Animal Genetic Resources, 2016, 59, 47–54. © Food and Agriculture Organization of the United Nations, 2016
doi:10.1017/S2078633616000102

Mitochondrial DNA hypervariable region 1 diversity in Nigerian goats

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Summary
Goats make up the largest group of ruminant livestock in Nigeria and are strategic in bridging animal protein supply gap and improving the economy of rural households. The hypervariable region 1 (HVR1) of the caprine mitochondrial genome was investigated to better understand genetic diversity important for improving selection for animal breeding and conservation programs. We sequenced and analysed the mitochondrial DNA (mtDNA) HVR1 in 291 unrelated indigenous Nigerian goats (West African Dwarf (WAD), Red Sokoto (RSO) and Sahel (SAH)), randomly sampled from around the country, and compared them with the HVR1 sequences of 336 Indian goats and 12 other sequences in five different species in the genus *Capra* (*C. falconeri, C. ibex nubiana, C. aegagrus, C. cylindricornis* and *C. sibirica*). A total of 139 polymorphic sites from 291 individuals were captured in 204 haplotypes. Within and among population variations were 77.25 and 22.74 percent, respectively. Nigerian goats showed high genetic diversity (0.87) and high FST values, and separate from Indian goats and other wild species. Haplogroups in WAD separates it from RSO and SAH concomitant with a different demographic history. Clear genetic structure was found among Nigerian goat breeds with appreciable variation in mtDNA HVR1 region. This study grouped Nigerian goat breeds into two major groups suggesting two different demographic origins for Northern and Southern breeds. High genetic admixing denotes different maternal origins and in contrast to evidence from goats from Levant and Central Asia, where goats were originally domesticated.

Keywords: *genetic diversity, goats, hypervariable region, mitochondrial DNA, Nigeria*

Résumé
Les caprins constituent le plus grand groupe de ruminants domestiques au Nigéria et jouent un rôle stratégique dans l'approvisionnement en protéines animales et dans l'amélioration de l'économie des ménages ruraux. Une recherche a été menée à propos de la région hypervariable 1 (HVR1) du génome mitochondrial caprin dans le but de mieux comprendre l'importance de la diversité génétique pour améliorer la sélection dans les programmes d'amélioration génétique et de conservation des animaux. La région hypervariable 1 de l'ADN mitochondrial (HVR1) a été séquencée et analysée chez 291 chèvres indigènes du Nigéria, sans rapport entre elles (Naine d'Afrique Occidentale (NAO), Rouge de Sokoto (RS) et Sahel (S)), échantillonnées de manière aléatoire à travers le pays et comparées avec les séquences HVR1 de 336 chèvres indiennes et avec 12 autres séquences de 5 espèces différentes du genre *Capra* (*C. falconeri, C. ibex nubiana, C. aegagrus, C. cylindricornis* et *C. sibirica*). Un total de 139 sites polymorphes de 291 individus a été rassemblé en 204 haplotypes. La variation intra- et inter-populationnelle a été de 77,25 pour cent et de 22,74 pour cent, respectivement. Les caprins nigérians ont montré une grande diversité génétique (0,87) et des valeurs de FST élevées et différentes de celles des chèvres indiennes et de celles des autres espèces sauvages. D'après les haplogroupes, la chèvre NAO serait à séparer des populations concomitantes de RS et S avec une histoire démographique différente. Une structure génétique claire a été décelée entre les races caprines du Nigéria, avec une variation substantielle dans la région HVR1 de l'ADN mitochondrial. Cette étude a regroupé les races caprines nigérianes en deux groupes principaux, ce qui suggère deux origines démographiques différentes pour les races du Nord et du Sud. Le fort degré de mélange génétique dénote des origines maternelles différentes, contrairement à ce qui a été observé chez les chèvres du Levant et d'Asie Centrale, où les caprins furent d'abord domestiqués.

