Genetic differentiation and structuration of the Gobra zebu cattle breeds reared in Senegal

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Babacar Souleymane SAMBE*

Laboratoire National de l'Elevage et de Recherches Vétérinaires (LNERV), Dakar, Sénégal.

Département de Biologie Animale, Université Cheikh Anta Diop (UCAD), Dakar, Sénégal.

Current address: Institut Pasteur de Dakar, Pôle Immunophysiopathologie et Maladies Infectieuses (IPD/IMI), Dakar, Sénégal.

ORCID: 0000-0001-5983-2248.

Mame Nahé DIOUF

Laboratoire National de l'Elevage et de Recherches Vétérinaires (LNERV), Dakar, Sénégal.

Bakary NDIAYE

Laboratoire National de l'Elevage et de Recherches Vétérinaires (LNERV), Dakar, Sénégal.

Département de Biologie Animale, Université Cheikh Anta Diop (UCAD), Dakar, Sénégal.

Isidore HOUAGA

Centre International de Recherche-Développement sur l'Elevage en zone Subhumide (CIRDES), Bobo-Dioulasso, Burkina Faso.

Current address: Centre for Tropical Livestock Genetics and Health (CTLGH), Roslin Institute, University of Edinburgh, Midlothian, United Kingdom.

Marc Noël BADJI

Laboratoire National de l'Elevage et de Recherches Vétérinaires (LNERV), Dakar, Sénégal.

Département de Biologie Animale, Université Cheikh Anta Diop (UCAD), Dakar, Sénégal.

Mamadou DIOP

Laboratoire National de l'Elevage et de Recherches Vétérinaires (LNERV), Dakar, Sénégal.

Mbacké SEMBENE

Département de Biologie Animale, Université Cheikh Anta Diop (UCAD), Dakar, Sénégal.

***Corresponding author**: Babacar Souleymane SAMBE, IMI/IPD, BP: 220, Dakar Sénégal.

E-mail: babs602@hotmail.com or babacarsouleymane.sambe@ucad.edu.sn

Abstract

The Gobra zebu genetic breeding programme has resulted in a population with genetic characteristics that differ from other cattle populations exploited in Senegal. These differences seem to be due to the reproductive isolation and selection to which this population of the "Centre de Recherches Zootechniques" of Dahra has been subjected since the 1950s. The objective of this study is to evaluate the genetic differentiation and structuration of this population in relation to the main cattle breeds used in Senegal. A sample of 180 individuals from the Gobra selection nucleus and six other bovine populations from the four main breeds exploited in Senegal was thus constituted. The genotyping of these individuals was done with 21 microsatellite markers recommended by the Food and Agriculture Organization. The basic parameters of differentiation and structuration genetic were calculated using various bioinformatics software. The results of this study, notably the degrees of genetic differentiation (Fst), the coefficient of genetic homogeneity (Gst) and the gene flow (Nm), show a significant genetic differentiation of the Gobra from the station compared to the other populations studied. The analysis of genetic structuring reveals a micro-structuring within the Gobra population. This micro-structuring clearly identifies the centrally-bred Gobra individuals from the other Gobra populations studied. The main causes of these observations would be reproductive isolation and the selection pressure exerted on this population for several decades.

Keywords: genetic characterization; Gobra zebu; local cattle breeds; microsatellites; Senegal.

Introduction

Indigenous animal genetic resources are known for heat and draught tolerance, disease resistance and subsistence on poor feed, opening scope for allele mining for these traits (Sharma et al., 2013). However, usually in animals breeding program, many traits of local breeds are neglected at the expense of productivity traits of exotic breeds. This leads in some countries to a continuous decline of the indigenous cattle population. As a result, the introduction of highly

productive breeds and population pressure contribute to the loss of valuable traits or to the decline in the population of local breeds (Sharma et al., 2015). Description of cattle biodiversity is important as an aid to conservation of animal genetic resources and national heritage (Mannen et al. 2004). Indeed, genetic characterization (in particulary elucidate genetic variability and genetic relationship) of breeds has direct relevance with the issues of sustainable use of domestic animal genetic resources (Mannen et al., 2004; Sodhi et al., 2005). Furthermore, such information should contribute to the formulation of rational breeding programs with the goal of increasing output in the production system (Mannen et al., 2004; Sodhi et al., 2005).

