Genetic diversity and population structure of Nigerian indigenous goat using DNA microsatellite markers

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Additional keywords

Allele.
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SUMMARY

Twenty-nine microsatellite markers were used to evaluate genetic diversity and relationships among three Nigerian goat breeds and to compare with one South African and one European goat breeds as outgroups. A total of 244 goats from the Sahel (47), Maradi (47), and West African Dwarf (67) breeds; and as outgroup: Kalahari (47) and Saanen (36) breeds were included. DNA was extracted from blood preserved on FTA Classic cards according to manufacturer's protocol. The microsatellite regions were amplified using thermal cycler. Mean number of allele (MNA), expected and observed Heterozygousities (He and Ho, respectively), Hardy-Weinberg Equilibrium (HWE) and genetic distances between populations were calculated. A dendogram was constructed to reveal evolutionary trend in the studied breeds. A genetic structure of the populations was performed using STRUCTURE. Genetic diversity was high with MNA per locus ranging from 6.69 to 8.79 for Kalahari and West African Dwarf, respectively. Ho values ranged from 59 % for West African Dwarf to 64.9 % for Saanen. The highest He estimates were observed in the West African Dwarf (70 %). The lowest He (66.5 %) was observed in Saanen population. The Mean Fis values for the studied populations ranged from 0.055 to 0.148 for Kalahari and West Africa Dwarf, respectively. Genetic distances between populations revealed the least genetic relationship between Saanen and Maradi (0.386) and highest between Maradi and Sahel (0.025). The HWE test revealed eighteen, seventeen, thirteen, twenty-three, and twenty-one loci were in HWE ($p>0.05$) in Maradi, West African Dwarf, Sahel, Saanen, and Kalahari, respectively. A graphic representation of the STRUCTURE analysis revealed that Nigerian goats descended from a common ancestor different from South African and European breeds used as outgroups.

Diversidad genética y estructura de población de cabras autóctonas nigerianas usando marcadores microsatélites DNA

Palabras clave adicionales

Alelo.
Distancias genéticas.

RESUMEN

Se analizaron 29 microsatélites para evaluar la diversidad genética de tres razas caprinas Nigerianas y establecer las relaciones genéticas entre ellas utilizando las razas Saanen y Kalahari como poblaciones *outgroup*. Se analizaron 244 distribuidas de la siguiente manera: en Sahel (47), Maradi (47) y WestAfrican Dwarf (67), Kalahari (47) y Saanen (36). El ADN se extrajo a partir de sangre conservada en tarjetas FTA Classic siguiendo las instrucciones del fabricante y se amplificaron los microsatélites mediante PCR. Se calcularon el número medio de alelos (MNA), las heterocigocidades observada (Ho) y esperada (He) y las distancias genéticas entre pares de poblaciones. Se hizo una prueba de equilibrio Hardy-Weinberg (HWE) y un análisis de la estructura genética de las poblaciones mediante el programa STRUCTURE. La diversidad genética encontrada fue alta con valores de MNA entre 6,69 y 8,79 para Kalahari y West African Dwarf, respectivamente. Los valores de Ho oscilaron entre un 59 % para West African Dwarf y un 64,9 % para Saanen. La He más alta se encontró en la raza West African Dwarf (70 %), mientras que el valor más bajo se observó en la raza Saanen (He= 66,5 %). Los valores medios de Fis para las poblaciones estudiadas variaron entre 0,055 en Kalahari y 0,148 en West African Dwarf. La distancia genética más elevada fué la encontrada entre Saanen y Maradi (0,386) y la menor entre Maradi y Sahel (0,025). La prueba de equilibrio de HWE reveló que dieciocho, diecisiete, trece, veintitrés y veintiún *loci* estaban en equilibrio HWE ($p>0,05$) en las razas Maradi, West African Dwarf, Sahel, Saanen y Kalahari, respectivamente. Una representación gráfica del análisis de estructura genética reveló que las cabras de Nigeria descienden de un ancestro común diferente de las razas sudafricanas y europeas que fueron utilizadas como grupos externos.

