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Diversity and Genetic Relationships among Seven West African Goat Breeds

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ABSTRACT : This study was carried out to determine the genetic relationships among seven west African goat breeds : Casamance Goat (Kolda, Senegal), Labe Goat (Fouta Djallon, Guinea), three Sahel Goat (Djoloff, Senegal ; Maradi, Niger; Gorgol, Mauritania) red Sokoto Goat (Maradi, Niger) and Guera goat (Atar, Mauritania).The polymorphism of six microsatellites and the α_{s1}-casein locus was analysed. The six microsatellite loci were polymorphic with a mean number of alleles ranging from 2.71 to 4.0. At the α_{s1}-casein locus, A and B were the most frequent alleles, which are known to be associated with a high level of protein synthesis. A neighbour-joining tree and a Principal Component Analysis were performed and the reliability of both methods was tested. Our study shows that the genetic relationships among the breeds analysed correspond to their geographical distribution and in addition, that the Labe Goat is strongly separated from the other breeds. Among the seven markers used, four have an effect on the distribution of breeds while three seem to be non-informative. (**Key Words :** Goats, West Africa, Microsatellites, α_{s1}-Casein, Genetic Relationship)

INTRODUCTION

The domestic goat *capra hircus* is an important livestock species throughout the entire asian and african continents. Goats are an important resource for agricultural, economic, cultural and religious purposes. Their origin remains uncertain and controversial, and the history of their domestication is more complex than indicated by previous studies. Archaeological evidence indicates that goats were one of the first animals to be domesticated by man around ten thousands years ago, in the ganj-darch in the zagros mountain pastures (Zeder et al., 2000). However, a world wide survey of domestic goat mtdna diversity has identified a multiple maternal origin with a possible centre of origin in asia as well as in the fertile crescent region (Luikart et al., 2001). In their study, three major mtdna lineages were revealed while in a more recent study (Joshi et al., 2004) concerning indian domestic goats two additional lineages were observed.

Apart from advances on the evolutionary and demographic history of humans and domesticated animals, these studies are also important for the management and conservation of today's animal resources. Unfortunately, many livestock breeds are still weakly characterised to date especially locally adapted breeds.

According to Doutressoulle (1947), West Africa presents a unique geographic mixture of two basic types of goats, particularly adapted to the local environmental conditions :

• Savanah or Sahel goats in the Sahel belt south of the Sahara, extending from lake Chad to Senegal. This type which is long legged and not resistant to trypanosomiasis is found in an area free of tsetse flies.

• Dwarf and trypanotolerant goats in humid zones, extending from South-Senegal through Nigeria.

Among these types, breed classification is still unclear. For instance, the red Sokoto Goat is classified as a Sahel type by Epstein (1971), a dwarf type by Doutressoulle (1947) and a crossbreed of both by Wilson (1992). The Guera Goat was first described by Kane (1995) simply as a breed from Mauritania. Moreover, some breeds are known by the same name in different places, but are phenotypically different from one place to another. Conversely, there are breeds that look alike but have different names in different places (ILRI, 1996).

Our study concerns the characterisation of seven west African goat breeds : Casamance Goat (Kolda, Senegal); Labe Goat (Fouta Djallon, Guinea); Sahel Goat from Djoloff (Senegal), from Maradi (Niger) and fom Gorgol (Maurtania); red Sokoto Goat (Maradi, Niger) and Guera Goat (Atar, Mauritania) with six microsatellites and with