In Senegal, four local cattle breeds and one exotic breed are generally found on pastoral farms (Missohou et al., 1997; Diack et al., 2016). The African breeds are the Gobra zebu in the Sahelian area of the country (in the north and centre - sylvo-pastorale area), the N'dama taurine in the Sudano-Sahelian area of the country (in the south and east), the Djakoré (resulting from cross-breeding between Gobra zebus and N'dama taurines in transitional zones) and the Moorish zebu in the north of the country (Missohou et al, 1997; Mbengue et al., 2007; Diack et al., 2016; Wane et al., 2017). Among the exotic breeds, the Guzera zebu is the most commonly encountered in pastoral farms, especially in the sylvo-pastoral area (Diack et al., 2016).

The Gobra zebu is, from a socio-economic point of view, one of the most important bovine genetic resources in the country and the "Centre de Recherches Zootechniques" (CRZ) of Dahra hosts the genetic breeding programme of this breed (Missohou et al., 1997; Sambe et al., 2019). Its genetic selection programme aims to: conserve the Gobra breed *in vivo in situ* at the CRZ of Dahra and to provide breeders in the sylvo-pastoral zone with animals that are better adapted and perform better in this particular production environment. The genetic breeding programme of this breed was carried out by an intra-racial closed-nucleus mass selection initiated in 1952 (Sow et al., 1988). Together with the maintenance of reproductive isolation, this desire to preserve this breed within the CRZ of Dahra for so long has had an impact on the genetic

diversity within this population (Sambe et al., 2022). However, the impact on genetic differentiation and structuration between these populations and the wild populations is not documented. The objective of this study is to assess the impact of this selection and isolation on the genetic differentiation and structuration of this population compared to mainly other cattle populations exploited in Senegal.

Materials and methods

Study areas

The study involved 180 individuals randomly selected from the 7 study sites shown in Figure 1. The study areas other than the CRZ of Dahra were chosen either to obtain animals preserved as much as possible from inter-racial crossings (CRZ of Kolda and EMAAP farm), or because of the accessibility of the individuals (Dakar slaughterhouses), or because the foundation herd would have been made up of cattle that notably came from these areas (Amaly, M'beuleukhé and N'diané).

Study population and blood collection

The study population is made up of the venous blood of 4 breeds: N'dama taurines, Gobra zebus, Guzera zebus and Moorish zebus. Thus, 41 samples of Gobra from the CRZ of Dahra were compared to: 68 samples of Gobra from 3 villages located close to CRZ of Dahra (21 in Amaly, 22 in M'beuleukhé and 25 in N'diané); 29 samples of N'dama from the selection nucleus of the CRZ of Kolda; 22 samples of Moorish zebu from the Dakar slaughterhouses; and 20 Guzera individuals from the EMAAP industries farm in Thiès. The 41 animals from the CRZ of Dahra are made up of: i) 29 animals from the genetic breeding programme (native); ii) and 12 animals (from the 33 animals from villages close to CRZ of Dahra) introduced in 2017 to reinforce the nucleus selection (acquired).

Blood collection was carried out between October 2016 and March 2017. On each of the individuals sampled, blood was taken from the jugular vein of the animal in tubes with ethylene diamine-tetra-acetic acid (EDTA) as an anticoagulant. The samples thus obtained are

centrifuged at 8,000 rpm during 10 minutes to collect the buffy coat. The buffy coat is then placed in 1.5 ml Eppendorff tubes and stored at -20°C until the genomic DNA is extracted.

DNA extraction and genotyping of individuals

Genomic DNA was extracted from the buffy coat using the Zymo Research commercial kit (Quick-DNATM Universalt Kit) following the protocol described by the manufacturer. The extracted DNA was stored at -20°C until the individuals were genotyped. Individuals were genotyped with 21 of the 30 microsatellite markers recommended by FAO (2011). The genotyping protocol is described by Sambe et al. (2022).

