSSM66* (N_A = 14), while *ETH3* (N_A = 7) and *ILSTS005* (N_A = 5) were the least informative in our study. Besides a large N_A (Naveen Kumar *et al*., 2006), a large average H_{OA} determines the strength of microsatellites markers to genetically differentiate livestock breeds (Blott *et al*., 1999). Based on H_O, the two loci *ILSTS005* and *ETH3* were again two of the least informative markers. Surprisingly, the microsatellite marker with the greatest N_A (*TGLA53*) in our study had one of the smallest H_O.

F-statistics were all positive which indicates a deficiency in heterozygosity at the level of the population structure (Ngono Ema *et al*., 2014). The global deficiency of heterozygotes (F_{IT}) in peri-urban cattle herds in Burkina Faso was estimated at 0.10. This value is lower than the overall F_{IT} value reported for cattle populations across different regions of Burkina Faso (0.16) (Soudré *et al*., 2019) as well as for Cameroonian native cattle populations (0.13) (Ngono Ema *et al*., 2014), but still higher than the F_{IT} value reported for Zimbabwean Sanga cattle breeds (0.06) (Gororo *et al*., 2018). In our study, *TGLA53* had the largest F_{IT} value (0.35), which is comparable to 0.32 reported in (Soudré *et al*., 2019). On the contrary, the lowest value in our study was observed for locus *BM2113* (−0.197), for which Soudré *et al*. (2019) calculated a F_{IT} value of 0.227. Overall, four loci had a negative F_{IS} value, while most of the studied loci showed a positive value. In total, 12 (57 %) of the studied loci were not in HWE, of which 11 departed from HWE due to the heterozygosity deficiency. Only one locus (*BM2113*) significantly deviated from HWE due to heterozygosity excess. The deviation from HWE due to heterozygosity deficiency that we observed in the studied microsatellite loci may have several potential reasons. One possibility includes the Wahlund effect. Our sample of 112 cows in Burkina Faso comprised cows of different genetic background that have diverged sufficiently to observe an overall reduction in heterozygosity. Deficiency of heterozygotes caused by the Wahlund effect has been also proposed in other indigenous cattle breeds, e.g. in Ethiopia (Bora *et al*., 2023) and Senegal (Sambe *et al*., 2022). Inbreeding, or the mating of closely related individuals, can also be a contributing factor to this deviation. In our sample of 112 cows in Burkina Faso, the observed overall reduction of heterozygosity was strongly due to within-population inbreeding (F_{IS} = 0.077), while the genetic drift among the populations only explained a minor proportion of the reduction in heterozygosity (F_{ST} = 0.026). Especially cows with pure zebuine origin had a comparatively high (yet insignificant) within-group inbreeding coefficient (F_{IS}) as compared to the other genetic groups derived through cluster analyses. Based on the F_{ST} value, the most powerful microsatellite markers were *ETH152* (9.0 %) and *ETH225* (7.7 %). Finally, it has been proven that numerous microsatellite markers in cattle are shaped by selective breeding because they are associated with genes influencing traits of economic interest. For instance, the selection for intramuscular fat resulted in significant differences in allele frequencies for *ETH10, INRA23*, and *TGLA53* between different lines of Japanese Black cattle (Smith *et al*., 2001). Chu *et al*. (2005) have demonstrated a connection between *BM1818* and the somatic cell score (SCS). Accordingly, certain alleles of this microsatellite are shown to either support or hinder resistance to mastitis in Beijing Holstein cows. In another study, directional changes in allele frequencies of *ETH3, ETH225, TGLA122, TGLA126* and *TGLA227*, that align with the history of artificial selection in the German Holstein population, have been described by Brenig & Schütz (2016).