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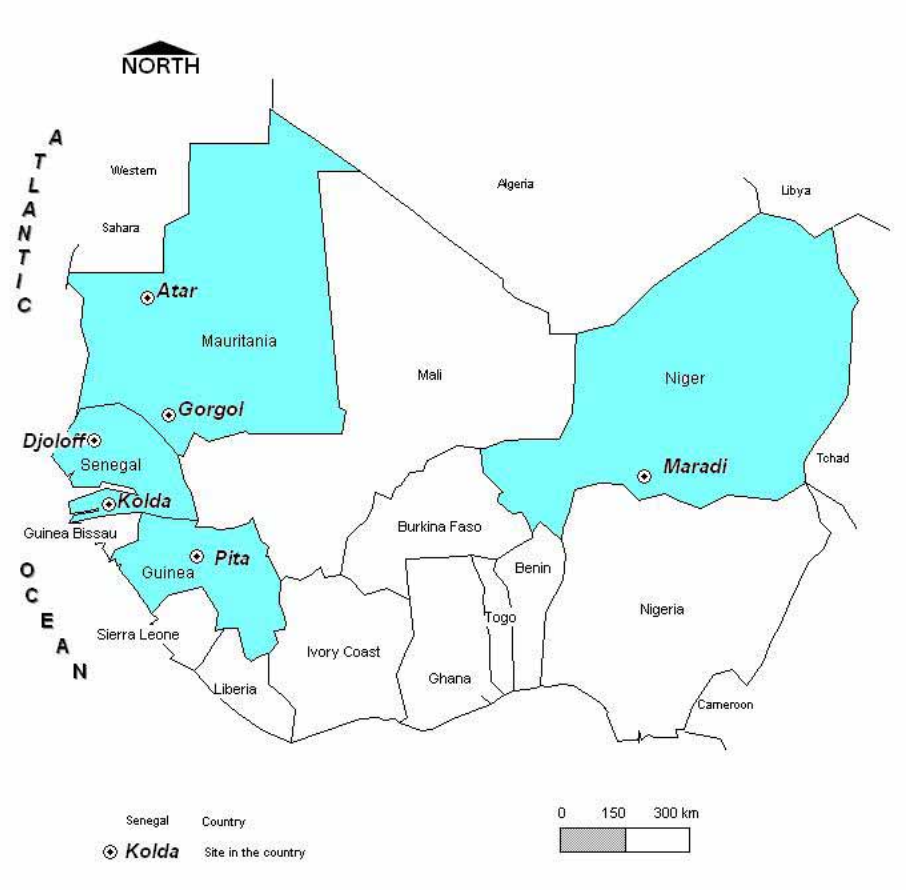

Figure 1. Geographical location of milk and blood samples collected in the 7 west African goat breeds of this study.

the α_{s1}-casein locus. This study contributes to the global process initiated by the FAO to document the world's Animal genetic resources.

MATERIALS AND METHODS

Sampling

The sampling process is of great importance since it will determine the kind of inferences which can be made. In order to reflect the current genetic composition and to try to ensure that the animals chosen were unrelated, individuals were sampled in herds from different locations (breeding centres and surrounding areas of the main goat breeds of West Africa). Between 74 to 100 blood and milk samples were collected per breed in lactating goats from at least 30 different villages with an average distance of two to 10 km. Within these samples, 20 were chosen for microsatellite typing procedures (one per village).

Dwarf samples were provided from Kolda (Casamance, Southern Senegal) for the Casamance Goat and from Fouta Djallon (Guinea) for the Labe Goat. The three Sahel Goat were provided from Djoloff (Central Senegal); from Maradi (Niger) and from Gorgol (Mauritania). The red Sokoto Goat and the Guera Goat were provided respectively from Maradi (Niger) and Atar (Mauritania) (Figure 1). The Casamance Goat and the Labe Goat are dwarf and trypanotolerant while the other breeds are long legged and trypanosusceptible.

Blood and milk samples were frozen and were respectively sent to the Inter-States School of Veterinary Medecine (EISMV), Dakar, Senegal and to the Laboratory of Biochemical Genetics and Cytogenetics (LGBC), INRA, France, for analysis. DNA was extracted by LABOGENA (Laboratory of genetic analysis for animal species). Microsatellites and α_{s1}-casein polymorphism analysis were carried out respectively in EISMV and LGBC.