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INTRODUCTION

One of the earliest features of human civilization was the cultivation of plants and domestic animals from ancestral wild stocks by selecting those members of the species which showed a favourable variation. Individuals with favorable traits such as increased size or improved flavour were artificially bred by selective mating (Taylor *et al*., 1997). It is often said that variation in genes is necessary to allow organisms to adapt to ever-changing environments (Orr and Unckless, 2014). However, it is actually the variation in alleles that is critical. According to Dubey (2009), variation in alleles or markers can be detected at three different levels: morphological or phenotypic which corresponds to quantitative traits scored visually; biochemical due to differences in proteins; and molecular (a sequence among which the differences can be detected and monitored in the subsequent generations). Measurement of genetic diversity in goats has been imprecise because earlier studies were based on morphological and biochemical markers. Because of the influence of both natural and artificial selection on phenotypic traits as well as great influence of environment on both of these types of markers, it is unlikely that observations based on the study of differences between breeds would produce reliable results. Molecular markers such as microsatellite markers are more accurate because of their dense distribution in the genome, great variation, co-dominant inheritance and easy genotyping at DNA level. Microsatellites are repeats of simple sequences, the commonest being dinucleotide repeats which are abundant in genomes of all higher organisms, including livestock (Weber and May, 1989). Polymorphism of microsatellites takes the form of variation in the number of repeats at any given locus and is generally revealed as fragment length variation in the products of polymerase chain reaction (PCR) amplification of genomic DNA using primers flanking the chosen repeat sequence and specific for a given locus (Kemp and Teale, 1991).

The conservation of farm animal genetic resources is important for coping with future breeding needs and for facilitating the sustainable use of marginal areas. The increasing availability of molecular markers for most farm animal species and the development of techniques to analyze molecular variation are widening our capacity to characterize the genetic variation of breeds.

Goats play an important role in food production systems in developing countries. Their great popularity can be explained by their good adaptation to many different climates, ecological adaptation and the many uses for which they can be kept (Carl and Kees, 2004). Goats are of high importance to rural people because of their socio-cultural value. Furthermore goats provide milk and meat which are high-grade foodstuffs for people. Goats' meat is much tougher than beef from cattle (Carl and Kees, 2004), however they are small animals and cost less per animal compared to cattle, sheep and pigs. Efforts to document genetic diversity in goats will aid sustained increases in goat production.

There are three recognized indigenous breeds of goats in Nigeria. The hardy short legged West African Dwarf is confined to the humid forest belt of the south. The relatively small sized Maradi is found in the semi-desert. The long-legged Sahel is found in the Savannah zone of the country (Attah *et al.,* 2004). The Maradi is characterized by its uniformly dark red coat colour, short and horizontal ear, and horns in both sexes (Adu *et al*., 1979). The skin of the Maradi is among the most valuable of all goat skins and it commands a premium in the world market (Adu *et al*., 1979; Devendra and Burns, 1983). The breed is also a good meat animal. The West African Dwarf goats in the semi-arid zone resemble Maradi goats in their body proportions. It is a meat and milk type. The Sahel has varying coat colours usually white pied with black or brown. The coat is short and it has long legs. The horns are long, flat and twisted in the male, and sickle shaped in female. The ears are usually long and horizontal, but sometimes moderately long and pendulous (Devendra and Burns, 1983). The breed is adapted to nomadic or long range grazing and used for meat, milk and skin production.