Data analysis

Impact of technical errors and linkage disequilibrium between loci

The impact of technical errors during genotyping was assessed using MicroChecker software version 2.2.3 (Oosterhoot et al., 2004). These analyses consisted of checking: dropout, stuttering, and the presence and proportion of null alleles for each locus and each population. Furthermore, the proportion of null alleles expected under the double null hypothesis of panmixing and that null alleles explain the variance of the inbreeding coefficient deficit is calculated according to the second method of Brookfield (1996). Microchecker analyses were performed after 10,000 replicates and with a confidence level of 95%. A binomial test, performed with R software, was used to compare the significance at the 5% level of the differences between the proportions of null alleles observed and calculated by the second method of Brookfield (1996).

Linkage disequilibrium (between pairs of loci) was assessed using Genepop version 4.2.2 (Rousset, 2008). The linkage disequilibrium signal was tested on R with a binomial test as described by De Meeûs (2012). The significance level of the tests performed is set at 5%.

Genetic differentiation

For each locus, genetic differentiation was assessed using the Wright (1978) degree of genetic differentiation reported by Weir and Cockerham (1984) (θ denoted Fst in the following) and

the Nei (1973) genetic homogeneity coefficient (Gst) reported by Nei and Chester (1983). These analyses were carried out using SPAGeDi version 1.4 software (Hardy and Vakemans, 2002) after 20,000 randomisations using the Jackknife resampling method.

Genetic differentiation was also assessed between the different populations by calculating: the degree of genetic differentiation (Fst per population pair), gene flow (Nm) and genetic distances (Dcs) according to the method of Cavalli-Sforza and Edwards (1964). The results of these analyses were generated with the Genepop version 4.2.2 and Populations version 1.2.32 software (Langella et al., 1999). A significance level of 5% was retained for the tests performed.

Genetic structuration

In a first step, a Correspondence Analysis (CA) was performed to visualize the relationships between individuals of the different populations, to estimate the distribution of genetic diversity between populations and to visualize their degrees of admixture. Given the high sensitivity of this analysis to outliers (De Meeûs, 2012), analyses were performed at different hierarchical levels to detect micro-structuring. The hierarchical levels are defined by considering all the samples and then progressively subtracting the populations that show significant genetic differentiation with the others (Fst significantly greater than or equal to 0.05). These analyses were performed with Genetix software version 4.0.5.2 (Belkhir et al., 2014).

In a second step, a genetic assignment test was performed using the method described by Paetku et al. (1995). This method, based on allelic frequencies, makes it possible to estimate the probability of each individual belonging a posteriori to the different populations considered. This analysis was carried out using the GeneClass version 2.0 software (Piry et al., 2004), considering 10 000 simulations and a significance threshold of 1%.

Finally, the structure of the study population was inferred using the Bayesian method implemented in the Structure software version 2.3.4 (Pritchard et al., 2000). This method makes it possible to infer the likelihood with which certain individuals can be grouped together and

considered to belong to the same group or cluster. The analyses were carried out considering: a priori 1 to 8 groups or clusters (K), a preheating chain consisting of: 10^4 iterations, 10^6 iterations of the Marcov Monte Carlo Chain (MCMC) and 10 replications for each value of K. The likelihood and Evanno methods (Evanno et al., 2005), available on the online platform Structure Harvester (Earl and VonHoldt, 2012) were used to determine the most likely numbers of genetic clusters. Analyses were performed on the hierarchical levels described for CA to detect micro-structuring.

Results and discussion

Results

Impact of technical errors and linkage disequilibrium

After cleaning the data, the HEL5 marker and 5 zebus (1 Gobra from Amaly, 3 Guzera and 1 Moorish) were eliminated due to poor amplification. The analyses therefore covered 20 microsatellite markers and 175 individuals, representing 3,500 data points or genotypes. Among these 3,500 genotypes, only 74 (or about 2%) were identified as null alleles (Appendix 1). On average, in each population and for each locus, a maximum of 2 individuals showed null alleles. For all populations combined, each locus had on average 3 to 4 individuals with null alleles (Appendix 1). The proportion of null alleles observed per loci is very low as it is less than 5% for all loci except for HEL1 and INRA063. These two loci present a proportion of null alleles equal to approximately 5.7% (which represents 10 null alleles for 175 targeted genotypes).

