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Genetic Diversity and Population Structure of Taurine Cattle Using STR Markers in Burkina Faso, West Africa

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ABSTRACT

Burkina Faso relies on its substantial bovine population for meat and milk production, ensuring food security. The country hosts three primary taurine cattle populations: Lobi, Gourounsi Nahouri, and Gourounsi Ténado. These cattle are adapted to local conditions and exhibit valuable trypan tolerant traits, playing a crucial role in sustaining local communities and holding cultural and socio-economic significance. This study aimed to assess the genetic diversity and structure of Burkina's primary taurine cattle populations using 27 microsatellite markers. Blood samples from 143 cattle representing these populations were genotyped. The analysis included assessing genetic diversity, deviations from Hardy-Weinberg equilibrium, calculating genetic distances, and population structure. The results revealed that all loci were polymorphic, indicating high allelic diversity. The overall mean F_{IS} was moderate (0.028), ranging from -0.36 (CSRM60) to 0.73 (INRA035). Genetic differentiation between populations was moderate, accounting for 4% of the total differences. The highest pairwise F_{ST} was observed between Lobi and Gourounsi Ténado. The neighbor-joining tree displayed high admixture levels between Gourounsi populations, while Lobi cattle clustered as a distinct population. The population structure analysis indicated significant zebu gene introgression in Burkina taurine populations with relatively higher levels of admixtures in Gourounsi cattle compared to Lobi. The study provided a thorough genetic analysis of Burkina Faso's taurine cattle populations, uncovering the diversity and population structure. The study also revealed the differences in the prevalence of tsetse flies and associated trypanosomosis across the native tracts of Burkinabe taurine cattle populations had shaped the level of zebu introgression in them.

Keywords: diversity; introgression; structure; taurine cattle

INTRODUCTION

In Burkina Faso, livestock farming plays a vital role in enhancing household food security and nutrition by supplying nutrient-rich products like meat, milk, and eggs. In 2019, the bovine population stood at approximately 9.8 million (MRAH, 2019). These bovines hold great importance, as they play a substantial role in meat production (45%), milk production (90%), and serve as a vital source of labor.

Despite the substantial size of the livestock population, animal production falls short in meeting the increasing demands of the growing population. The prevalence of extensive production systems, coupled with the limited genetic potential of local breeds, constrains their production efficiency (Rouamba, 2016). To address this issue and enhance overall performance, suggestions have emerged over the past decades for intensifying livestock management systems and genetically improving the local livestock. Subsequently, campaigns for bovine artificial insemination have been garnering increasing attention within development programs (PNPDL, PDRDP/BK, PAPSA, PDES, MCA-BF, PDRI, and PDEL/ZPO) (Blagna *et al.*, 2017). As part of these crossbreeding initiatives, specialized breeds in the form of semen or live animals are regularly introduced through imports. However, the lack of a coordinating institutional framework allowed the

uncontrolled introduction of exotic genetic material into livestock breeding, leading to unregulated crossbreeding without proper guidance or regulations (Blagna *et al.*, 2018). While local cattle breeds can contribute to the resilience of livestock-oriented livelihoods through their suitability to the specific environment, robustness, and tolerance to diseases, livestock keepers have reduced their number in favor of "exotic" or crossbreed animals, which tend to have higher productivity and market value (Leroy *et al.*, 2015). Furthermore, in West Africa as a whole, and specifically in Burkina Faso, among the local cattle, zebus are favored over taurine cattle due to their larger size and comparatively higher productivity (Traoré *et al.*, 2015; Ouédraogo *et al.*, 2020).

Burkina Faso hosts three taurine cattle populations: Lobi/Baoulé in the southwest and Gourounsi in the central-western and central-southern regions. These cattle are adapted to local conditions and display trypanotolerant characteristics, crucial in tsetse fly-infested areas where African animal trypanosomiasis is prevalent. They are vital in supporting local communities with meat, milk, and labor and hold cultural and socio-economic significance. However, these taurine cattle populations are generally smaller than zebu cattle and may offer lower milk yields, making them less economically attractive. Crossbreeding with zebu cattle is also risky, potentially diluting the genetic purity of these trypanotolerant breeds. Moreover, a lack of research on indigenous taurine cattle breeds in Burkina Faso, particularly Gourounsi taurines, hinders their development and preservation. While taurine cattle are known for their trypanotolerance (Flori *et al.*, 2014; Yougbaré *et al.*, 2021), protecting them from genetic introgression by zebu cattle is essential. Human activities, such as deforestation and urban expansion, combined with tsetse fly control efforts, have encroached on taurine habitats, increasing the infiltration of zebu cattle into humid forested areas. Regular genetic assessments of Burkina Faso's primary taurine cattle populations are necessary to maintain their integrities and prevent excessive gene flow from zebu cattle. This study's primary goal is to scrutinize the genetic diversity and structure of Burkina Faso's three main taurine cattle populations, focusing on indicine ancestry levels. Short Tandem Repeats (STRs) serve as invaluable tools for understanding genetic diversity and gene flow in populations. To accomplish this, Short Tandem Repeats (STRs) are utilized as invaluable tools to understand genetic diversity and gene flow in populations, given their high variability and utility in genetic profiling, individual identification, and population genetic studies (Lokugalappatti *et al.*, 2023; Bora *et al.*, 2023; Gargani *et al.*, 2015; Solodneva *et al.*, 2023; Chang *et al.*, 2023). In the context of Burkina Faso's taurine cattle populations, this study leverages STR markers to explore the extent of indicine ancestry, offering insights into genetic integrity and potential challenges associated with crossbreeding with zebu cattle.

MATERIALS AND METHODS

Ethical Approval

The study protocol was approved by the Institutional Animal Care and Use Committee (IACUC) (agreement code: CE-UJKZ/2023-09).