Mots-clés: *diversité génétique, caprins, région hypervariable, ADN mitochondrial, Nigéria*

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https://doi.org/10.1017/S2078633616000102 Published online by Cambridge University Press

Resumen
Las cabras constituyen el mayor grupo de ganado rumiante en Nigeria y desempeñan un papel estratégico en el aporte de proteína animal y en la mejora de la economía de los hogares rurales. Se investigó acerca de la región hipervariable 1 (HVR1) del genoma mitocondrial caprino con el fin de comprender mejor la importancia de la diversidad genética para mejorar la selección en los programas de mejora y conservación animal. Se secuenció y se analizó la región hipervariable 1 del ADN mitocondrial (HVR1) en 291 cabras autóctonas de Nigeria no relacionadas (Enana de África Occidental (EAO), Roja de Sokoto (RS) y Sahel (S)), seleccionadas aleatoriamente a lo largo del país y comparadas con las secuencias HVR1 de 336 cabras indias y con otras 12 secuencias de 5 especies diferentes del género *Capra* (*C. falconeri, C. ibex nubiana, C. aegagrus, C. cylindricornis* y *C. sibirica*). Un total de 139 sitios polimórficos de 291 individuos se concentraron en 204 haplotipos. La variación intra- e interpoblacional fue de 77,25 por ciento y de 22,74 por ciento, respectivamente. Las cabras nigerianas mostraron una elevada diversidad genética (0,87) y unos valores de FST elevados, distintos de los de las cabras indias y de los de las otras especies salvajes. De acuerdo con los haplogrupos, la cabra EAO se desliga de poblaciones concomitantes de RS y S con una historia demográfica diferente. Se identificó una estructura genética clara entre las razas caprinas de Nigeria, con una variación apreciable en la región HVR1 del ADN mitocondrial. Este estudio agrupó las razas caprinas nigerianas en dos grupos principales, sugiriendo así dos orígenes demográficos distintos para las razas septentrionales y meridionales. El alto grado de mezcla genética denota orígenes maternos distintos, a diferencia de lo observado en cabras del Levante y Asia Central, donde se domesticaron originalmente las cabras.

Palabras clave: *diversidad genética, cabras, región hipervariable, ADN mitocondrial, Nigeria*

Submitted 25 October 2015; accepted 17 May 2016

Introduction

The domestic goat, *Capra hircus* L., also known as "poor man's cow" is an important livestock species that contributes to the economy of many developing countries through the production of meat, milk, fiber, and skin (MacHugh and Bradley, 2001; Abdul-Aziz, 2010; Rout *et al.*, 2012). In Nigeria, goats play diverse roles in the economy, culture and religion of the people, with wide distribution across all agro-ecological zones of the country from the coastal South to the Arid North (Okpeku *et al.*, 2011a, 2011b). Goats are the largest group of ruminant livestock in Nigeria totalling about 55.8 million (FAOSTAT, 2013), with various surveys showing that up to 85 percent of rural households, poor farmers, small business owners of both sexes and all age groups raise them (Bayer, 1986). Nigerian goats are able to tolerate harsh climates, thrive on poor-quality diets provided by scarce grazing on marginal lands (Okpeku *et al.*, 2011a, 2011b), and the presence of trypanotolerance in some breeds (Abdul-Aziz, 2010) are advantages for their production and management. Moreover, their small size, low maintenance requirements and short generation interval (Okpeku *et al*., 2011b) underscores their importance for increasing production efficiency in rural agricultural systems verses other livestock species (Amills *et al.*, 2009; Rout *et al.*, 2012).

Recent archaeological and molecular biological studies suggested that goats originated in West Asia. However, very little is known of the processes leading to their domestication such as the timing of population expansion and the dynamics of their selection pressures (Nomura *et al.*, 2013).

The hypervariable region I (HVR1) of mitochondrial DNA (mtDNA) contains highly informative polymorphic sites due to its: (1) simple maternal inheritance without recombination, (2) relatively rapid evolution rate; endpoints useful for diversity studies in many organisms and species (Brown *et al.*, 1986; Bradley *et al.*, 1996; Luikart *et al.*, 2001; Amills *et al.*, 2009; Zhong *et al.*, 2013; Akis *et al.*, 2014; Zhao *et al.*, 2014). The mtDNA polymorphisms have been largely applied not only to better understand phylogenetic relationships in many animal species, including cattle (Bradley *et al.*, 1996; Mannen, Nagata and Tsuji, 2001; Troy *et al.*, 2001; Kim *et al.*, 2010; Taberlet *et al.*, 2011), chickens (Niu *et al.*, 2002; Liu *et al.*, 2006), horses (Vilà *et al.*, 2001; Lira *et al.*, 2010) and goats (Mannen, Nagata and Tsuji, 2001; Sultana, Mannen and Tsuji, 2003; Chen *et al.*, 2005; Pereira *et al.*, 2005; Naderi *et al.*, 2007; Okpeku *et al.*, 2011a, 2011b; Zhong *et al.*, 2013; Akis *et al.*, 2014; Zhao *et al.*, 2014), but also to understand maternal origin and migration of livestock. Based on the phylogenetic analyses of caprine mtDNA polymorphisms, at least four mtDNA lineages (A–D) have been discovered, with the lineage A group being the most diverse and widely distributed in comparison with other lineages (Luikart *et al.*, 2001; Sultana, Mannen and Tsuji, 2003; Chen *et al.*, 2005; Akis *et al.*, 2014). Luikart *et al.* (2001) assessed the phylogenetic history and matrilineal population structure of 406 domestic goats representing 88 breeds across the world and identified three highly divergent lineages A–C. More recently, Naderi *et al.* (2007) analysed 2 430 domestic goat samples from all over the old world and identified three additional lineages (A–G).

