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Short communication

Genetic characterisation of Burkina Faso goats using microsatellite polymorphism

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ABSTRACT

A total of 133 reproductive individuals belonging to the 3 Burkina Faso goat breeds (Djallonké, Mossi and Sahelian) were analysed for 27 microsatellites. Additionally, 72 blood samples belonging to two reproductively isolated subpopulations of the endangered Spanish Bermeya goat were used as outgroup. The between-Burkinabé goat breeds molecular coancestry varied from 0.418 ± 0.006 (Mossi–Sahelian) to 0.450 ± 0.007 (Djallonké–Mossi) and exceeded that computed between the Bermeya subpopulations (0.372 ± 0.006). Moreover, the computed between-Burkinabé F_{ST}'s varied from 0.023 ± 0.003 (Djallonké–Mossi) to 0.038 ± 0.004 (Djallonké–Sahelian). Structure and degree of admixture of the Burkinabé goat population were assessed using the program STRUCTURE and showed a significant introgression of the Sahelian goat southwards. The classification of the Burkinabé goat into different breeds did not have strong genetic support at the microsatellite level due to the rough definition of livestock breeds in Africa, historical gene flow patterns and desertization. The Mossi goat can be considered a transition breed between the two major Burkinabé goat populations (Djallonké and Sahelian).

1. Introduction

Documentation of existing genetic resources, including the description of the population phenotypic characteristics, performance, cultural importance and genetic uniqueness is one of the main areas of the livestock conservation activities (Duchev and Groeneveld, 2006; Ruane 1999). Description of genetic diversity can also inform on further sustainable intensification of animal production.

In Burkina Faso, there are about 10 million goat heads being the 69.5% of the domestic ruminants of the country (ENEC II, 2004). Goat plays a major role in maintenance of rural populations and also has a particular cultural importance due to its traditional use in rites and celebrations. However, studies on goat resources of Burkina Faso are scarce and basically limited to morphological traits (Sanfo et al., 2000; Traoré et al., 2006, 2008). A recent analysis of mitochondrial DNA variation failed in finding genetic differences among Burkina Faso goat populations (Royo et al., 2008).

The aim of this research was to assess the genetic relationships between Burkina Faso goat populations using microsatellite marker polymorphism. This aim focused mainly on the ascertainment of the Burkinabé goat population structure and degree of admixture. To address this task,

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two geographical subpopulations of the endangered Bermeya goat of Spain were used as outgroup.

2. Materials and methods

2.1. Description of breeds and territory

Burkina Faso is a sub-Saharan West African country that can be divided into three main environmental areas according to climate conditions and types of vegetation (Ouadba, 1997; see Fig. 1): a) the arid Sahel area, covering the Northern part of Burkina Faso (from latitude 13° 5′ N to 15° 3′ N, approximately); b) the Sudan area, covering the Southern part of Burkina Faso (latitude from 9° 3′ N to 11 °3′ N) with annual rainfall higher than 900 mm; and c) the Sudan–Sahel area, covering the central part of the country and very variable rainfall, with an average of 750 mm/year.