If we assume that the populations studied were panmictic and that null alleles explain the Fis deficits, the p-values of the binomial tests are not significant. Furthermore, no cases of stuttering and/or dropout were detected (Appendix 1).

Out of 190 pairs of loci, only 12 show a significant p-value in the linkage disequilibrium test (Appendix 2). The linkage disequilibrium signal test gives a non-significant p-value. This

means that the observed linkage disequilibrium for the 12 loci pairs can be explained by chance. Therefore, all loci are used for further analysis as they are considered independent.

Genetic differentiation and structuration

All loci show a degree of differentiation (Fst) and a coefficient of genetic homogeneity (Gst) significantly different from 0 (Table 1). Nineteen of the twenty loci have Fst values indicating moderate genetic differentiation (Fst between 0.053 and 0.157). Only BM1818 (Fst = 0.045) shows weak genetic differentiation. The Gst values are very close to the Fst values. The multi-loci analyses lead to the same conclusions. Indeed, Fst and Gst are also significantly different from 0 and indicate moderate genetic differentiation.

From a racial point of view, Table 2 shows that: i) the Gobra and Moorish breeds show little genetic differentiation from each other (Fst < 0.05); ii) these breeds show moderate genetic differentiation from the Guzera (0.05 < Fst < 0.15); and iii) all the breeds studied are strongly differentiated from the N'dama (Fst > 0.15).

From a population point of view, Tables 3 and 4 confirm the slight differentiation between the Gobra and Moorish populations studied. These populations show low to moderate degrees of differentiation (Fst between 0.002 and 0.077), significant gene flow and genetic distance (Nm between 1.042 and 3.238 and Dcs between 0.258 and 0.362). In addition, the Guzera and N'dama show greater genetic differentiation with the Gobra and Moorish (Fst ranging from 0.067 to 0.271; Nm ranging from 0.538 to 1.512; and Dcs ranging from 0.395 to 0.602).

It should be noted that the Gobra from the CRZ of Dahra selection nucleus are more differentiated from the other Gobra and Moorish populations sampled, while the N'dama are the most differentiated from all other populations.

Considering all populations into account, the first three axes of the CA give an overall inertia of 70.19% (Figure 2). The populations contributing most to the construction of these axes (Appendix 3) are: the N'dama (with a contribution of 64.7% for axis 1 and 12.6% for axis 2); the Guzera (with a contribution of 45.2% for axis 2 and 31.2% for axis 1); the Gobra of Amaly and the natives of the CRZ of Dahra for the construction of axis 3. Thus, a projection of the individuals on the two main axes of the CA makes it possible to distinguish a genetic structuration of our population into three sub-populations. These are a population of N'dama, one of Guzera and another population, not differentiated at this scale, made up of Gobra and Moorish.

Considering only the zebu populations (Figure 3), the overall variance explained by the first three axes is 69.71%. The Guzera contribute almost exclusively (79%) to the construction of axis 1 (Appendix 3) and the construction of the other two axes mainly involves the native Gobra of the CRZ of Dahra (49% for axis 2 and 12.8 for axis 3). This CA allows us to distinguish the Guzera, the native Gobra of the CRZ of Dahra, from the other zebu populations sampled.

At the local zebu level (Figure 4), the overall inertia is 71.87% and a micro-structuring of the population is visible. Three populations contribute significantly to the construction of the first two axes (Appendix 3). These are the Gobra native to the CRZ of Dahra (axis 1: 61.8%; axis 2: 12.6%), the Gobra of Amaly (axis 1: 32.6%; axis 2: 26%) and the Gobra of N'diané (axis 1: 0%; axis 2: 57.7%). These three populations are the ones that are identifiable on the CA.

The percentages of individuals correctly assigned to their population of origin according to the Paetku method are very high (Table 5). The populations with the lowest assignment scores are the new acquisitions of the CRZ of Dahra and the Guzera zebus with more than 83% and 88% of individuals correctly assigned, respectively. All other populations have correct assignment percentages of at least 90%.