Sample Collection

A total of 143 blood samples were collected, with 38 adult individuals from the Gourounsi Nahouri population, 43 from the Lobi population, and 62 from the Gourounsi Ténado population. The Gourounsi cattle were sampled in the Sanguié and Nahouri Provinces, while the Lobi cattle were sampled in the Poni Province (Figure 1). The farmers were interviewed in detail to ensure the unrelatedness of sampled cattle. These interviews gathered information about the cattle's lineage and familial relationships, confirming that the selected cattle were genetically

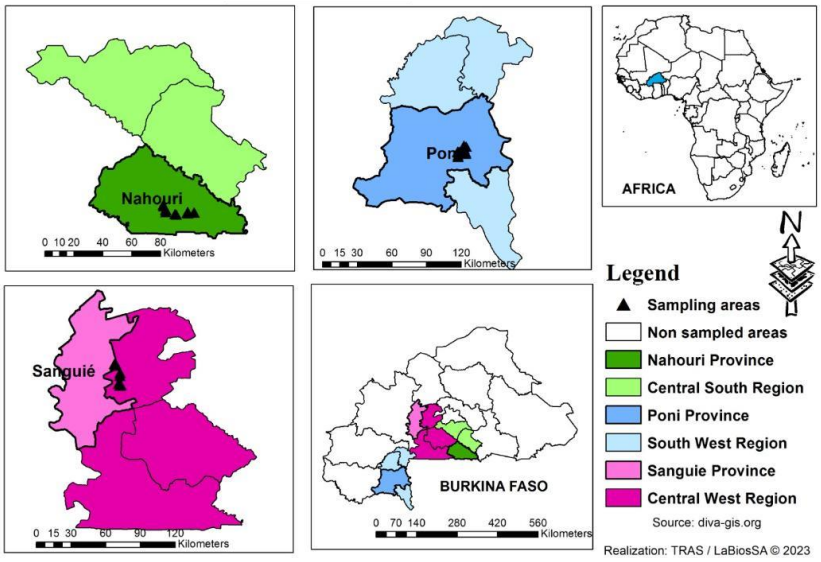


Figure 1. Sampling areas in Burkina Faso, West Africa

diverse and unrelated. This process aimed to prevent bias in the genetic analysis by excluding closely related animals. Blood samples were collected after jugular venipuncture in EDTA coated Vacutainer tubes. In Burkina Faso, the territory can be classified into three distinct agroecological zones based on their patterns of rainfall and vegetation: Sahelian, Sudano-Sahelian, and Sudanian. The Sudano-Sahelian zone, covering nearly one-third of Burkina Faso's total area, is characterized by a diverse landscape of plains and low mountains that can reach altitudes of up to 500 meters. The soil in this region is predominantly poor and composed of laterite, while the vegetation consists of a mixture of thorny scrubland and savanna grassland. The average annual rainfall in the Sudano-Sahelian zone ranges between 500 mm and 900 mm. This particular zone is the natural habitat of Gourounsi cattle from Tenado (TEO). On the other hand, Lobi cattle (BB) and Gourounsi cattle from Nahouri (NAO) are predominantly found in the Sudanian agroecological zone, which is the wettest area in Burkina Faso. This zone receives more than 1,000 mm of annual rainfall, resulting in fertile soil and a varied landscape, including bushy savannas and forests along watercourses. Notably, these riverside areas are the preferred habitats for tsetse flies. The Sudanian zone is characterized by rugged terrain with numerous hills. In all these agroecological zones, Burkina Faso experiences a single rainy season, typically stretching from May to June through September to October. This rainy season is marked by significant temporal and spatial variability in rainfall patterns. Subsequently, Burkina Faso enters a prolonged dry season, commencing at the end of October and lasting until May. Livestock farming in Burkina Faso predominantly relies on free grazing and the utilization of naturally occurring herbaceous and ligneous plant species during the wet season. However, during the dry season, when both the quality and quantity of forage diminish, farmers resort to exploiting crop residues like rice straw, millet, sorghum, and corn stalks, as well as utilizing fodder from trees and shrubs to meet the nutritional needs of their animals.

DNA Extraction

DNA was extracted from whole blood using MasterPure DNA Purification Kit (Biozym, Illumina Inc, USA). DNA samples were then stored at 4 °C until PCR amplification and genotyping.

Genetic Markers and Genotyping

Twenty-seven FAO-recommended short tandem repeat (STR) markers (FAO, 2011) with forward primers conjugated to one of the three fluorescent dyes (FAM, HEX, and ATTO550) were used for diversity analysis. Polymerase chain reaction was performed under the following conditions: initial denaturation for 5 min at 95 °C, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at the respective temperature of each marker locus for 1 min, elongation at 72 °C for 1 min with a final extension at 72 °C for 10 min. The PCR products were then electrophoresed after multiplexing in an automated DNA analyzer ABI3100 (Applied Biosystems, USA) with ROX500 (Applied Biosystems, USA) as an internal lane control. All 27 STR loci were multiplexed in six sets for genotyping, as shown in Table 1. The allele size data for each sample were then extracted using GeneMapper v.4.1 software (Applied Biosystems, USA).