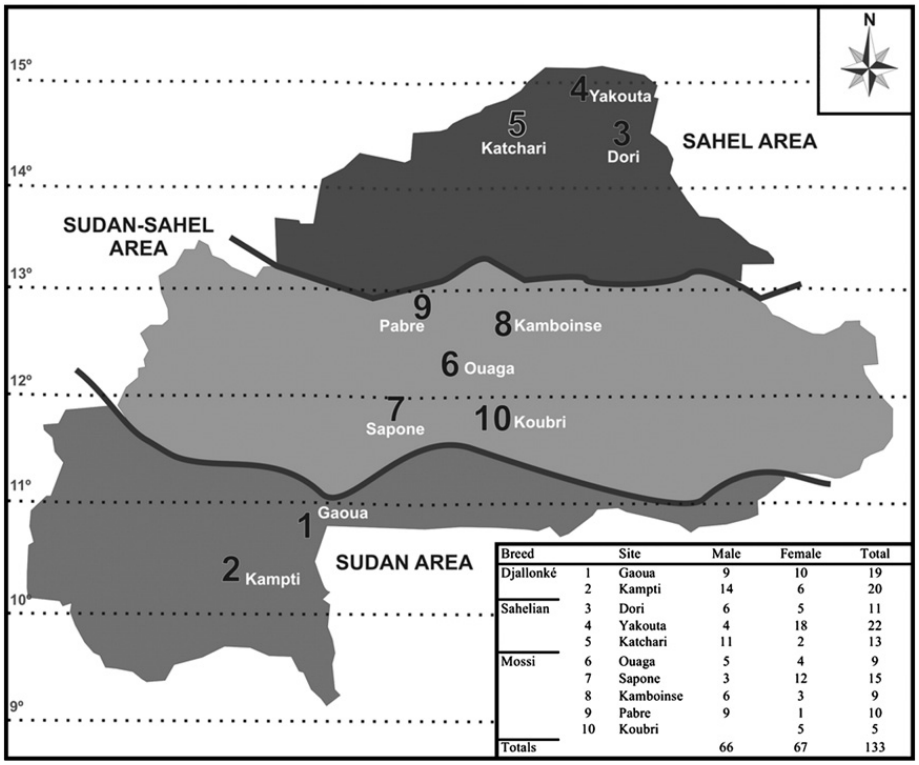
Each of these environmental areas is the habitat of a different goat breed: a) the Sahelian breed, which is the Burkina Faso representative of the long-legged goat group spread throughout the Sahel region of West Africa; b) the Djallonké breed, located in Southern Burkina Faso (the Sudan area), is a short-eared and small-horned goat belonging to the West African Dwarf goat population; and c) the Mossi breed, highly related to the Djallonké breed (Traoré et al., 2006), located in the central area of Burkina Faso (the Sudan–Sahel area). A complete description of the morphological characteristics of the three Burkinabé goat breeds can be found in Traoré et al. (2008).

2.2. Sampling and genotyping

Blood samples were obtained from a total of 133 reproductive individuals (66 bucks and 67 does) belonging to the 3 Burkinabé goat populations (see Fig. 1). From 2 to 5 different villages were sampled in each environmental area. Within each village, from 2 to 5 different flocks were sampled. In addition, 72 blood samples from reproductive individuals (34 bucks and 38 does) belonging to the endangered Spanish Bermeya goat (Figueroa et al., 2003) were obtained to be used as outgroup. Up to 37 Bermeya samples belonged to the Eastern Asturias population and the other 35 to the Western Asturias population. These two geographical subpopulations of Bermeya goat are known to be reproductively isolated, at least, from the last quarter of the 20th century (Álvarez et al., 2008) thus allowing their use to ascertain the degree of gene flow between Burkinabé goat breeds. Total DNA was isolated from blood samples following standard procedures (Sambrook et al., 1989). A microsatellite set, including 27 markers, was analysed on all the individuals (see Table 1). Genotyping was performed on an Automatic Sequencer ABI 310 (Applied Biosystems, Barcelona).

2.3. Statistical analyses

The following parameters were computed using the program MolKin (current version 3.0; Gutiérrez et al., 2005): number of observed alleles, observed (H_o) and expected (H_e), polymorphic informative content (PIC), Wright's *F*-statistics and raw (A) and rarefacted (A_g) average number of alleles per



Breed		Site	Male	Female	Total
Djallonké	1	Gaoua	9	10	19
	2	Kampti	14	6	20
Sahelian	3	Dori	6	5	11
	4	Yakouta	4	18	22
	5	Katchari	11	2	13
Mossi	6	Ouaga	5	4	9
	7	Sapone	3	12	15
	8	Kamboinse	6	3	9
	9	Pabre	9	1	10
	10	Koubri		5	5
Totals			66	67	133

Fig. 1. Map, adapted from Ouadba (1997), illustrating the division in provinces of Burkina Faso and the limits of the main environmental area of identified in the country. A description of sampling carried out in Burkina Faso is also given by breed, village and sex of the individuals. The numbers on the map correspond to the sampling locations listed.

Table 1
Number of alleles per marker (n), chromosome location (Chr), observed (H_o) and expected (H_e) heterozygosity polymorphic informative content (PIC), and F-statistics (F_{IT}, F_{IT} and F_{IT}) values per marker in the analysed dataset.