226 The likelihood and Evano methods (Figure 5 A and B) indicate that the number of probable
227 genetic groups when considering the whole study population is 2 (K = 2). The resulting structure
228 shows 2 main multi-loci groups (red and green) which are present in different proportions in
229 the inferred groups (Figure 5 D). Our populations, constituted *a priori*, have varying proportions
230 of these multi-loci groups (Figure 5 C). The N'dama are mainly composed of the red multi-loci
231 group, while the zebus are mainly composed of the green multi-loci group. The N'dama group
232 shows a slight introgression of the green multi-loci genotype (zebu group) and vice versa. The
233 percentage of individuals assigned to the different groups (Appendix 4) confirms these results.
234 Indeed, 97% of the N'dama are assigned to group 1, while the zebus are assigned to group 2 in
235 proportions varying between 83 and 99%.
236 When we consider only zebu cattle, the maximum likelihood is obtained with K = 3 (Figure 6
237 A and B). The genetic structuring according to our *a priori* populations is less obvious (Figure
238 6 C and D). Nevertheless, it should be noted that the Gobra native to the CRZ of Dahra and the
239 Guzera have a multi-loci genotype that is in the majority. The Gobra native of the CRZ of Dahra
240 are predominantly composed of the blue multi-loci genotype, whereas the Guzeras seem to
241 possess almost exclusively the green multi-loci genotype. The other populations are mostly
242 composed of the blue and red multi-loci genotypes. These populations are distributed in various
243 proportions in the three groups inferred by the Bayesian method, while the Guzera and the
244 Gobra native to the CRZ of Dahra are mostly assigned to groups 2 and 3 respectively (Appendix
245 5).
246 Considering only Gobra and Moorish zebu, Evano's method gives a most likely K equal to 4
247 (Figure 7). The four groups inferred by the Bayesian method are each predominantly composed
248 of a Gobra population (Appendix 6) and a particular multi-loci genotype (Figure 7). Group 1 is
249 predominantly made up of the red multi-loci genotype and 53.3% of the N'diane Gobra. The
250 green multi-loci genotype is predominantly identified in group 2 which contains 67% of the

Gobra native of the CRZ of Dahra. The blue and yellow multi-loci genotypes are respectively in the majority in groups 3 and 4. These groups respectively hold 60% of the Gobra of M'beuleukhé and Amaly. The Moorish zebus and the new acquisitions of the CRZ of Dahra are mainly distributed in groups 3 and 4.

Discussion

The indices of genetic differentiation (Fst, Gst, Nm and Dcs) indicate overall low differentiation between the Gobra and Moorish zebu and moderate genetic differentiation between these populations and the N'dama populations of the CRZ of Kolda and Guzera of the EMAAP. It also appears that, among the Gobra and Moorish, the population of Gobra native of the CRZ of Dahra has the greatest degree of genetic differentiation from the Guzera and N'dama populations. The analysis of the population structure shows little introgression between the N'dama taurines and the zebu breeds studied, but also little introgression between the Guzera and the local zebu breeds. Furthermore, it appears from this analysis that genetic exchanges between local populations (Gobra and Moorish zebus) are very important. All this leads to the structuring of our study population into three clearly differentiated populations, namely: a population mainly comprising the Gobra and the Moorish (population 1); a population composed of Guzera (population 2); and a population of N'dama (population 3). The first two populations (populations 1 and 2), although clearly distinguishable, are not as distinct as population 3 (N'dama of the Kolda CRZ). The analyses also highlighted a micro-structuring within population 1, allowing the individuals from the CRZ of Dahra to be clearly identified from the other Gobra and Moorish individuals. Various studies to define the genetic differentiation and structuration of cattle breeds have resulted in a genetic distinction between zebu and bull populations (Bradley et al., 1994; Loftus et al., 1994; MacHugh et al., 1997; Bradley et al., 1998; Hanotte et al., 2000; Freeman et al., 2004; Dayo et al., 2009). These studies also show a clear genetic differentiation between African and other cattle breeds.