Data Analysis

Basic diversity indices like the observed number of alleles, observed and expected heterozygosity, pairwise and global F statistics were calculated using Microsatellite Analyzer (MSA) version 3.15 (Dieringer & Schlötterer, 2003). Deviations of heterozygosity from Hardy–Weinberg equilibrium (HWE) were estimated with exact tests of heterozygote excess for each marker and in each breed, as implemented in Genepop (Raymond & Rousset, 1995). Polymorphism information content was calculated using the Cervus program (Kalinowski *et al.*, 2007). Pairwise allele sharing distance between populations and inter-individual allele sharing distances were calculated using MSA. The Neighbor-joining circular tree was constructed in PHYLIP version 3.5 (Felsenstein, 1993) using Pairwise interindividual allele sharing distance. The Neighbor-joining tree was visualized using MEGA version X (Kumar *et al.*, 2018). Burkina taurine populations were tested for mutation drift equilibrium following three statistical approaches (sign test, standardized differences test, and Wilcoxon sign rank test) under different models of microsatellite evolution as implemented in BOTTLENECK (Piry *et al.*, 1999). Genotype assignment based on likelihood (Paetkau *et al.*, 1995) and Bayesian (Rannala & Mountain, 1997) methods were performed as implemented in GeneClass 2 software (Piry *et al.*, 2004). The underlying genetic structure in the studied populations was further investigated using the Bayesian clustering approach as implemented in the STRUCTURE program (Pritchard *et al.*, 2000). To identify the optimal 'K', the second order rate of change in LnP (D) concerning different 'K' was calculated by following the procedure of Evanno *et al*. (2005).

RESULTS

Biodiversity and Inbreeding Estimates

A total of 3861 genotypes were generated across the 27 STR loci used in this study. The mean polymorphic information content (PIC) was calculated to gauge biodiversity across populations. The computed PIC values were 0.54, 0.62, and 0.66 for the Lobi, Gourounsi Nahouri, and Gourounsi Ténado breeds, respectively (Table 1). Most of the loci exhibited PIC values above 0.5. The overall mean PIC for the total population was 0.61, with the lowest value observed at locus SPS115 (PIC= 0.18).

A total of 219 alleles were observed across the loci, ranging from 3 alleles (INRA035) to 14 alleles (TGLA53). The mean observed number of alleles (n_a) varied between breeds, ranging from 6.04 (Lobi) to 7.41 (Gourounsi Ténado).

Table 1. Microsatellite loci, Multiplex PCR parameters, allele sizes, and genetic diversity measures for taurine cattle populations in Burkina Faso

Locus panel	Multiplex	Anneal (Temp.)	Dye	Allele size (Range)	Primers F/R	All locus (PIC)	Gourounsi Nahouri			Gourounsi Ténado			Lobi		
							n_a	PIC	R_s	n_a	PIC	R_s	n_a	PIC	R_s
CSRM60	1	60 °C	FAM	89-107	AAGATGTGATCCAAGAGAGAGGCA AGGACCAGATCGTGAAAGGCATAG	0.67	8	0.70	7.81	9	0.71	9.00	7	0.61	6.94
CSSM66	1	60 °C	FAM	177-197	ACACAAATCCTTTCTGCCAGCTGA AATTTAATGCACTGAGGAGCTTGG	0.64	8	0.75	7.74	10	0.62	9.87	6	0.55	5.97
HEL1	1	56 °C	HEX	98-114	CAACAGCTATTTAACAAGGA AGGCTACAGTCCATGGGATT	0.63	6	0.64	5.95	7	0.71	6.93	7	0.54	6.56
INRA063	1	56 °C	HEX	173-183	ATTTGCACAAGCTAAATCTAACC AAACCACAGAAATGCTTGGAAG	0.53	5	0.56	4.97	5	0.52	4.93	4	0.50	3.99
BM1824	2	61 °C	ATTO550	183-197	GAGCAAGGTGTTTTTCCAATC CATTCTCCAACTGCTTCCTTG	0.55	4	0.57	4.00	4	0.51	4.00	4	0.58	3.83
ETH152	2	60 °C	FAM	185-199	TACTCGTAGGGCAGGCTGCCTG GAGACCTCAGGGTTGGTGATCAG	0.60	6	0.69	5.85	6	0.67	5.99	4	0.45	3.85
HAUT27	2	54 °C	HEX	140-150	TTTTATGTTCATTTTTTGACTGG AACTGCTGAAATCTCCATCTTA	0.61	6	0.64	5.66	6	0.60	5.93	5	0.58	4.97
INRA05	2	54 °C	FAM	134-140	CAATCTGCATGAAGTATAAATAT CTTCAGGCATACCCTACACC	0.54	4	0.59	4.00	4	0.52	4.00	4	0.51	3.81
BM1818	3	60 °C	HEX	256-272	AGCTGGGAATATAACCAAAGG AGTGCTTTCAAGGTCCATGC	0.80	7	0.78	7.00	9	0.83	8.93	7	0.78	7.00
ETH3	3	63 °C	FAM	99-125	GAACCTGCCTCTCCTGCATTGG ACTCTGCCTGTGGCCAAGTAGG	0.60	5	0.57	4.83	8	0.70	7.99	8	0.52	7.67
HEL9	3	56 °C	ATTO550	155-175	CCCATTCAGTCTTCAGAGGT CACATCCATGTTCTCACCAC	0.75	9	0.77	8.62	9	0.82	8.93	8	0.65	7.67
ILSTS006	3	54 °C	FAM	284-300	TGTCTGTATTTCTGCTGTGG ACACGGAAGCGATCTAAACG	0.54	5	0.61	4.99	6	0.59	6.00	4	0.41	3.90
TGLA53	3	55 °C	HEX	151-183	GCTTTCAGAAATAGTTTGCATTCA ATCTTCACATGATATTACAGCAGA	0.80	13	0.87	12.15	14	0.79	13.69	9	0.75	8.98
HAUT24	4	53 °C	HEX	103-125	CTCTCTGCCTTTGTCCCTGT AATACACTTTAGGAGAAAAATA	0.70	7	0.69	6.59	8	0.77	7.76	8	0.64	7.50
HEL5	4	54 °C	FAM	148-164	GCAGGATCACTTGTTAGGGA AGACGTTAGTGTACATTAAC	0.70	8	0.74	7.61	7	0.67	6.97	7	0.70	6.96
INRA032	4	56 °C	ATTO550	164-208	AAACTGTATTCTCTAATAGCTAC GCAAGACATATCTCCATTCCTTT	0.68	7	0.68	6.68	9	0.75	8.76	8	0.62	7.61
SPS115	4	61 °C	FAM	243-255	AAAGTGACACAACAGCTTCTCCAG AACGAGTGTCCTAGTTTGGCTGTG	0.23	4	0.18	3.59	5	0.31	4.87	4	0.20	3.67
ETH185	5	65 °C	ATTO550	224-242	TGCATGGACAGAGCAGCCTGGC GCACCCCAACGAAAGCTCCCAG	0.52	6	0.44	5.48	8	0.56	7.79	6	0.57	5.88
HEL13	5	54 °C	HEX	182-194	TAAGGACTTGAGATAAGGAG CCATCTACCTCCATCTTAAC	0.53	5	0.58	4.81	5	0.59	5.00	4	0.43	4.00
ILSTS05	5	56 °C	FAM	178-190	GGAAGCAATGAAATCTATAGCC TGTTCTGTGAGTTTGTAAGC	0.46	3	0.42	3.00	6	0.56	5.89	4	0.40	3.85
INRA035	5	60 °C	FAM	99-117	ATCCTTTGCAGCCTCCACATTG TTGTGCTTTATGACACTATCCG	0.27	4	0.19	3.62	5	0.44	4.90	3	0.18	2.88
TGLA126	5	54 °C	HEX	114-128	CTAATTTAGAATGAGAGAGGCTTCT TTGGTCTCTATTCTCTGAATATTCC	0.71	7	0.64	6.67	7	0.76	6.89	7	0.72	6.89
BM2113	6	63 °C	FAM	118-142	GCTGCCTTCTACCAAATACCC CTTCCTGAGAGAAGCAACACC	0.72	7	0.75	6.98	9	0.77	9.00	7	0.64	6.97
ETH10	6	61 °C	FAM	207-223	GTTCAGGACTGGCCCTGCTAACA CCTCCAGCCCACTTTCTCTTCTC	0.62	6	0.66	5.97	7	0.73	6.97	7	0.47	6.74
ETH225	6	63 °C	ATTO550	140-160	GATCACCTTGCCACTATTTCCT ACATGACAGCCAGCTGCTACT	0.71	8	0.72	7.02	8	0.76	7.97	9	0.65	8.65
INRA023	6	58 °C	ATTO550	199-219	GAGTAGAGCTACAAGATAAACTTC TAACTACAGGGTGTTAGATGAACTC	0.61	6	0.63	6.00	8	0.73	7.97	7	0.46	6.56
TGLA122	6	58 °C	HEX	134-174	CCCTCCTCCAGGTAAATCAGC AATCACATGGCAAATAAGTACATAC	0.60	9	0.65	8.08	11	0.74	10.92	5	0.40	5.00
Mean	-	-	-	-		0.61	6.41	0.62	6.14	7.41	0.66	7.33	6.04	0.54	5.86