Marker[a]	n	Chr	H_o	H_e	PIC	F_{IT}	F_{ST}	F_{IS}
BM2504	4	9	0.024	0.022	0.024	−0.008 (0.004)	−0.007 (0.005)	−0.001 (0)
BM6526*	19	27	0.825	0.864	0.807	0.091 (0.063)	0.044 (0.024)	0.049 (0.047)
BM757	3	14	0.490	0.500	0.372	0.203 (0.191)	0.148 (0.112)	0.063 (0.189)
BMS2626	4		0.117	0.142	0.114	0.055 (0.088)	−0.001 (0.005)	0.056 (0.090)
BMS356	8		0.678	0.506	0.641	0.253 (0.090)	0.222 (0.093)	0.042 (0.048)
CSSM15***	10		0.840	0.801	0.819	0.276 (0.019)	0.109 (0.037)	0.190 (0.050)
CSSM43	9	27	0.705	0.643	0.668	0.147 (0.022)	0.055 (0.019)	0.098 (0.036)
CSSM66***	33	14	0.934	0.909	0.930	0.242 (0.059)	0.047 (0.019)	0.206 (0.077)
FCB128	7		0.265	0.148	0.256	0.122 (0.032)	0.078 (0.040)	0.049 (0.042)
ILSTS11	9	14	0.611	0.463	0.580	0.169 (0.052)	0.139 (0.047)	0.037 (0.052)
LSCV29	11	18	0.747	0.703	0.715	0.126 (0.043)	0.052 (0.027)	0.079 (0.062)
McM53	17		0.822	0.831	0.801	0.089 (0.015)	0.036 (0.012)	0.055 (0.022)
McMA26	10		0.692	0.663	0.634	0.067 (0.098)	0.070 (0.031)	−0.005 (0.082)
RBP3	5	28	0.278	0.147	0.246	0.270 (0.166)	0.127 (0.064)	0.157 (0.128)
BM8125	7	17	0.759	0.744	0.728	0.002 (0.036)	0.050 (0.037)	−0.050 (0.036)
BMS2461	9		0.385	0.321	0.365	0.029 (0.025)	0.048 (0.021)	−0.020 (0.010)
BMS2843	11		0.738	0.668	0.704	0.042 (0.033)	0.082 (0.020)	−0.043 (0.031)
BMS975	10		0.515	0.563	0.492	0.639 (0.053)	0.009 (0.015)	0.635 (0.049)
CSRD2111	17		0.864	0.780	0.851	0.128 (0.058)	0.108 (0.038)	0.022 (0.046)
CSSM31*	19	24	0.850	0.840	0.833	0.193 (0.045)	0.061 (0.021)	0.142 (0.053)
ILSTS005	8	10	0.419	0.368	0.387	0.080 (0.085)	0.065 (0.026)	0.019 (0.106)
INRA23*	12		0.810	0.785	0.787	0.128 (0.063)	0.082 (0.032)	0.049 (0.043)
INRA26	14	22	0.853	0.772	0.838	0.154 (0.101)	0.116 (0.041)	0.040 (0.070)
McM527*	8	7	0.727	0.723	0.679	0.152 (0.050)	0.018 (0.006)	0.136 (0.051)
OarHH64	8	4	0.765	0.771	0.727	0.119 (0.051)	0.104 (0.044)	0.017 (0.026)
SPS115	5		0.406	0.289	0.342	0.324 (0.219)	0.219 (0.177)	0.120 (0.073)
TGLA53	13	16	0.452	0.451	0.435	0.063 (0.048)	0.010 (0.009)	0.054 (0.051)

[a] One, two and three asterisks as superscripts mean a significant deviation from Hardy–Weinberg equilibrium for, respectively, $p<0.05$, $p<0.01$ and $p<0.001$.

locus. Here, g was fitted to 50, which is twice the minimum number of individuals within a breed with genotype known for all the microsatellites. Using also the program MolKin, the between-individuals and populations shared allele distance (D_{AS}), molecular coancestry (f_{ij}), kinship distance (D_k) and F_{ST} matrices were computed. See Gutiérrez et al. (2005) and the User's Guide of the program MolKin (freely available at http://www.ucm.es/info/prodanim/html/JP_Web.htm) for a detailed description of the methodologies used. When necessary for descriptive purposes, multidimensional scaling analysis was carried out on the genetic distance matrices using the Proc MDS of SAS/STAT™ (1999). Following Achmann et al. (2004) a bubble plot was also constructed on the between-individuals D_{AS} matrix using the IML module of SAS.

The program GENEPOP v. 1.2 (Raymond and Rousset, 1995) was used to compute the deviations from the Hardy–Weinberg proportions at marker and population levels. The program FSTAT 2.9.3 (Goudet, 1995) was used to compute the Wright's F-statistics at the marker level.