In the sylvo-pastoral area, although herders are increasingly introducing Guzera into their herds, the proportion of individuals of this breed is still very low in the said area (Diack et al., 2016). Due to sociological considerations such as the black colour of the Guzera's coat, although it has a desirable size, the breeders does not prefer an animal with this phenotypic appearance. Thus, farmers in this area only introduce males (generally only one male as a sire) to improve the meat production of their animals. MacHugh et al. (1997) and Ndiaye et al. (2015) also describe a strong genetic proximity between the Gobra and Moorish zebus of Senegal. Indeed, African zebu populations, having overlapping areas of distribution and being most often subject to a transhumant breeding system, retain a high genetic diversity and have a low degree of genetic differentiation between them (Freeman et al., 2004; Dayo et al., 2009).

The genetic micro-structuring observed between the Gobra individuals native to the CRZ of Dahra and the other Gobra and Moorish individuals is the result of the reproductive isolation and long selection to which this population has been subjected since 1950. In fact, since the beginning of the Gobra genetic breeding programme, every effort has been made to obtain "pure bred" and high-performance animals (Sow et al., 1988). It is with this in mind that the programme is based on an intra-racial selection of individuals in a system where, overall, there has been very little blood supply from outside (Sambe, 2021).

This study reveals that the Gobra population, the result of the genetic breeding programme conducted at the CRZ of Dahra since nearly 1970, is clearly different from the other bovine populations studied. These include populations of other breeds (i.e. the N'dama, the Guzera and the Moorish) as well as populations of the same breed that are very close historically and geographically (i.e. the Gobra of Amaly, M'beuleukhé and N'diané). This differentiation would be due to the long years of reproductive isolation and selection to which this population has been subjected since the beginning of the genetic breeding programme. However, in the future

this genetic differentiation should disappear or be less important due to the introduction of new individuals from neighbouring villages (i.e. the Gobra population acquired in 2017).

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Appendix

Appendix 1: Impact of technical errors on panmixia.

Appendix 2: Significance matrix for the linkage disequilibrium test (red boxes represent loci pairs with a significant p-value in the linkage disequilibrium test. grey boxes represent loci pairs without a significant p-value in the linkage disequilibrium test).

Appendix 3: Contributions of each population to the construction of the first 3 axes of the CA.

Appendix 4: Percentages of individuals correctly assigned to genetic clusters (N'dama and zebu combined).

Appendix 5: Percentages of individuals correctly assigned to genetic clusters (zebu only).

Appendix 6: Percentages of individuals correctly assigned to genetic clusters (local zebus only).

Figure

Figure 1: Study areas for genotypic characterisation

Figure 2: Correspondence Analysis performed on the entire study population.

Figure 3: Correspondence Analysis performed on all zebu populations.

Figure 4: Correspondence Analysis performed on the Gobra and Moorish zebu populations.

Figure 5: Genetic structure of the studied cattle populations.

Figure 6: Genetic structure of the zebu populations studied.

Figure 7: Genetic structure of the local zebu populations studied.

Table

Table 1: Indices of genetic differentiation by locus, calculated on the study population.

Table 2: Degree of genetic differentiation (Weir and Cockerham Fst) per population pair between the breeds studied.

Table 3: Degree of genetic differentiation (Weir and Cockerham Fst) and gene flow (Nm) per population pair.

Table 4: Cavalli-Sforza genetic distance between populations.

Table 5: Assignment of individuals to their populations of origin according to the method of Paetku (1995) at the 1% significance level.

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Data available on request from the authors.

Conflict of interest

The authors declare no conflict of interest.

Ethics statement

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to and that no ethical approval was required for this particular case report.

Authors contribution

Babacar Souleymane Sambe: Investigation, Formal analysis, Funding acquisition, Methodology, Writing original draft, Writing-review & editing; **Mame Nahé Diouf**: Conceptualization, Project administration, Investigation, Funding acquisition, Methodology, Supervision, Writing original draft, Writing-review & editing; **Bakary N'diaye**: Investigation, Formal analysis; **Isidore Houaga**: Formal analysis, Methodology, Supervision; Writing original draft; **Marc Noël Badji**: Investigation, Formal analysis; **Mamadou Diop**: Conceptualization, Methodology, Supervision, Validation; **M'backé Sembène**: Methodology, Supervision, Validation. All authors have read and approved the final manuscript.

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