DNA extraction, PCR amplification and electrophoresis of milk samples

DNA was extracted from 10 ml of frozen blood as described by Jean-Pierre (l987). Eleven microsatellites chosen from the most polymorphic ones published by Luikart et al. (1999) were tested. In our samples, only six were polymorphic: ILSTS011, INRABERN172, MAF65, OarFCB20, OarFCB48 and SRCRSP9. References and annealing temperature are described in Luikart et al. (1999). PCR was carried out in 25 µl reactions containing 1-30 ng of template DNA, 100 µM of each dNTP, 0.1 µM of each

Table 1. Mean number of alleles per locus and average heterozygosity values of 7 West African goat breeds of this study

Breed	Mean number of alleles	Average observed heterozygosity	Average expected heterozygosity
Casamance dwarf	2.86	0.880±0.274	0.468±0.106
Sahel goat, Senegal	2.86	0.730±0.329	0.423±0.167
Red sokoto	4.0	0.812±0.226	0.587±0.08
Sahel goat, Niger	3.14	0.686±0.310	0.518±0.138
Guera	2.86	0.882±0.263	0.542±.061
Sahel goat, Maurtania	3.28	0.708±0.372	0.492±0.223
Labe goat	2.7	0.799±0.183	0.534±0.073

primer, $MgCl_2$ (25 mM), 1 U of Taq polymerase, 1×PCR Buffer (500 mM Tris-Hcl pH 7.2 at 25°C, 100 mM MgSO4, 1 mM DTT). Cycling involved initial denaturation at 95°C for 5 min, 35 cycles of 15 s at 95°C, 15 s at 55°C or 50°C and 30 s at 72°C and a final extension step at 72°C for 10 min using a Perkin Elmer Gene Amp PCR System 2400. The PCR products were typed by electrophoresis on polyacrylamide gels (10%) and allele identification was performed by silver staining (Budowle et al., 1991).

The polymorphism of milk proteins was determined by isoelectric focusing according to Mahé and Grosclaude (1993).

Statistical analysis

Allele frequencies, estimates of heterozygosities (Ht = $1-\sum(\bar{Pi}^2)$), expected heterozygosities, F-statistics (Fis, Fit, Fst) and gene flow were calculated using the GENETIX package version 4.03 (Belkhir et al., 1998). The goat breeds studied were considered to be closely related and the main factor describing their genetic variability is random drift. Under this assumption, the Reynolds distance (Reynolds, 1983) is the most appropriate genetic distance to measure the degree of diversification (Eding et al., 1999, Laval et al., 2002). The Reynolds distances estimation, the neighbour-joining tree construction and bootstrap analysis were performed using the PHYLIP package (Felsenstein, 1993).

Prior to multivariate analysis, we tested the congruence of loci following the two step procedure developed by Moazami-Goudarzi and Laloë (2002), because a consensus representation of breed relationships is not meaningful if single markers are not congruent. First, distance matrixes among all the breeds were generated for each locus and correlations estimated using the Mantel procedure (Mantel, 1967). Next, marker congruence was investigated by performing a Principal Component Analysis (PCA) on the matrix of correlations and a Kruskal-Wallis test (NPAR1WAY procedure; SAS Institute, 2000) on rank scores of standardized distances among breeds. The correlation circle produced by the analysis gives a visual representation of marker congruity, while a significant Kruskall-Wallis test indicates that a compromise structure exists because distances are unequal among breeds. If a compromise structure exists, then a PCA using all the markers will be meaningful. The contribution of each marker in the structure of the principal components have been computed to see if these components are due to the action of a few markers only or to the whole set of markers. All computations relative to PCA were performed with ADE-4 package (Chessel et al., 2004) of R software (Ihaka and Gentleman, 1996).

RESULTS AND DISCUSSION

Markers polymorphism

A total of 34 distinct alleles were detected from the 137 goats studied with a mean number of alleles ranging from 2.71 to 4.0 (Table 1). Among the seven loci analysed, five private alleles were detected. These alleles were present with a relatively high frequency (15%) for three of them and low frequencies (2.5%) for the two others.