In all cases, the statistical significance of the obtained values was estimated by bootstrapping using 1000 replications.

The program STRUCTURE (Pritchard et al., 2000) was used to ascertain a possible cryptic genetic structure in the analysed dataset. The program estimates, using the Markov Chain Monte Carlo method, the natural logarithm of the probability that a given genotype X is part of a given population K ($\ln \Pr(X|K)$). This ensures that the groups are, as representatively as possible, samples from a single population. As the implemented algorithm

Table 2
Number of individuals analysed (N), within-population molecular coancestry (f_{ii}), heterozygote deficiency within population (F_{IS}), average number of alleles per locus (A) and average number of alleles per locus rarefacted to 50 copies ($A_{(50)}$) per analysed breed and for the whole dataset.

Breed		Within-population parameters				Between-populations parameters				
	N	f_{ii}	F_{IS}	A	$A_{(50)}$	1	2	3	4	5
1. E_Bermeya[a]	37	0.416 (0.007)	0.031 (0.021)	6.0	5.7		0.037 (0.004)	0.09 (0.005)	0.07 (0.005)	0.066 (0.004)
2. W_Bermeya[b]	35	0.417 (0.007)	0.031 (0.021)	6.1	5.8	0.372 (0.006)		0.088 (0.005)	0.072 (0.005)	0.068 (0.004)
3. Djallonké	48	0.497 (0.010)	0.076 (0.019)	5.4	5.1	0.350 (0.006)	0.352 (0.006)		0.024 (0.003)	0.037 (0.004)
4. Mossi	39	0.453 (0.009)	0.107 (0.028)	8.2	6.9	0.349 (0.006)	0.348 (0.006)	0.450 (0.007)		0.024 (0.003)
5. Sahelian	46	0.437 (0.008)	0.030 (0.019)	7.3	6.4	0.345 (0.006)	0.344 (0.006)	0.426 (0.006)	0.418 (0.006)	
Totals	205	0.389 (0.003)	0.054 (0.010)	10.7	6.7					

The between-populations molecular coancestry (below diagonal) and F_{ST} (above diagonal) matrices are also given. Standard deviations of the estimates are in brackets.

[a] Eastern population of the Spanish Bermeya goat breed.

[b] Western population of the Spanish Bermeya goat breed.

uncovers 'hidden structure' without using a priori knowledge about the number of clusters (populations or breeds) present in a dataset, following Druml et al. (2007) we carried out 10 different runs from $K=2$ to $K=10$ to identify the most likely number of clusters present in the dataset (the most likely parameter K). All runs used a burn-in period of 100,000 iterations and a period of data collection of 100,000 iterations under and admixture model with allele frequencies correlated.

3. Results

Table 1 gives information on the polymorphism of the genotyped markers. Up to 20 out of 27 markers had 8 or more alleles per locus and 15 and 16 markers had, respectively, expected heterozygosity and PIC values above 0.5. Overall, the microsatellite set used was useful to obtain sound assessments of among-breeds genetic relationships. Five markers (CSSM15, CSSM66, CSSM31, INRA23, and McM527) showed statistically significant deviations from Hardy–Weinberg proportions. However these significant deviations were not consistent across populations and could be due to a chance sampling effect (Type I Error). This was checked running all the analyses with and without including these five microsatellites. Results obtained with the full and the reduced set of microsatellites were highly consistent (not shown). This was also truth for results obtained using the program STRUCTURE in accordance with Álvarez et al. (2004). Therefore, results obtained from the 27 genotyped markers are further reported.