Note: : n_a = Observed no. alleles; PIC= Polymorphism Information Content; R_s = Allelic richness; F/R= Forward primer sequence on top and Reverse primer sequence on the bottom.

The allelic richness values were 7.33, 6.14, and 5.86 for Gourounsi Ténado, Gourounsi Nahouri, and the Lobi breed, respectively.

The range of observed heterozygosity per locus spanned from 0.05 (INRA035) to 0.92 (CSRM60). Expected heterozygosity varied from 0.2 (SPS115) to 0.9 (TGLA53).

In Gourounsi Nahouri, the observed heterozygosity averaged 0.64, and the expected heterozygosity was 0.67. Gourounsi Ténado exhibited similar values, with both observed and expected heterozygosity around 0.70 and 0.71, respectively. Meanwhile, Lobi cattle displayed a mean observed heterozygosity of 0.58, with expected heterozygosity at 0.6. The overall F_{IS} value of 0.045 in the population indicates a moderate level of inbreeding at the examined genetic loci. Among breeds, the F_{IS} values ranged from -0.36 (CSRM60) to 0.73 (INRA035) at the locus level. The Gourounsi Nahouri cattle showed the highest mean estimated inbreeding of 0.06, while the Gourounsi Ténado population had the lowest mean of 0.00. The test for Hardy-Weinberg equilibrium (HWE) revealed 11 locus x breed combinations (13.58%) with significant departures ($p<0.05$) from panmictic equilibrium (Table 2). Among populations, the highest number of loci deviating from HWE equilibrium ($p>0.05$) for heterozygosity deficiency was noticed in Gourounsi Nahouri cattle with 4 loci (ETH152, TGLA53, HEL13, and INRA035) followed by Gourounsi Ténado and Lobi cattle with 2 loci each (INRA032, ILSTS05, TGLA53, and CSRM60). Moreover, the HWE test for heterozygosity excess revealed significant deviations in 2 (ETH225 and ILSTS006), 0 and 2 (HEL9 and ETH152) loci in Gourounsi Nahouri, Gourounsi Tenado, and Lobi cattle, respectively.

Genetic Relationships and Population Structure

The genetic differentiation values (F_{ST}) per locus varied from -0.006 (TGLA122) to 0.09 (ILSTS05) with an average of 0.034 across all the loci (Table 2). At the locus level, the F_{IT} values ranged from -0.09 (CSRM60) to 0.41 (ILSTS05) and the overall F_{IT} value was 0.077 (Table 2).