Heterozygosities (Ht) for the seven loci ranged from 0.468 to 0.587 across breeds with an overall average of 0.534. The red Sokoto Goat had the highest heterozygosity (Hexp = 0.587) and the Casamance Goat the lowest (Hexp = 0.47). This polymorphism is comparable with results published by Luikart et al. (1999), Yang et al. (1999), Wang et al. (2004), Selvi et al. (2004) and Chenyambuga et al. (2004) who also worked on the Casamance Goat (also called Djallonke) and on a long legged breed (Maure) but is lower than those published by Yang et al. (2004), Sun et al. (2004), Jin et al. (2005) and Yoon et al. (2005).

Population differentiation was examined by fixation indices Fis, Fit and Fst for each locus and across all loci. On average, we observed no significant deficit of heterozygotes for each of the breeds analysed (Fis = -0.52 ($p<0.001$)) or for the whole population (Fit = -0.19 ($p<0.001$)). We can thus suggest that the consanguinity of the analysed samples is probably weak. The average of genetic differentiation among breeds, measured as the Fst value, was 21% ($p<0.001$) with all loci contributing significantly to this differentiation. Thus, seventy nine percent of the genetic diversity in the total population could be attributed to differences among individuals. This value is similar to the values reported for Swiss goat breeds, Fst = 0.170 (Saitbekova et al., 1999), and Sub-Saharian goats Fst = 0.146 (Chenyambuga et al., 2004), Chinese pig breeds Fst = 1.63 and is higher than the values reported for horses Fst = 0.078 (Cañon et al., 2000), river buffalo breeds Fst = 0.038

Table 2. Allelic frequencies of α_{s1}-casein in samples of the 7 west African goat breeds of this study

Populations	Locations	N	α_{s1}-cn		
			A	B	C,E,F
Casamance goat	Senegal	100	0.193	0.807	0.000
Sahel goat	Senegal	100	0.06	0.923	0.015
Red sokoto goat	Niger	74	0.132	0.811	0.019
Sahel goat	Niger	75	0.211	0.778	0.011
Guera	Mauritania	90	0.268	0.619	0.113
Sahel goat	Mauritania	82	0.034	0.933	0.002
Labe goat	Guinea	99	0.316	0.684	0.000

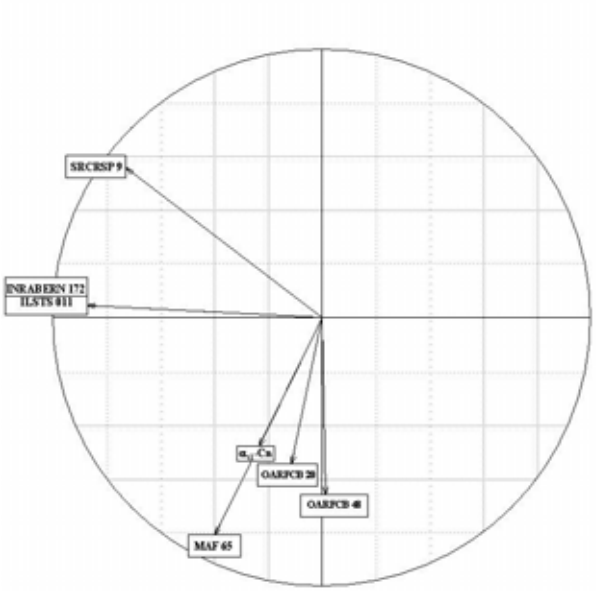

Figure 2. Correlation circle constructed from single-marker distances.

(Barker et al., 1997) or cattle Fst = 0.107 (Kantanen et al., 2000). The differences in allele frequencies may be due to migration, random genetic drift or mutations. In our study, the genetic migration would have played an important role between breeds of close geographical vicinity. The gene flow ranges from 0.46 to 6.21 between pairs of breeds. The greatest gene flow (N_em = 6.21) is between the Sahel Goat from Niger and red Sokoto Goat and the lowest is between the Labe Goat and other breeds (on average N_em = 0.65). Thus, the Labe Goat has maintained an important genetic isolation from all other breeds.