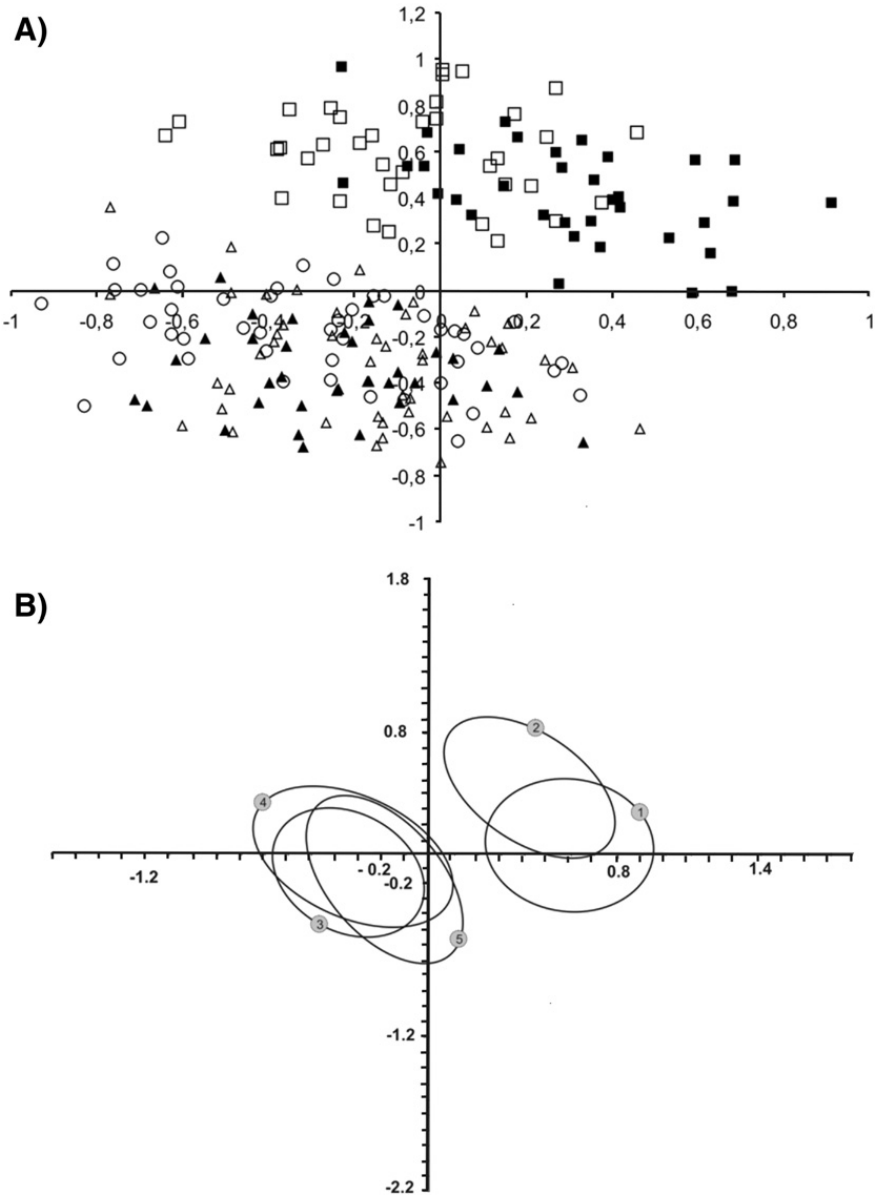


Fig. 2. Plot A shows a bidimensional scaling plot constructed using the between-individuals shared -allele distance (D_{AS}) matrix. Dimension 1 is on the X-axis while Dimension 2 is on the Y-axis. Eastern Bermeya individuals are in open squares, Western Bermeya individuals are in black squares, Djallonké individuals are in black triangles, Mossi individuals are in open triangles and Sahelian individuals are in open circles. Plot B shows a contour plot with 75% confidence region of the molecular genetic relationship among the analysed individuals constructed on the two dimensions computed on the shared allele distance (D_{AS}) matrix. Eastern Bermeya: 1; Western Bermeya: 2; Djallonké: 3; Mossi: 4; Sahelian: 5.

In any case, Table 1 also gives loci-wise *F*-statistics values to allow readers further assessment of potential non-neutrality of the markers used.

Parameters characterising genetic variability of the analysed goat populations are given in Table 2. The African breeds had higher genetic identity values (f_{ii}) than those computed within the endangered Bermeya subpopulations being the highest f_{ii} value that of the Djallonké breed (0.497 ± 0.010). The Djallonké breed had the lowest rarefacted average number of alleles per locus (5.1). The Mossi breed had the highest heterozygote deficiency ($F_{IS} = 0.107 \pm 0.028$) and average number of alleles in the dataset. The F_{ST} value computed for the whole analysed population was 0.090 ± 0.003 whilst this parameter computed for the three Burkinabé breeds was 0.035 ± 0.003.