Across different breed pairs, maximum differentiation was observed in the Lobi-Gourounsi Tenado (0.05) pair, whereas the Gourounsi Tenado - Gourounsi Nahouri was the least differentiated couple (0.02) (Table 3). Further, pairwise gene flow (Nm) based on F_{ST} values was calculated for all possible pairs of populations. Similarly to F_{ST}, gene flow was high within Gourounsi populations (Gourounsi Ténado and

Table 2. Summary of diversity statistics and global F statistics of Burkina Faso taurine cattle populations

Locus	F_{ST}	F_{IT}	F_{IS}	Gourounsi nahouri			Gourounsi ténado			Lobi		
				H_o	H_e	F_{IS}	H_o	H_e	F_{IS}	H_o	H_e	F_{IS}
CSRM60	0.04	-0.09	-0.13	0.84	0.75	-0.12	0.71	0.74	**0.04**	0.92	0.68	-0.36
CSSM66	0.04	0.08	0.04	0.71	0.79	0.09	0.63	0.67	0.05	0.67	0.63	-0.06
HEL1	0.03	0.01	-0.02	0.76	0.69	-0.10	0.83	0.76	-0.09	0.51	0.59	0.13
INRA63	0.03	0.04	0.02	0.61	0.64	0.04	0.68	0.61	-0.11	0.50	0.58	0.13
BM1824	0.08	0.22	0.15	0.44	0.63	0.29	0.68	0.57	-0.2	0.69	0.67	-0.04
ETH152	0.01	-0.06	-0.08	0.61	0.75	**0.18**	0.55	0.73	0.25	0.56	0.55	**-0.03**
HAUT27	0.00	0.01	0.01	0.82	0.70	-0.18	0.70	0.66	-0.07	0.64	0.64	-0.01
INRA05	0.02	0.03	0.01	0.59	0.66	0.09	0.64	0.58	-0.12	0.56	0.58	0.03
BM1818	0.02	0.02	-0.01	0.78	0.82	0.04	0.90	0.87	-0.05	0.78	0.82	0.04
ETH3	0.05	0.09	0.05	0.62	0.65	0.03	0.75	0.75	0.00	0.64	0.60	-0.08
HEL9	0.03	0.00	-0.03	0.70	0.81	0.13	0.80	0.86	0.06	0.74	0.69	**-0.08**
ILSTS006	0.04	0.20	0.16	0.83	0.68	**-0.23**	0.68	0.65	-0.04	0.38	0.50	0.22
TGLA53	0.06	0.04	-0.03	0.76	0.90	**0.15**	0.74	0.83	**0.10**	0.62	0.79	0.22
HAUT24	0.04	0.05	0.01	0.82	0.74	-0.11	0.74	0.81	0.08	0.76	0.70	-0.10
HEL5	0.01	0.03	0.02	0.73	0.79	0.07	0.74	0.72	-0.03	0.76	0.75	-0.01
INRA032	0.00	-0.07	-0.08	0.68	0.73	0.07	0.86	0.79	-0.09	0.62	0.68	**0.09**
SPS115	0.01	0.04	0.03	0.21	0.20	-0.08	0.38	0.33	-0.15	0.21	0.22	0.01
ETH185	0.01	0.13	0.13	0.51	0.49	-0.07	0.59	0.60	0.02	0.55	0.62	0.10
HEL13	0.05	0.07	0.02	0.53	0.65	**0.19**	0.59	0.65	0.09	0.49	0.53	0.07
ILSTS05	0.09	0.41	0.36	0.54	0.54	0.00	0.71	0.64	-0.11	0.39	0.49	**0.19**
INRA035	0.02	0.04	0.02	0.05	0.20	**0.73**	0.36	0.51	0.29	0.18	0.20	0.14
TGLA126	0.02	0.11	0.10	0.69	0.70	0.01	0.76	0.80	0.05	0.79	0.77	-0.04
BM2113	0.05	0.10	0.05	0.65	0.79	0.18	0.78	0.81	0.02	0.64	0.70	0.08
ETH10	0.04	0.08	0.04	0.57	0.71	0.19	0.79	0.78	-0.02	0.53	0.51	-0.04
ETH225	0.06	0.08	0.02	0.89	0.78	-0.16	0.74	0.80	0.08	0.59	0.71	0.17
INRA023	0.08	0.08	0.00	0.61	0.68	0.09	0.76	0.77	0.00	0.54	0.52	-0.04
TGLA122	-0.006	0.047	0.053	0.64	0.71	0.10	0.84	0.77	-0.10	0.44	0.43	-0.02
Mean	0.034	0.077	0.045	0.64	0.67	0.06	0.70	0.71	0.00	0.58	0.60	0.02

Note: H_o= Observed heterozygosity; H_e= Expected heterozygosity; F_{IS}= Estimated Heterozygosity deficit; F_{IT}= Overall genetic variation; F_{ST}= Fixation Index among Subpopulations; The bold values refer to the deviation of Hardy-Weinberg Equilibrium.

Gourounsi Nahouri: 12.25) and was lower for the Lobi-Gourounsi Tenado pair (4.75).

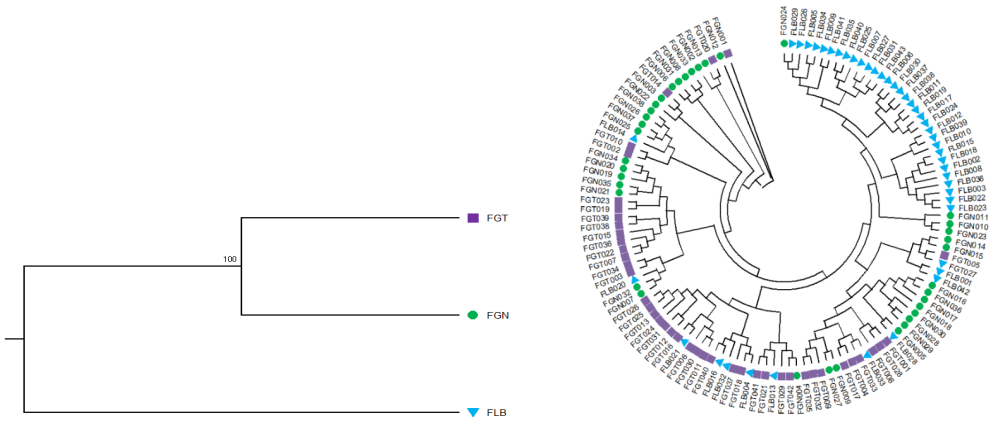
The dendogram obtained exhibited a clustering pattern where Gourounsi Ténado and Gourounsi Nahouri populations appeared to be closely related, while the Lobi population appeared relatively distinct from them (Figure 2a). However, the phylogenetic tree revealed a more complex pattern of genetic relationships (Figure 2b). Notably, a subset of Lobi individuals formed a distinct cluster, suggesting a subgroup within the Lobi population with specific genetic characteristics. Additionally, some Gourounsi Nahouri individuals were found within clusters formed by Lobi and Gourounsi Ténado individuals, indicating potential genetic exchange or shared ancestry between these populations.