α_{s1}-Casein polymorphism

The α_{s1}-casein locus is characterized by a high qualitative and quantitative genetic variability. In particular, milk coagulation properties are strongly influenced by this locus (Grosclaude et al., 1987, 1994). The nucleotide sequence of the whole goat α_{s1}-casein-encoding gene (CSN1S1) has been determined, and at least, 15 alleles have been characterized (Ramuno et al., 2004). They are distributed among seven different classes of variants (A, B, C, E, F, G and O) and associated with four different synthesis efficiencies ranging from 3.5 g/L (α_{s1}-Cn A, B, C) to 0 g/L (α_{s1}-Cn0) per allele (Grosclaude et al., 1994). In this study, among the 620 animals analysed, it is clear that α_{s1}-cnA and α_{s1}-CnB were the major alleles, while α_{s1}-CnC, α_{s1}-CnE and α_{s1}-CnF were rare alleles present only in some breeds (Table 2). For example, the α_{s1}-CnB frequency varied from 0.62 in the Guera Goat to 0.93 in the Sahel Goat from Mauritania. The relatively high frequency of the α_{s1}-CnE (11%) in the Guera Goat is interesting. In addition, at the DNA level the null allele is detected with a high frequency 25%, while not observed or only in one animal in the Casamance Goat and in the Sahel Goat from Mauritania (data not shown). As these alleles have been reported to be highly present in European goat breeds (Grosclaude et al., 1994), the specific distribution pattern of α_{s1}-casein in the Guera Goat (also known as Spanish Goat or Western Sahara Goat) could be explained by crossbreeding with Spanish breeds introduced in Mauritania throughout Western Sahara. It is important to specify that due to selection programs the frequencies of α_{s1}-CnA, α_{s1}-CnB and α_{s1}-CnC have considerably increased during the last decade. For example, the frequency of these groups of alleles has increased from 20% (1985) to 83% (2000) for the Alpine breed.

It is surprising to note that the most frequent variant in these African goats (α_{s1}-B) is also the phylogenetically oldest variants reported (Grosclaude et al., 1994, Bevilacqua et al., 2002). Even if goats have multiple maternal origins, possibly arising through multiple independent domestications, Africa may likely be one of the centres of domestication (Luikart et al., 2001).

Relation between breeds

Genetic distances were significantly unequal among breeds (Kruskall-Wallis test, x^2 = 41.55, 20 d.f, p-value = 0.003), indicating the existence of a multivariate compromise structure. The correlation circle (Figure 2) suggested that the markers are congruent. Since all the markers are clustered in the same half-circle, PCA was performed.

Due to the fact that the first two principal components (PC) explained 73% of the total variation, the four others were not considered. The first PC accounts for 45% of the total variance and it clearly distinguished the Labe Goat

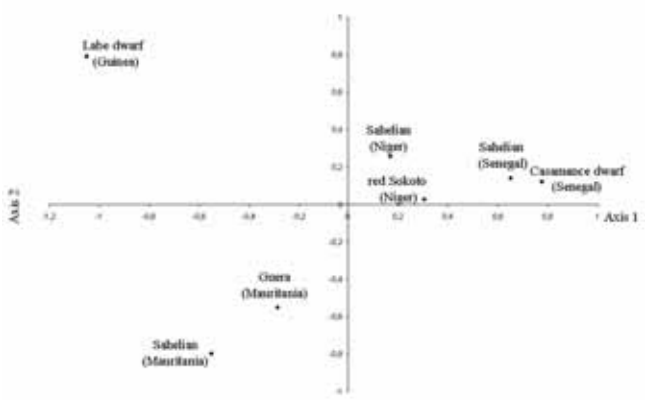

Figure 3. Scatterplot of principal component analysis of allelic frequencies of 7 west African goat breeds of this study.