Although a few studies examining the nuclear microsatellite DNA of Nigerian goats have been reported (Adebambo, 2003; Muema *et al.*, 2009; Okpeku *et al.*, 2011a, 2011b), there is no published report on mtDNA diversity in Nigerian goats. Therefore, we have investigated

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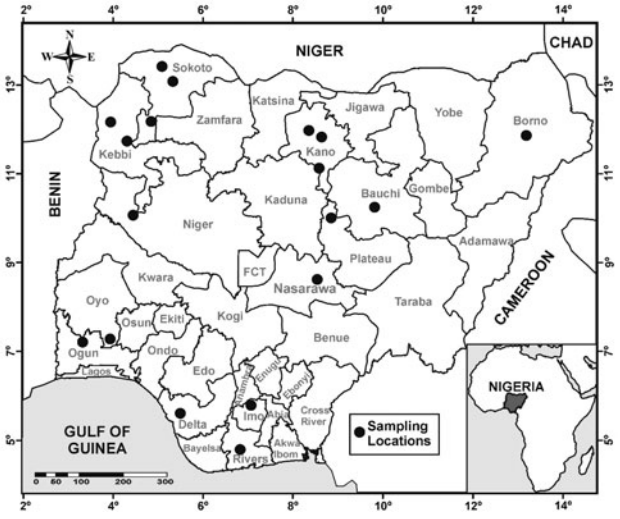


Figure 1. Map of Nigeria showing sampled locations.

the HVR1 of the caprine mitochondrial genome in three major Nigerian goat breeds sequences along with archived sequences from Africa and Asia available on NCBI to gain a better understanding of matrilineal origin of Nigerian goats, gain insight into demographic distribution and understanding goat domestication and adaptation. This will be important in facilitating the development of new approaches to improve selection and mating systems for animal breeding and conservation programmes.

Materials and methods

Sample collection and DNA isolation

Whole blood was collected from 291 unrelated goats belonging to three major goat breeds [140 Red Sokoto (RSO); 53 Sahel (SAH) and 97 West African Dwarf (WAD)]. Samples were collected from 19 different locations covering the five agro-ecological zones in the country (Figure 1). Efforts were made to collect samples from unrelated goats, based on the pedigree information provided by owners. Blood samples were collected by jugular venipuncture and DNA was isolated using ZymoBead™ Genomic DNA kit (Zymo Research Corporation, Irvine, CA, USA) following the manufacturer's instructions. Quantification of DNA yield and assessment of quality were done using a Nanodrop; ND-100 UV/Vis Spectrophotometer (Nanodrop Technologies, Inc., Wilmington, DE, USA).

PCR amplification and DNA sequencing

To amplify the HVRI of goat mtDNA, a pair of primers was designed using the known goat mtDNA sequence (AB044304, FAOSTAT, 2013) in the GENETOOL package and synthesized in an ABI 392 Oligosynthesizer (Perkin Elmer, Foster City, CA). Primer sequences were as follows: forward 5′-CATCCATATAACGCGGACAT-3′ and reverse 5′-GTGTGAGCATGGGCTGATTA-3′. PCR amplification was carried out in a 10 µl reaction volume containing 5 ng of DNA, 10 pM of each primer, 200 pM of dNTPs, 1× PCR buffer containing 2 mM $MgCl_2$, and 2 U of AmpliTaq Gold (Perkin Elmer, Foster City, CA). Amplification was performed in a Veriti thermal cycler (Applied Biosystems, Carlsbad, CA) employing the following conditions: 94 °C for 5 min; 35 cycles at 94 °C for 30 s, 54 °C for 45 s and 72 °C for 2 min; and final extension at 72 °C for 5 min. The amplicons were sequenced using BigDye™ (Applied Biosystems, Foster City) Terminator cycle sequencing kit in ABI Prism 3730 DNA Analyser (Applied Biosystems, Foster City) following manufacturer's protocol.