Table 3. Pairwise FST (lower triangle) and Nm (Upper triangle) among Burkina Faso taurine cattle and zebu Bororo Populations

	Gourounsi nahouri	Lobi	Gourounsi ténado
Gourounsi nahouri	-	8.08	12.25
Lobi	0.03	-	4.75
Gourounsi ténado	0.02	0.05	-

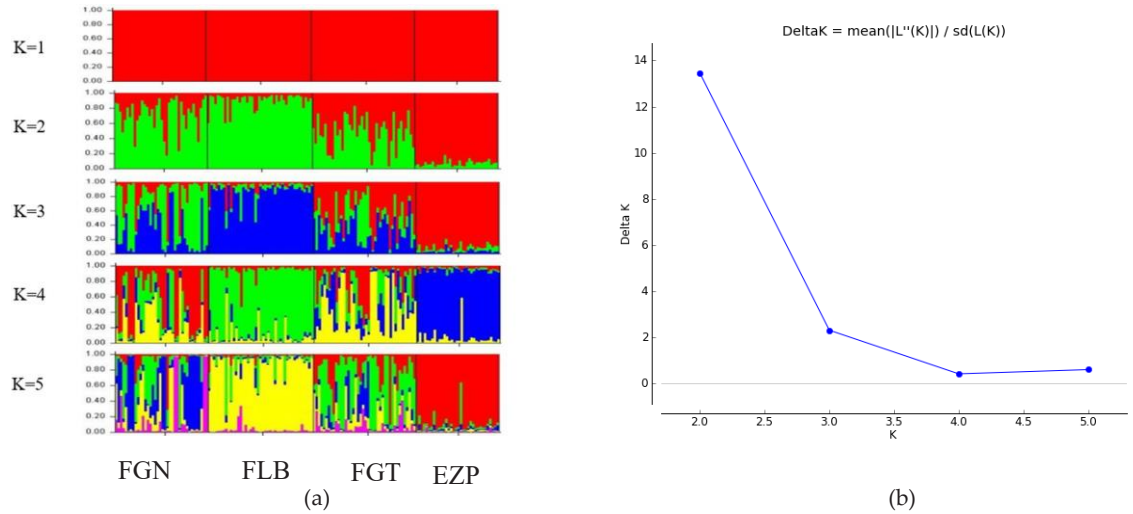
To investigate the presence of cryptic genetic structure in Burkina Faso taurine cattle populations, a Bayesian clustering analysis was conducted without any prior population information. The analysis revealed that the data best fit a model with K=2 genetic ancestors, determined by the point at which the second order rate of change in the logarithm of the probability of the data (LnP(D)) was the highest (Figure 3). Assuming that the most likely progenitor populations are two, it was observed that all Burkina taurine populations showed evidence of introgression with zebu genes. However, the extent of introgression appeared comparatively lower in the Lobi breed compared to the Gourounsi cattle populations. Within the Gourounsi taurine cattle populations, Gourounsi Ténado cattle exhibited the highest level of introgression.

Genotype assignment based on Bayesian and likelihood methods was assessed for Lobi cattle and



(a) (b)

Figure 2. Neighbor joining tree based on pairwise (a) population and (b) inter-individual allele sharing distances (FGN= Gourounsi Nahouri; FGT= Gourounsi Tenado; FLB= Lobi).



(a) (b)

Figure 3. (a) Bayesian clustering under assumption of 1 to 5 clusters without a priori population information. (b) Determination of the correct number of clusters Delta L (K) over 10 runs for each K value of 2-5 (FGN= Gourounsi Nahouri; FGT= Gourounsi Tenado; FLB= Lobi; EZP= Peuls zebu).

Gourounsi taurine cattle populations. The results revealed that Lobi cattle individuals were consistently and perfectly assigned to their source population (100%) across all classification methods. For Gourounsi taurine cattle, the assignment accuracy varied between the two subpopulations, Gourounsi Nahouri and Gourounsi Ténado. Gourounsi Nahouri exhibited higher percent correct assignment rates, ranging from 89% to 94.74%, consistently outperforming Gourounsi Ténado. The assignment accuracy of Gourounsi Ténado ranged from 47% to 97.67% across the different classification algorithms utilized (Table 4).

The sign test results of bottleneck analysis revealed that Gourounsi Nahouri, Gourounsi Tenado, and Lobi cattle populations exhibited heterozygosity excess in 23, 21, and 18 loci, respectively, under the IAM mutation model (Table 5). The expected numbers of loci with heterozygosity excess under the IAM model were 15.98 for Gourounsi Nahouri, 15.70 for Lobi, and 15.97 for Gourounsi Tenado. However, only the values for Gourounsi cattle populations were statistically significant ($p<0.01$), indicating a departure from mutation drift equilibrium. On the other hand, comparisons of observed heterozygosity excess with expected heterozygosity excess under the TPM model showed significant heterozygosity excess only in Gourounsi populations, while no deviation from drift mutation equilibrium was found under the SMM model for any of the three populations.