For effective utilization of goat genetic resources, it is necessary to genetically characterize different populations. Such characterization would provide a database with information on which of the populations represent homogeneous breeds and which are genetically distinct. This characterization, contributes to the understanding of the evolutionary history of goats as well as future conservation and management of goat genetic resources. Studies on genetic diversity using microsatellite markers have been reported on indigenous goat breeds of Nigeria (Muema *et al*., 2009; Okpeku *et al*., 2011), Kalahari Red of South Africa (Kotze *et al*., 2004; Visser *et al*., 2004) and Saanen. In these studies, 10 or 11 microsatellite markers were utilized with indication that there was appreciable diversity in the populations for the loci considered. A more comprehensive knowledge of the existing genetic variability and how it is partitioned among breeds could be obtained with the use of more microsatellite markers as intended for this study. In the working hypothesis, we assumed that the populations of different breeds have different allele frequencies and will form separate clusters. This study was therefore designed to investigate genetic diversity in the Nigerian goat populations compared with outgroups from Europe and South Africa using 29 DNA microsatellite markers.

MATERIAL AND METHODS

DNA was extracted from blood obtained from 244 unrelated goats from different breeds: Sahel (47), Maradi (47), and West African Dwarf (67); with Kalahari (47) and Saanen (36) as out-group breeds. The blood was collected through the jugular vein using needle and syringe, applied immediately onto FTA® Classic cards (Whatman Biosciences, Maidstone, UK) and allowed to dry for about 1 hour at room temperature. DNA was extracted using 3 punches (2 mm^2) of the cards in 100 µl of 5 % chelex resin and incubating at 56 °C for 1 hour and at 95 °C for 15 minutes.

PCR amplification and genetic analysis of PCR products

A total of 29 microsatellites markers were selected from the ISAG/FAO advisory group recommended markers on sheep and goat genetic diversity study **(Table I)**. Microsatellites amplification and amplicon genotyping were carried out using fluorescent labeled primers. The amplification reactions were carried out using a programmable thermal cycler (MJ Research, USA). Each 25 µl PCR reaction contained 10-20 ng of the extracted genomic DNA as a template for the PCR reaction; 5 pmol of each primer (Microsynth, Switzerland); 200 µM each of dNTPs (Sigma-Aldrich, USA); 1 unit of Taq DNA polymerase (Biotools, Madrid ES); 2.5 mM $MgCl_2$. The PCR reaction cycle was accomplished by initial denaturation for 3 mins at 95 °C follow by 35 cycles at denaturation temperature of 95 °C for 45 sec, primer annealing for 45 sec at 50-63 °C depending on the primer and an extension for 45 sec at 72 °C. The final extension step was given at 72 °C for 10 min. Size call were carried out after separation using a DNA capillary sequencer ABI Prism® 377 Genetic Analyzer (Applied Biosystems) with GS Rox 400 HD internal size marker.

Measure of molecular genetic variability and relationships between the breeds

The mean number of allele (MNA) which is the average number of alleles observed in a population was calculated using GENEPOP, version 4.2 (Rousset, 2008). Genetic diversities of Nigerian goat at the studied microsatellite loci were measured by calculating the average heterozygousity, which is the H_e in a population that is assumed to be in HWE using GENEPOP, version 4.2 (Rousset, 2008). Just how far the population deviates from Hardy-Weinberg is an indication of the intensity of external factors, and was determined by chi-square analysis using the exact test for POPGENE software, version 1.31. (Yeh *et al*., 1999). The genetic relationship between populations was measured by determining the genetic distance between populations. Nei's standard genetic distance (D_{ST}) (Nei, 1972) whose value is proportional to evolutionary time was calculated using GENEPOP, version 4.2 (Rousset, 2008). A dendogram was constructed from Nei's standard genetic distance (D_{ST}) using Nei's genetic distance method implemented in the POPTREE software package (Takezaki *et al*., 2000). Bootstrap values were calculated from 100 000 replications of re-sampling loci (Ota, 1993). The probability of individuals correctly assigned into populations was computed using the Geneclass software package (Cornuet *et al*., 1999). Structure analyses were performed to determine level of sub-structure among the population with STRUCTURE (Pritchard *et al*., 2000) based on admixture unlinked loci model set at 200 000 burn-in followed by 1 000 000 MCMC repetitions K= 2 through to 8, for all the goat samples.