The between-breeds molecular coancestry (f_{ij}) and F_{ST} matrices are also given in Table 2. The between-breeds shared allele distance (D_{AS}; not shown) gave similar information than F_{ST}. The between-Burkinabé goat breeds molecular coancestry, varied from 0.418 ± 0.006 (pair Mossi–Sahelian) to 0.450 ± 0.007 (pair Djallonké–Mossi). These values exceeded the molecular coancestry computed between the Bermeya subpopulations (0.372 ± 0.006). The between-Burkinabé breeds genetic differentiation assessed using F_{ST} varied from 0.023 ± 0.003 for the pair Djallonké–Mossi to 0.038 ± 0.004 for the pair Djallonké–Sahelian. The

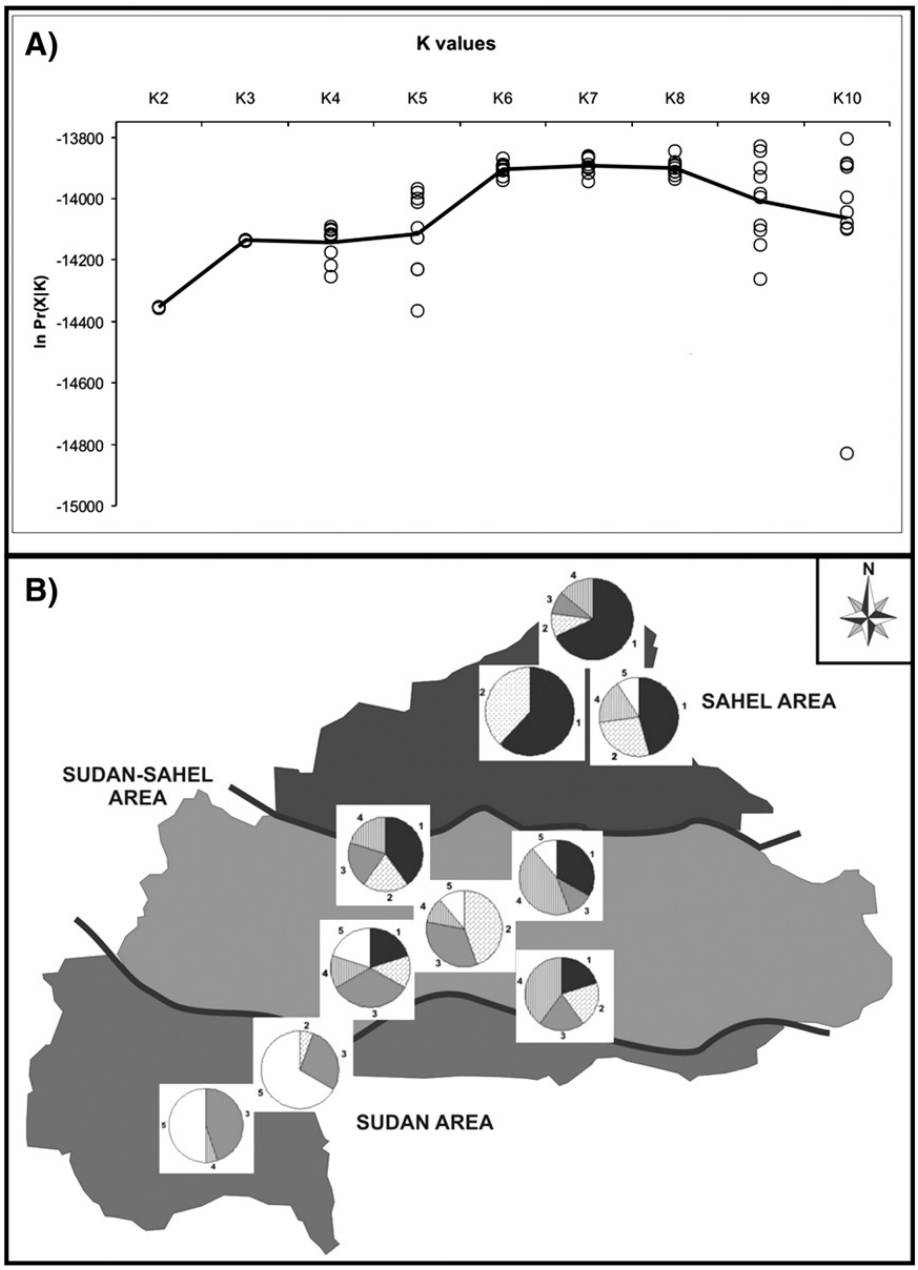


Fig. 3. Plot A gives the ln Pr($G|K$) values of 10 different runs of the program STRUCTURE for each K value varying from 2 to 10. Mean ln Pr($G|K$) of 10 runs for each K values is shown in a solid line. Plot B gives the proportion of membership of each of the sampling locations in each of the 5 clusters inferred in the most likely run of the program STRUCTURE using only the Burkinabé samples. Note that the numbers attached to the clusters are not consistent with those of Table 3. The individuals sampled in the Sudan area belonged basically to clusters 'white' and 'grey' whilst the individuals sampled in the Sahel area belonged basically to clusters 'black' and 'dashed'. The fifth inferred cluster (in bars) basically includes Mossi and Sahelian individuals.

between-populations D_{AS} matrix (not shown) gave similar information than F_{ST}'s. The between-individuals D_{AS} matrix was described using a bidimensional scaling plot (Fig. 2A). The Burkinabé individuals are separated from the Bermeya individuals and mainly spread on negative values of Dimension 1 (*X*-axis) and Dimension 2 (*Y*-axis). However, no clear separation could be assessed between the individuals assigned to each Burkinabé breed. Fig. 2B shows the genetic relationship among individuals as a contour plot. The contour plot showed a high between-Burkinabé breeds genetic overlap due to a significant degree of genetic similarity. Note that the overlap among Burkinabé breeds is higher than that assessed between the Bermeya goat subpopulations.

Population structure and degree of admixture were assessed using the program STRUCTURE. The most likely number of clusters (*K*) present in the dataset was ascertained using 10 different runs of the program (see Fig. 3). In $K=6$, across-runs average ln Pr($G|K$) was maximised and also mean variance of the ln Pr($G|K$) estimates was the lowest. Table 3 gives the membership (in percentage) of each of the analysed goat breeds in each of the 6 most likely clusters inferred using the program STRUCTURE. Cluster 4 included the Bermeya individuals and Cluster 1 gathered most Djallonké individuals (89.3%). A total of 31.6% of the Mossi individuals clustered separately in the inferred population 6. However, a significant proportion