Data analysis

Five hundred and thirty three (503) base pairs from the mtDNA HVRI region of 291 goats of three Nigerian breeds, 366 sequences from 11 breeds of Indian goats, one breed each from Kenya, China and Korea and a sequences from Sheep (*Ovis aries*) was used as an outgroup (downloaded from NCBI; accession numbers AY155674 to AY156039, KJ420485, KJ420476, KJ420443, KJ420458, KJ420481, KJ420480.1 KJ420474, EU126792, AY853293, KP164694, KP164705, DQ188864, GQ141240, DQ188851, DQ121618, KP120664, KP120665, KP120646, KP120646, KP120622, EF490471 and AJ317864 to AJ31787 respectively), were aligned using ClustalW software package (Thompson, Higgins and Gibson, 1994). The MEGA 6.0 (Tamura *et al*., 2013) and DNASP software package version 5.10.01 (Librado and Rozas, 2009) were used for formatting the sequences to make them compatible with the desired software. Median joining networks (Bandelt, Forster and Rohl, 1999) were drawn using the Network 3.1.1.1 software (http://www.fluxus-engineering.com). Haplotype diversity, SE, Fu's Fs statistics (Fu, 1997), mismatch analysis (Schneider *et al.*, 1999), analysis of molecular variance (AMOVA), mean number of pairwise differences and population pairwise F_{ST} values were computed using ARLEQUIN version 2.001 (http://anthropologie.unige/arlequin) (Excoffier, Smouse and Quattiro, 1992). F_{ST} values were calculated using 1 000 bootstraps. These F_{ST} values were used to reconstruct an NJ/UPGMA tree in comparison with Indian and wild goat breeds using the MEGA package version 6.0 (Tamura *et al*., 2013). DnaSP program, version 5.10.01 (Librado and Rozas, 2009) was used for estimating haplotype and nucleotide diversity.

Results

mtDNA HVR1 variation in Nigerian goats

The sequences from the study have been deposited in GenBank and published with accession numbers KM582169–KM582416. Analysis of mitochondrial HVR1 sequences in Nigerian goats revealed 204 different

https://doi.org/10.1017/S2078633616000102 Published online by Cambridge University Press

Table 1. Genetic diversity parameters for HVRI sequences of the Nigerian goat breeds.

	Diversity parameters										
Breed	**NS**	***H***	H_d	***K***	π	π_s	π_a	***S***	**SP**	**PIP**	**d*N*/d*S***
Wd	98	58	0.982	6.203	0.0259	0.0237	0.2708	76	42	34	1.0112
So	140	24	0.465	0.764	0.0070	0.0059	0.0078	23	9	14	1.3220
Sh	53	40	0.985	7.143	0.0204	0.0386	0.0154	56	27	29	0.3989
All sequences	291	7	0.245	0.270	0.0079	0.0158	0.0073	6	0	6	2.6524

NS, number of sequences; *H*, number of haplotypes; H_d, haplotype diversity; *K*, average number of nucleotide differences; π, nucleotide diversity π_s, synonymous nucleotide diversity; π_a, non-synonymous nucleotide diversity; *S*, number of polymorphic sites; SP, singleton variable sites; PIP, parsimony informative sites; d*N*/d*S*, Tajima ratio of non-synonymous to synonymous nucleotide diversity.

haplotypes. In addition to base substitutions and deletions, a 75 base insertion was observed in one individual belonging to WAD breed. The number of haplotypes found in each breed ranged from 24 in RS to 58 in WAD. Haplotype diversity values for the breeds were 0.465, 0.985 and 0.982 for RSO, SAH and WAD, respectively (Table 1). Transition–transversion ratios were found to be 1.6:1, 2:1 and 3.5:1 for RSO, SAH and WAD, respectively, while the total calculated for the study was 7.1:1. Median joining networks (Figure 2) were constructed based on the data obtained from transition and transversion ratios using the Network for phylogeny software. The network indicated considerable diversity, with the central node having the highest haplotype frequency of 105 made up of 3.81 percent SAH goats, 5.71 percent RS and 90.48 percent WAD. Of interest, other nodes in the network also contained more than one haplotype group.