The standardized differences test revealed negative T2 values for all three breeds under different mutation models, except for Gourounsi Nahouri under TPM and all populations under IAM. Furthermore, the one-tail Wilcoxon sign rank test for gene diversity excess demonstrated significant deviations ($p<0.01$) in Gourounsi Nahouri and Tenado under the IAM model, while no departures from drift equilibrium were observed under the TPM and SMM models in all populations, except for Gourounsi Nahouri cattle under TPM.

Additionally, a qualitative graphical method based on mode-shift distortion displayed a normal L-shaped curve in all three Taurine cattle populations, indicating that these populations have not undergone recent size reduction events (Figure 4).

DISCUSSION

Biodiversity and Inbreeding Estimates

The average polymorphic information content (PIC > 50%) of the loci investigated demonstrates their high capacity for providing informative data. This informative nature of the markers has also been observed in the bovine characterization study conducted by Moussa *et al*. (2019) in Niger, where a PIC value of 0.650 was reported. According to previous research, only Locus SPS115 falls below the threshold of 0.25, which is necessary for reliable and usable data in characterization studies. However, the PIC value of 0.42 observed for this locus in the study of Moussa *et al*. (2019) allows us to retain and consider the data for this particular locus as reliable. In terms of the taurine cattle under investigation, the average number of alleles (n_a) and allelic richness (R_s) per locus were higher than the minimum threshold of 4 alleles per locus recommended by the Food and Agriculture Organization (FAO, 2011) to reflect average genetic variability. Hence, these loci provide dependable information on the diversity and genetic structure of the local taurine cattle population in Burkina Faso.

Table 4. Assignment of genotypes to different cattle populations with various methods

Breeds	N	Rannala & Mountain (1997)		Baudouin & Lebrun (2001)		Paetkau *et al*. (1995)	
		No. correctly assigned	% correctly assigned	No. correctly assigned	% correctly assigned	No. correctly assigned	% correctly assigned
Gourounsi nahouri	38	34	89	36	94.74	36	94.74
Gourounsi ténado	43	20	47	42	97.67	41	95.35
Lobi	42	42	100	42	100	42	100
Total	123	96	78.05	120	97.56	119	96.75

Note: N= headcount; No= Number.

Table 5. Analysis of recent population bottleneck signatures using the Wilcoxon test

Test	Parameters	Gourounsi nahouri			Lobi			Gourounsi ténado		
		IAM	TPM	SMM	IAM	TPM	SMM	IAM	TPM	SMM
Sign test	Expected number of loci with H_e excess	15.98	15.95	16.05	15.7	16.04	16.07	15.97	16.06	15.89
	Observed number of loci with H_e excess	23	20	8	18	10	2	21	17	5
	P value	0.003	0.079	0.001	0.243	0.015	0	0.035	0.436	0
Standardized differences test	T2 value	3.032	0.61	-4.145	0.864	-2.604	-9.131	2.686	-0.343	-6.392
	P value	0.001	0.27	0	0.193	0.004	0	0.003	0.365	0
Wilcoxon sign rank test	P value (one tail for H_e excess)	0.001	0.027	0.998	0.097	0.984	1	0	0.365	0.999

Note: IAM= Infinite Alleles Mode, TPM= Two-Phase Mutation Model, SMM= Stepwise Mutation Model.

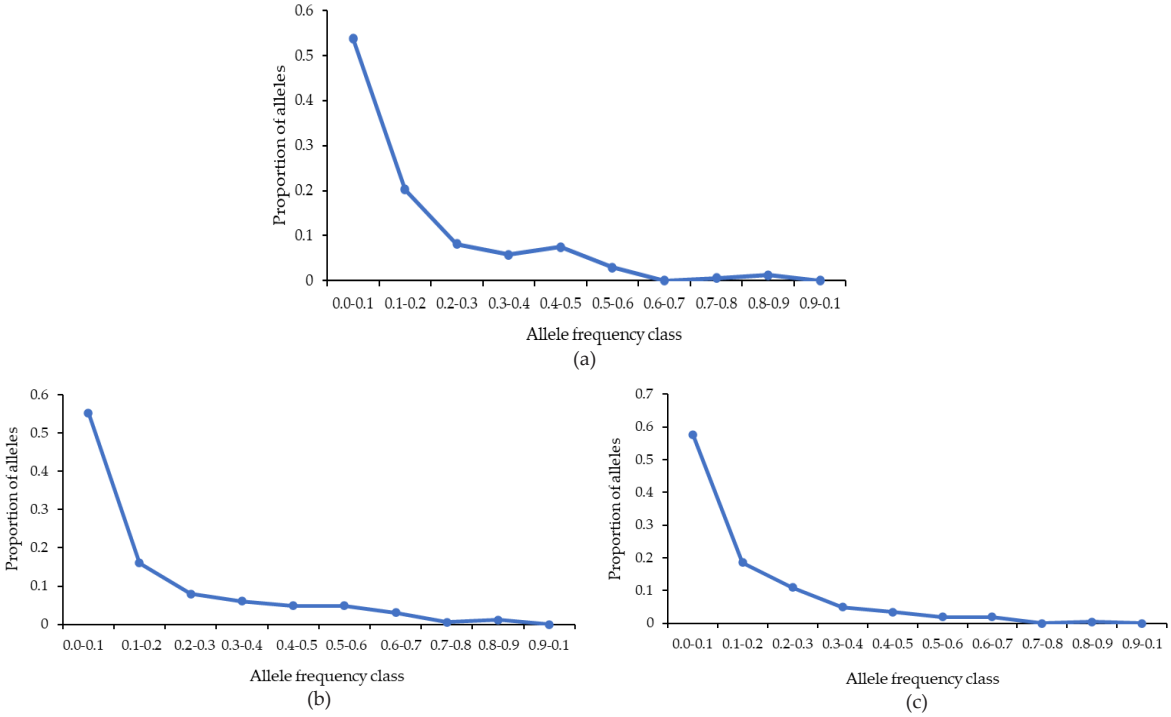


Figure 4. Mode Shift analysis showing L-shaped distribution of allele frequencies in (a) Gourounsi Nahouri, (b) Lobi, and (c) Gourounsi Ténado populations.