of Mossi individuals clustered with the other Burkinabé breeds. The program STRUCTURE was re-run using only the Burkinabé samples as input. Consistently with the general analysis, the most likely *K* was 5. The mean of the posterior distribution of each individual's admixture coefficient ($\hat{q}$), which represents an estimate of the amount of an individual's genome that is derived from the inferred clusters, were estimated and plotted on each sampling location to ascertain local processes of admixture (see Fig. 3B and the corresponding legend text). Plot 3B shows the existence of population structure within the Djallonké and the Sahelian breeds with their individuals being basically included into two different clusters each. A fifth cluster (basically represented in the Sudan–Sahel and Sahel areas) could be a result of local processes of admixture between Mossi and Sahelian individuals.

4. Discussion

Here we carried out the first genetic analysis of Burkina Faso goat using microsatellite markers. Although these studies are relatively frequent in Europe and Asia (Barker et al., 2001; Glowatzki-Mullis et al., 2008; Li et al., 2002), to our knowledge this is the first microsatellite analysis carried out on Sub-Saharan goat.

As noted in cattle (Hanotte et al., 2002; Dadi et al., 2008), it is not easy to assess genetic relationships among African livestock because definition of breeds is mainly based on the farmholding ethnic groups or geographical areas into which the individuals are found. In such a scenario, the use of appropriate outgroups is needed to obtain sound assessments of the between-African breeds genetic relationships. The use here of the two geographic subpopulations of the endangered Spanish Bermeya goat breed allows us to ascertain correctly the genetic relationships among Burkinabé breeds. Note that the Bermeya subpopulations are known to be reproductively isolated for the past 40 years and under severe population bottleneck (Figueroa et al., 2003; Álvarez et al., 2008). In consequence, the genetic identity assessed via molecular coancestry between Bermeya subpopulations is likely to be due to their membership to the same ancestral goat population (Álvarez et al., 2005). In this respect, the current analysis showed that the gene flow among Burkinabé goat populations is very high. Assuming 0.372 (see Table 2) as the 'minimum' molecular coancestry between subpopulations of the same breed, the increase in molecular coancestry $\left(\Delta f_{ij} = \frac{f_{ij} - 0.372}{1 - 0.372}\right)$ between Burkinabé goat breeds (interpreted as the degree of between-breeds gene flow) varied from 0.073 (pair Mossi–Sahelian) to 0.124 (pair Djallonké–Mossi). This high among-breed gene flow explains the low genetic differentiation observed between Burkinabé breeds (see Table 3 and Fig. 2) and the lack of clear genetic structure within the Burkinabé goat population (see Table 3).