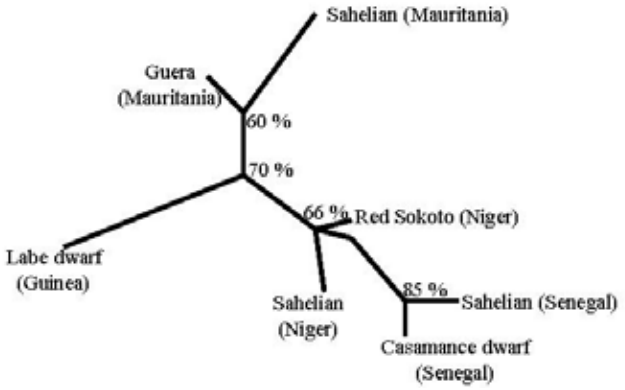

Figure 4. Phenogram showing genetic similarities among seven West African goat breeds from microsatellite and α_{s1}-casein. This tree is constructed by the neighbor-joining method from the Reynolds distance. Numbers at the node represent the percentage of group's occurrence in 500 bootstrap replicates.

from Senegalese breeds. The second PC accounted for 28% of the total variance and it clearly separated the Labe Goat from Mauritanian breeds. When plotted in a two-dimensional space (Figure 3), these two principal components revealed a pattern of association that was in concordance with the geographical origin of the breeds.

Figure 4 shows a neighbour-joining tree constructed from the matrix of Reynolds distances. The genetic relationships among the breeds correspond to their geographical distribution. Thus, four groups could be distinguished. The Labe Goat is strongly separated from other breeds and the most robust feature of the topology concerned the Senegalese breeds that are clustered with a bootstrap value of 85% while the occurrence of the node of breeds from Niger or Mauritania was 60%.

Whatever the method used, the seven breeds were clearly separated according to their geographical origin rather than their type or morphological grouping. This geographical grouping has also been reported in the recent study of Chenyambuga et al. (2004) who analysed 15 goat breeds from Europe, Asia, Middle east and eastern, southern and western Africa, with 19 microsatellites. In this study the separation between West African breeds and other African breeds was detectable at the third principal component which accounted for 9.1% of the total variance. Our study confirms this similarity but at a sub-regional scale. This alikeness between breeds of the same country rather than among types (trypanosusceptible, trypanotolerant) may suggest increasing crossbreeding as a consequence of increase in transhumance (due to drought episodes during these last decades) and farmers preference for larger animals. We confirmed the erosion of animal genetic diversity reported in other animal species from West Africa (Missohou and Adakal, 2004). MacHugh et al. (1997) and Hanotte et al. (2000; 2002) reported a declining north-to-south gradient of male zebu introgression among taurine breeds of West Africa. This was illustrated with the N'Dama breed across Senegal, The Gambia, Guinea Bissau and Guinea. For example N'Dama samples from Gambia have an average of 8.6% alleles that are of zebu origin, against 1.5% in Guinea Bissau and 0.2% for samples from the Fouta Djallon mountain of Guinea. These results lead the authors to qualify this area as representative of the last remnants of pure N'Dama left in West Africa. We have obtained similar results with the Labe Goat which has very weak values of gene flow estimates and a strongly separated position. Thus, the Fouta Djallon mountain has a very specific status with possibly the "most" pure breeds. This is probably due to the fact that this region is not easily accessible and have specific breeding practices.

Even if inferences among breeds made using a few number of markers should be interpreted with caution, our study confirms the need to define a higher priority for management strategies and conservation measures for specific breeds (dwarf) or specific regional breeding practices (Fouta Djallon mountains).

With the publication of the bovine genome sequence, the next step will be the combined use of random neutral markers and expressed genes. Thus, it will be necessary to use methods that can be applied to various types of markers and to check if the increase in the number of markers is really improving the reliability of the typology analysis.

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