The variation in observed heterozygosity (H_O) ranging from 0.580 in the Lobi breed to 0.700 in the Gourounsi Tenado breed signifies significant genetic diversity among taurine cattle in Burkina Faso. This diversity could potentially be attributed to gene flow occurring between taurine and zebu cattle. Similar instances of gene flow between these two cattle types have been observed in Niger (Grema *et al.*, 2017; Moussa *et al.*, 2019) and Senegal (Ndiaye *et al.*, 2015).

The highest values of R_s in Gourounsi taurine populations (7.327 and 6.134) compared to Lobi (5.832) can be explained by the likely hybridization of Gourounsi cattle relative to Lobi cattle, as hybrid populations tend to exhibit higher values of R_s.

Among the 81 combinations of breed and locus tested in Burkina cattle, 13.58% exhibited significant departures from Hardy-Weinberg equilibrium (HWE). The majority (72.7%) of these departures were caused by heterozygosity deficit (ETH152, TGLA53, HEL13, INRA035, CSRM60, INRA032, ILSTS05). Departures from HWE equilibrium due to heterozygosity deficiency may arise from fewer heterozygotes in a population than expected due to population subdivision (Waples, 2015). Additionally, the observed heterozygosity deficit could potentially be attributed to the Wahlund effect, considering that samples were collected from different geographical locations. Similar levels of departures from panmictic equilibrium have been reported by Grema *et al.* (2017) in Niger cattle populations (14.8% of breed x locus combinations, (Grema *et al.*, 2017).

Genetic Relationships and Population Structure

The overall F_{ST} value of 0.034 in the taurine cattle of Burkina Faso indicates that 95.4% of the total genetic variation observed can be attributed to differences between individuals within the same subpopulation. This suggests that the taurine breeds in Burkina Faso are not highly differentiated. The overall F_{ST} value observed in Burkina taurine cattle is more notable than those reported for Sudanese cattle (F_{ST}= 0.084, as per Hussein *et al.*, 2015) and Cameroonian cattle (F_{ST}= 0.061, as reported by Ema *et al.*, 2014).

Regarding pairwise F_{ST} values, the highest genetic differentiation is observed between the Lobi and Gourounsi Ténado breeds (F_{ST} = 0.05). This can be attributed to the geographical isolation of these breeds, with Lobi cattle primarily found in the southwest region of the country and Gourounsi cattle inhabiting the central part of Burkina Faso. The presence of hills and spatial distance in these respective provinces, along with their distinct landscapes and topography, may explain the relatively strong differentiation observed between these populations. On the other hand, Gourounsi Tenado and Gourounsi Nahouri exhibit the lowest pairwise F_{ST} value, indicating lower genetic differentiation. These two cattle populations are found within the Gourounsi ethnic area. It has been noted by Pitt *et al.* (2019) that neighboring domestic populations often exhibit limited differentiation due to significant gene flow between them. The proximity of Gourounsi cattle populations and their relatively strong genetic differentiation from Lobi cattle is further reflected in the Neighbor-joining tree, where Gourounsi cattle populations cluster together with strong bootstrap support. The individuals' phylogenetic tree also demonstrates successive overlaps between the Gourounsi Nahouri and Gourounsi Ténado clusters, indicating the existence of gene flow between these Gourounsi taurine cattle populations.

The weak structuration of Gourounsi cattle and their differentiation from Lobi cattle in Burkina Faso may be attributed to zebu gene introgression. Lobi cattle inhabit the South Sudan Savanna area, which is characterized by a humid climate, Sudanian tropical vegetation, and riverine habitats preferred by tsetse flies. Zebu cattle populations are generally susceptible to trypanosomosis, and tsetse flies in the Lobi distribution area make zebu introgression more challenging. On the other hand, Gourounsi cattle are found in the Central region of the country, which experiences average rainfall. Gourounsi Nahouri, in particular, inhabits a more wet area. In 1987, Planchenault (1987) referred to Gourounsi taurine cattle populations as "Mere," a term commonly used by the Fulani (Peul) people to describe crossbreeds between zebu and taurine cattle, similar to "sanga" cattle. Therefore, the differentiation between Lobi and Gourounsi cattle can be attributed to the introgression of zebu genes in all Gourounsi taurine cattle populations. This hypothesis is supported by the results obtained from the STRUCTURE analysis, which provide evidence of genetic admixture. Differences in the prevalence of tsetse flies and associated trypanosomosis have also shaped the level of zebu introgression in taurine cattle. This is reflected in the relatively high level of zebu admixture in Gourounsi Tenado cattle that inhabit the dry Sudano-Sahelian region, where the prevalence of trypanosomosis is relatively less. Lobi and Gourounsi Nahouri cattle inhabiting the Sudanian region, which has a high prevalence of trypanosomosis, showed relatively low zebu admixture Further, cultural factors also play a role in the genetic differentiation between these populations. In Lobi country, there is a cultural preference for purebred Lobi cattle, particularly for ceremonial purposes such as weddings and dowries (Zoma-Traoré *et al.,* 2020), leading to the preservation of the Lobi breed's purity.

CONCLUSION

The present study reports high genetic diversity in the three main taurine cattle populations of Burkina. The global F statistics showed low genetic differentiation among Burkina Faso cattle, with about 4% of the total variation being attributed to differences between breeds. High levels of admixture were evident from the distribution of pairwise sharing distances that showed individuals within Gourounsi taurine populations being more related. Moreover, strong introgression signals of the zebu gene in Burkina taurine populations have been noticed using Bayesian clustering of individuals without prior population information.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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