4.2 Genetic differentiation and diversity of genetic clusters

Both, unsupervised (discriminant analysis of principal components) and model-based (STRUCUTRE) clustering, confirmed the poor population structure of dairy cows from commercial herds in Burkina Faso, but clearly differentiated the cows in Burkina Faso from pure European taurine cattle breeds in the reference dataset. Almost all purebred zebu cows (P, A, G) had the same ancestry and were assigned together in one genetic cluster. The genetic relatedness of zebu cattle breeds probably results from historic genetic gene flow in the sub-region as previously reported for zebuine cattle in Niger (Grema *et al*., 2017) and in Senegal (Ndiaye *et al*., 2015). More recent isolated and unstructured breeding and selection decisions of livestock breeders (Roessler, 2019; Scheper *et al*., 2020) as well as transhumance practices (Scheper *et al*., 2020) further explain the close genetic distance between West African cattle breeds. The membership proportions obtained through the model-based clustering and the large genetic differences between the genetic clusters obtained through model-free clustering are an indication for a relatively low genetic contribution of European taurine cattle breeds to crossbred cows in commercial herds in Burkina Faso. Accordingly, these European crossbred cows were classified together with cows of pure zebuine origin into the same genetic cluster. The low genetic contribution of high-yielding dairy cattle breeds to local zebu cows in Burkina Faso, together with unfavourable environmental conditions, especially inappropriate feeding management (Schlecht *et al*., 2019), might explain the low production performances of European taurine crossbred dairy cows in commercial cattle herds in Burkina Faso, as previously reported by Roessler *et al*. (2019). Another explanation for the low production performances of European crossbred dairy cows in Burkina Faso could be the loss of unique alleles that are related to adaptation to the harsh local production conditions. Our genetic analysis showed that allele *ETH225-158* bp was unique to cows managed in dairy cattle herds in Burkina Faso. This group-specific allele may form the basis for important functions and adaptation to prevailing production conditions. Hence, it should be considered in population specific breeding programs to prevent its loss in these highly adapted indigenous African cattle breeds due to the introgression of other alleles through crossbreeding with European taurine cattle breeds.

At the same time, structured breeding programs focussing on conservation could also improve the reproduction management and reduce current practices of uncontrolled mating and random selection decisions of dairy cattle breeders in Burkina Faso (Roessler, 2019), which most likely explain the comparatively higher inbreeding coefficient of the group of dairy cows in Burkina Faso as compared to the groups of European taurine cattle breeds in the reference database. The results of the present study showed that the mean observed heterozygosity ($H_O = 0.68$) of dairy cows in Burkina Faso was significantly lower than the expected heterozygosity ($H_E = 0.74$). Still, the observed heterozygosity was clearly larger than that of four Nigerian indigenous cattle populations (mean $H_O = 0.36$) (Nwachukwu *et al*., 2022). Similar values to our study were reported for a cattle dataset containing seven indigenous African taurine, West and East African zebu, South African and European cattle breeds (mean $H_O = 0.65$) (Álvarez *et al*., 2014), for zebu Bororo ($H_O = 0.67$), Kuri ($H_O = 0.67$) and zebu Arabe ($H_O = 0.71$) cattle in Niger (Grema *et al*., 2017), and for South Meat cattle in Ukraine (mean $H_O = 0.65$ and $H_O = 0.70$) (Kramarenko *et al*., 2019). In contrast, H_O was comparatively higher for Hallikar cattle in India ($H_O = 0.75$) (Naveen Kumar *et al*., 2006). H_E is another measure of genetic diversity in livestock populations (Mahrous *et al*., 2013). The mean H_E value obtained in our study indicates that the cows in commercial dairy cattle herds in Burkina Faso maintained a substantial amount of genetic diversity. It was comparable to values reported for four Nigerian indigenous cattle populations (mean $H_E = 0.77$) (Nwachukwu *et al*., 2022), seven indigenous African taurine, West and East African zebu, South African, and European cattle breeds (mean $H_E = 0.74$) (Álvarez *et al*., 2014), zebu Arabe ($H_E = 0.73$) and Kuri cattle in Niger ($H_E = 0.72$) (Grema *et al*., 2017) but slightly lower than in Hallikar cattle in India ($H_E = 0.79$) (Naveen Kumar *et al*., 2019).

Finally, the original breed classification of the respective cattle breeder was largely confirmed by the microsatellite genotypes of our study. This confirms dairy cattle breeders' preferences for the local cattle breeds and the importance of adaptive traits under the prevailing production conditions of dairy production in Burkina Faso (Roessler, 2019).

Conclusion

This study was the first attempt to assess the genetic diversity and population structure of cows from commercial dairy cattle herds in Burkina Faso, using microsatellite markers. Microsatellite analysis reveals pronounced genetic diversity but limited genetic structuring of cattle populations in peri-urban production systems in Burkina Faso. Estimates of pairwise genetic distance and clustering results revealed that the local zebu Peul were closely related to the Azawak and Gudali breed. On the other hand, the genetic contribution of European *Bos taurus* breeds to crossbred dairy cows in the herds remains low. Effective strategies for structured cross-/breeding programs are needed to maintain high

genetic diversity and adaptability in local cattle breeds and for better exploitation of breed and heterosis effects in commercial dairy cattle herds in Burkina Faso to make most efficient use of productive and adaptive traits embedded in different cattle breeds.

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Declaration of interest statement

The authors report that there are no competing interests to declare. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Data availability

The data that support the findings of this study are available from the corresponding author, RR, upon reasonable request.

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