RESULTS

The number of alleles and allele size as well as global PIC for each of the twenty-nine microsatellite loci in the goat populations is presented in **table I**. The mean numbers of alleles per locus were 7.97, 8.79, 8.21, 6.69 and 6.88 in Maradi, West Africa Dwarf, Sahel, Kalahari, and Saanen, respectively. Breed-specific differences in genetic constitution are found at all the loci used in this study, where some alleles at those loci are not present in Sahel, Maradi, West African Dwarf, or Saanen. Global PIC values in most microsatellite loci genotyped are very high **(table I)** revealing acceptable informative capacity. The H_o values ranged from 59 % for West African Dwarf to 64.9 % for the Saanen population **(table II)**. Highest H_e estimates were observed in West African Dwarf population (70 %). Whereas, lowest H_e (66.5 %) was observed in Saanen population. The values of H_e obtained for these populations showed that the goat populations used in this study were highly diverse at the analysed loci. The Mean F_{is} values for the studied populations ranged from 0.055 to 0.148 for Kalahari and West Africa Dwarf, respectively (Weir and Cockarham approach) **(table II)**.

Table I. Allele range, number of alleles and PIC in the five goat breeds analyzed (Rango alélico, número de alelos y PIC en las cinco razas caprinas analizadas).

Locus	AR (bp)	NA	M	WAD	S	K	S	PIC
BM1329	155-185	11	6	6	6	6	7	0.73
BM 6506	200-224	12	8	8	10	7	6	0.65
BM 8125	108-126	10	8	9	7	7	6	0.81
BM1818	252-272	11	10	8	10	8	6	0.80
CSRD247	218-246	11	7	8	11	6	7	0.82
HSC	166-308	20	13	14	13	12	11	0.88
MM12	86-126	19	10	14	13	8	10	0.85
OarFCB48	141-169	12	10	7	9	6	8	0.76
SRCRSP8	214-250	16	7	11	10	7	9	0.67
INRA 63	159-169	6	4	5	4	5	5	0.60
MAF209	105-109	3	3	3	3	3	2	0.51
HAUT 27	130-154	13	7	9	7	8	6	0.83
ILSTS 011	268-288	11	8	6	8	8	8	0.54
SPS115	244-262	7	4	4	6	2	3	0.30
TGLA 122	128-152	12	4	6	4	4	7	0.34
BM6526	155-189	18	12	13	14	12	11	0.83
CRSM60	75-91	9	8	7	7	7	7	0.74
CSSM66	181-259	35	15	15	12	10	13	0.77
McM527	152-176	12	6	10	5	6	7	0.83
FCB11	131-161	16	9	12	10	8	8	0.85
FCB304	133-173	21	12	16	14	7	10	0.83
MAF65	124-146	12	10	11	9	7	6	0.81
ETH 225	134-154	7	6	3	4	3	3	0.18
ETH10	205-219	7	6	4	4	4	4	0.59
INRA5	131-147	7	3	6	5	3	2	0.44
ILSTS19	146-160	8	5	6	7	6	0	0.45
SRCRSP5	163-187	13	11	9	8	8	0	0.78
SRCRSP23	81-117	17	11	14	10	7	0	0.83
SRCRSP24	143-175	13	8	11	8	9	0	0.67
MNA		18.45	7.97	8.79	8.21	6.69	6.88	0.68
SD		0.7	3.09	0.6	3.2	2.44	2.83	1.88

AR (bp)= Allele range (bp); NA= Number of alleles; M= Maradi; WAD= West African Dwarf; S= Sahel; K= Kalahari; S= Saanen; PIC= Polimorphic information content.

Table II. Mean ± SD of H_o, H_e and F_{is} of the goat breeds genotyped (Media ± SD de H_o, H_e y F_{is} de las razas caprinas genotipadas).