The clusters inferred by the program STRUCTURE would theoretically correspond to the 'ancestral' populations from which the analysed breeds were derived. Although the definition of the Burkinabé breeds can have some genetic support, being the Djallonké, Sahelian and the Mossi individuals those contributing the most to the inferred clusters 1, 3 and 6, respectively, the Mossi and the Sahelian individuals contributed significantly to three of the inferred clusters (2, 3 and 5) thus giving an idea of the direction of the among-breeds gene flow assessed using molecular coancestry. As noted by Pritchard et al. (2000), the inferred clusters do not necessarily correspond to 'real' ancestral populations and they can be determined simply by the sampling scheme, being quite difficult to estimate the allelic frequencies of the 'original' populations when the sampled breeds are not well differentiated and many individuals have some degree of admixture. This scenario is likely to occur in Burkina Faso goat. Since no introgression of foreign (European or Asian) breeds is expected in our sample, the genetic structure observed here could be a consequence of major introgression of Sahelian individuals into the Mossi breed.

Recently, Traoré et al. (2008) analysing morphological information from 10,147 Burkina Faso does found low differentiation between the Djallonké and Mossi breeds. The Mossi goat took an intermediate position at both the quantitative and the qualitative morphological levels, between the two main well-differentiated Burkinabé goat populations: Djallonké and Sahelian. Traoré et al. (2008) suggested that the Mossi breed is the northerner representative of the West African Dwarf goat

Table 3
Number of individuals per breed (*N*) and proportion (in percentage) of membership of each of the analysed goat breeds in each of the 6 clusters inferred in the most likely run of the program STRUCTURE.

Breed	Inferred clusters						
	1	2	3	4	5	6	*N*
E_Bermeya [a]	0.011	0.021	0.018	0.915	0.012	0.024	37
W_Bermeya [b]	0.009	0.019	0.019	0.927	0.017	0.009	35
Djallonké	0.893	0.012	0.023	0.008	0.038	0.027	48
Mossi	0.198	0.140	0.184	0.011	0.151	0.316	39
Sahelian	0.058	0.129	0.556	0.010	0.219	0.027	46

[a] Eastern population of the Spanish Bermeya goat breed.
[b] Western population of the Spanish Bermeya goat breed.

population in Burkina Faso, showing differential characteristics due to the particularly arid ecosystem in which it is spread and to an ancient and sustained introgression southwards of the Sahelian goat. This introgression would be mediated by the action of the Peuls, nomadic ethnical group constituting a major force of exchange of genes from the Sahel over the more temperate zones of southern West Africa in search of grazing lands (Dossa et al., 2007; Traoré et al., 2008). Also, the increase of the duration of the dry seasons in West Africa since the 1980's would have favoured the migration of the Sahelian goat into the Sudan–Sahel and Sudan areas of Burkina Faso.

This suggestion coincides with the information given by the analysis carried out using STRUCTURE that is likely to be affected by the high between-Burkinabé goat breeds gene flow. The Mossi and the Sahelian individuals clustered together forming various groups in a scenario of poor genetic differentiation. In turn, the Djallonké individuals tended to form their own cluster with a little number of Mossi individuals (see Table 3). The introgression of the Sahelian goat into the Sudan areas can be limited and mediated by the Mossi population, as reflected by the STRUCTURE analysis. Sahelian goat is not trypanotolerant thus limiting its possibilities of use for reproduction in the southernmost Burkina Faso flocks, formed basically by Djallonké goats.

5. Conclusions

The classification of the Burkina Faso goat into different breeds does not have strong genetic support at the microsatellite polymorphism level due to the high between-breeds gene flow assessed. Genetic differentiation within Burkinabé goat was mainly due to the existence of two main goat populations (Djallonké and Sahelian) with probable different genetic origins (Royo et al., 2008) and large morphological differences (Traoré et al., 2008). The Mossi goat breed can be considered a transition population between the two major Burkinabé goat populations. The information reported here will be the basis for the establishment of further conservation and selection strategies in Burkina Faso goat.

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