Population	H_o±SD	H_e±SD	F_{is}±SD
Maradi	0.618±0.013	0.675±0.034	0.064±0.21
WAD	0.590±0.012	0.700±0.035	0.148±0.21
Sahel	0.605±0.014	0.686±0.034	0.109±0.22
Saanen	0.649±0.016	0.665±0.043	0.162±0.40
Kalahari	0.630±0.013	0.674±0.025	0.055±0.15

Table III. Matrix of pairwise Dst genetic gistances between five goat breeds (Matriz de las distancias genéticas Dst en cinco razas caprinas).

	WAD	Sahel	Saanen	Kalahari
Maradi	0.111	0.025	0.344	0.288
WAD	—	0.047	0.346	0.269
Sahel	—	—	0.242	0.049
Saanen	—	—	—	0.386

Per pair estimator of genetic relationship between populations **(table III)** whose value is proportional to evolutionary time, revealed the least genetic relationship between Saanen and Kalahari (0.386) and closest genetic relationship between Maradi and Sahel (0.025). The phylogenetic tree **(figure 1)** supports the genetic distance estimates where Maradi and Sahel formed a separate cluster independent of West African Dwarf, indicative of a common origin between Sahel and Maradi goats with the Saanen and Kalahari relatively diverged from Nigerian goat populations. HWE test revealed eighteen, seventeen, thirteen, twenty-three, and twenty-one loci were in HWE ($p>0.05$) in Maradi, West Africa Dwarf, Sahel, Saanen, and Kalahari, respectively. A graphic representation of cluster structure analysis depicts the goat populations having descended from 3 major ancestral populations.

The global mean F_{is}, F_{it} and F_{st} are 0.077; 0.249 and 0.186 respectively **(table IV)**. All markers had positive values of F_{is}, showing a relatively high inbreeding coefficient, meaning that the populations are inbred at those loci except at CSRD247, SPS115, CRSM60 and INRA5 which has negative value and thus showing excess heterozygote (outbred populations at these loci). F_{ST} values of genetic differentiation ranged from 0.035 (MAF65) to 0.707 (ILSTS19).

Genetic sub-structuring

A graphic representation of cluster structure analysis is depicted in **figure 2** at K= 2-5 inferred ancestral populations where K= 3 is the optimum number of cluster as derived from structure harvester analysis (Earl and von Holdt, 2012). This indicates that the goat populations descended from 3 major ancestral populations. The clusters were basically formed by Maradi, West African Dwarf and Sahel (cluster 1), Kalahari (cluster 2), and Saanen (cluster 3). **Table V** shows proportion of membership of each of the five goat populations in each of the 3 inferred clusters. The table also reveals level of fixation index (F_{ST}) for the inferred clusters. Cluster 2 had the least F_{ST} (0.055) the highest F_{ST} was in cluster 3 (0.1783).

DISCUSSION

The results clearly demonstrated high level of genetic diversity in the populations across most of the loci studied. Estimated H_o, effective number of alleles and PIC were high with, number of alleles ranging

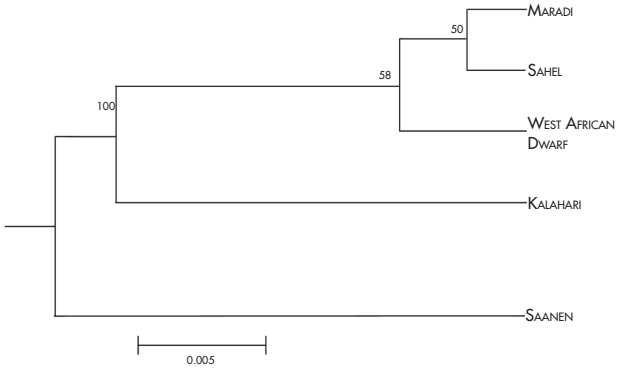

Figure 1. UPGMA Dendrogram of Dst genetic distances between five caprine breeds (Dendrograma UPGMA de las distancias genéticas Dst entre cinco razas caprinas).

Table IV. Global F_{is}, F_{it} and F_{st} values and gene flow for each locus over all breeds (Valores globales de F_{is}, F_{it} and F_{st} y flujo de genes para cada *locus* en todas las razas).

Locus	F_{is}	F_{it}	F_{st}	Nm
BM 1329	0.388	0.501	0.185	1.105
BM 6506	0.079	0.197	0.128	1.706
BM 8125	0.017	0.113	0.098	2.297
BM1818	0.025	0.134	0.117	1.989
CSRD247	-0.004	0.128	0.128	1.701
HSC	0.061	0.117	0.060	3.932
MM12	0.015	0.088	0.073	3.154
OarFCB48	0.008	0.088	0.080	2.862
SRCRSP8	0.062	0.205	0.152	1.395
INRA 63	0.104	0.160	0.062	3.785
MAF209	0.095	0.294	0.219	0.890
HAUT 27	0.052	0.191	0.147	1.455
ILSTS 01	0.069	0.172	0.111	2.008
SPS115	-0.071	-0.006	0.061	3.842
TGLA 122	0.047	0.204	0.164	1.273
BM6526	0.016	0.082	0.067	3.465
CRSM60	-0.021	0.061	0.080	2.885
CSSM66	0.370	0.446	0.121	1.814
McM527	0.058	0.223	0.175	1.177
FCB11	0.025	0.135	0.112	1.977
FCB304	0.135	0.229	0.109	2.054
MAF65	0.098	0.149	0.057	4.105
ETH 225	0.206	0.302	0.121	1.824
ETH10	0.029	0.063	0.035	6.815
INRA5	-0.090	0.256	0.318	0.537
ILSTS19	0.093	0.734	0.707	0.104
SRCRSP5	0.153	0.675	0.616	0.156
SRCRSP23	0.033	0.604	0.590	0.174
SRCRSP24	0.281	0.743	0.642	0.139
Mean	0.077	0.249	0.186	1.093

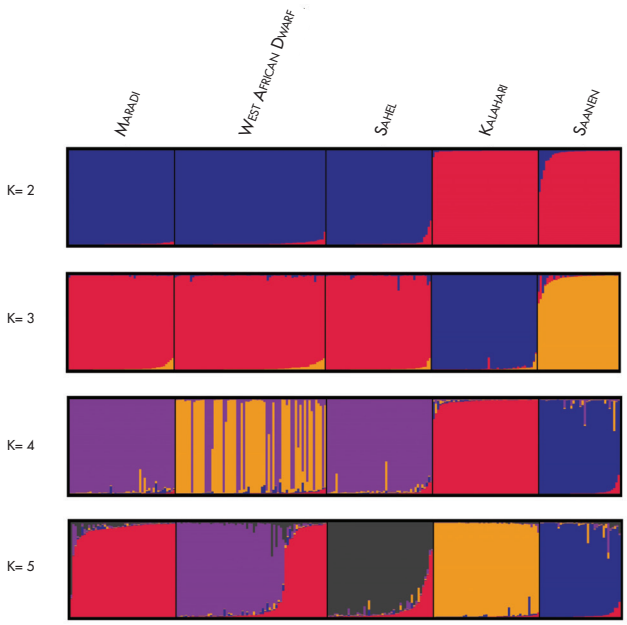

Figure 2. Estimated population structure for K= 2-5
(Estructura de la población estimada para K= 2-5).

Table V. Proportion of membership of each of the five goat populations in each of the 3 inferred clusters
(Proporción de miembros de cada una de las cinco poblaciones de cabra en cada uno de los 3 grupos inferidos).

	Cluster 1	Cluster 2	Cluster 3	N
Maradi	0.731	46.055	0.214	47
WAD	1.053	65.347	0.599	67
Sahel	0.549	45.814	0.641	47
Kalahari	0.537	0.371	46.096	47
Saanen	34.499	0.81	0.692	36
F_{ST}	0.1465	0.055	0.1783	—

from three to thirty-five, thus pointing to the suitability of the of the microsatellite markers in goat genetic diversity studies. In studies on genetic distance, Li *et al.* (2002) and Yang *et al.* (1999) suggested that microsatellite loci should have four or more alleles per locus to reduce the standard error of distance estimates. The range of number of alleles observed in the current study was higher than 2-14 reported by Garrine *et al.* (2010) for Mozambique goats and 2-19 reported by Saitbekova *et al*. (1999). This could either be implicated in the greater number of microsatellite markers utilized for this study, or greater diversity existing in the populations under consideration.

The expected heterozygousity (H_e) is an appropriate measure and good indicator of genetic variability within a population because genetic diversity can be measured as the amount of actual or potential heterozygousity. The H_e values per population were very close, ranging from 0.665 for the Saanen to 0.7 for the West African Dwarf. The observed and expected heterozygousities were higher than estimates (0.506 to 0.531) from earlier studies in Maradi, West African Dwarf and Borno white (Muema *et al.*, 2009) using different markers. The H_e value (0.674) recorded in this study for Kalahari was slightly higher than 0.63 reported by Kotze *et al*. (2004). The average observed heterozygousity was less than expected for all populations and this could be as a result of the following: segregation of non-amplified (null) alleles, selection against heterozygote or inbreeding. Similar results were reported by Barker *et al*. (2001) on indigenous South-East Asian goat populations. High value of average expected heterozygousity within the breed could be attributed to the large allele numbers detected at the tested loci (Kalinwski, 2002).

The genetic distance calculated according to Nei (1972) showed that the smallest genetic distance was between the Maradi and Sahel goats with a genetic distance of 0.025. Ngere *et al.* (1984) reported that population of the Maradi spread South and East from Sokoto through the savannah belts giving rise to the Kano Brown and, further east, to the Sahel types of Borno State, meaning that Sahel goat could be a strain of Maradi. Hence, a reason for the least genetic distance observed. The highest genetic distance was calculated between Saanen and Kalahari (0.386), which is indicative of least gene flow between the two populations. The genetic similarity observed among the populations could be attributed to migration among populations that might have a common origin and which have been selected mostly for morphological traits associated with the breed standard. Migration has a great effect on the reduction of genetic differentiation between populations (Laval *et al*., 2000).

The global inbreeding coefficients F_{IS} (0.077) and F_{IT} (0.249) observed in this study indicate a significant level of inbreeding and so it does probably encounter problems that results from inbreeding depression. This result may explain the lower H_o value than the H_e in each breed and the deviation from HWE which were detected in varying number of loci over all breeds. The results of genetic distance and structure analysis revealed 3 clusters associated with geographical locations viz European, south African and Nigerian goat populations. The West African Dwarf showed a separation from the other Nigerian goat populations at K= 4, indicating a sub-regional variation in the allelic composition of the populations. The West African Dwarf is adapted to the southern humid forest region of Nigeria, while Sahel and Maradi are adapted to dry, northern region of Nigeria. Some of the West African Dwarf goats carried alleles common in the other 2 goat populations which are indicative of interbreeding among the Nigerian goat breeds. This is expected due to free movement of the breeds within the country as northern herdsmen with Sahel and Maradi goats usually migrate southwards during the rainy season for better vegetation and more economic marketing of their stocks. In agreement with the working hypothesis, there was a clear and distinct separation of the Nigerian breeds from the South African and European breeds based on geographical locations.

CONCLUSION

The genetic diversity of the goat populations was high, as indicated by high mean number of alleles and expected heterozygousities recorded. The microsatel-

lite markers used in this study were quite informative for studying the genetic diversity of goats thus could be included in the formulation of effective conservation strategies and identification of quantitative trait loci for marker-assisted selection in goat genetic improvement. Inbreeding among the studied goat breeds occurred at varying levels: the highest in West African Dwarf and least in Kalahari population. The clusters were associated with the geographical region of the goat populations. The microsatellite makers used in this study suitable for molecular characterization of goat germplasm.

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