Genetic diversity and population expansion

For comparison, a neighbour-joining (NJ) tree (Figure 3) was constructed using MEGA 6.0 (Tamura *et al.*, 2013), with Nigerian goat sequences, 363 Indian goat sequences and ten sequences from wild goats. All Nigerian goats clustered together at the top of the NJ tree and were followed by a cluster of Indian domestic goats. The wild goat types used as an out-group diverged from Indian

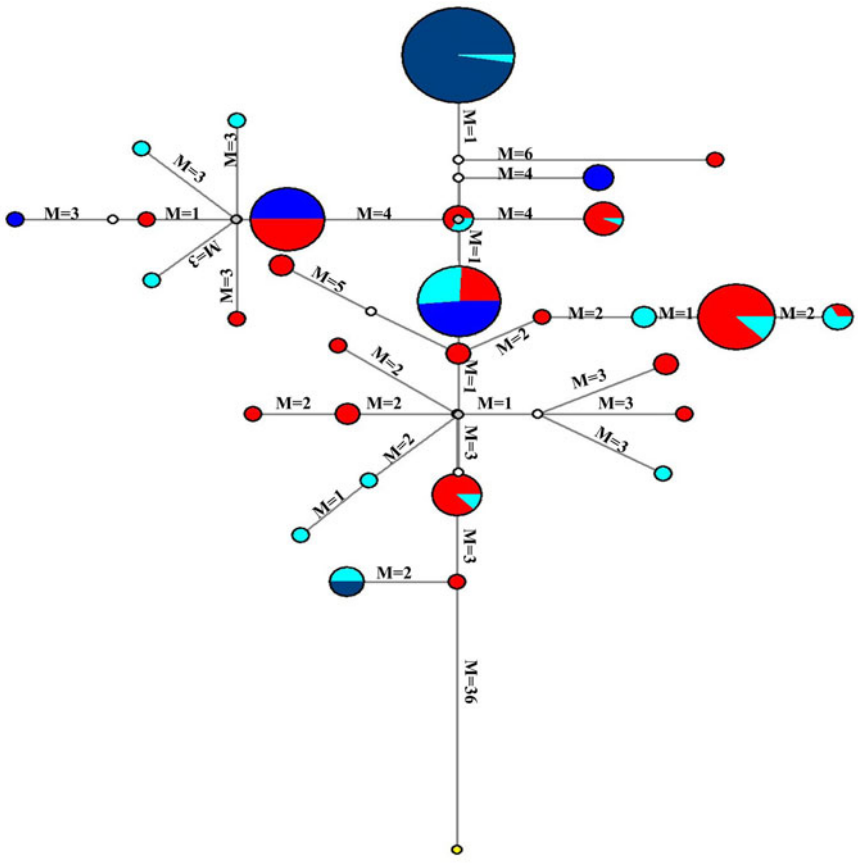


Figure 2. Median joining network of goat mtDNA distribution among Nigerian goat breeds with sheep mtDNA as an out group. Circles represent haplotypes and have a size proportional to frequency. Mutational differences are shown on lines. Colour Legend: Red Sokoto = Red, West African Dwarf (WAD) = Deep Blue, Sahel = Sky Blue, sheep = Yellow.

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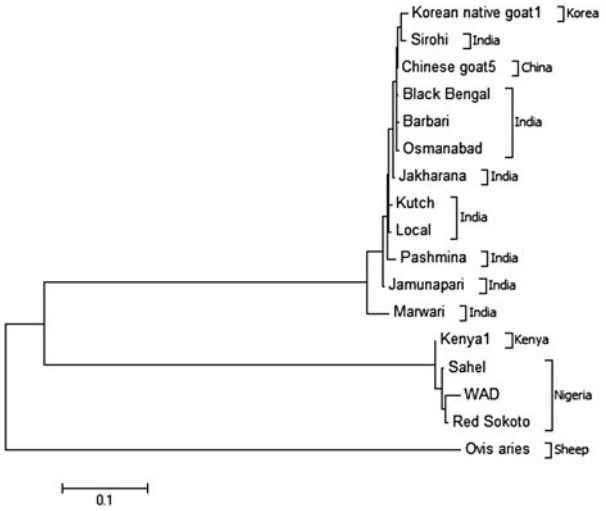


Figure 3. NJ tree of Nigerian, Indian and wild goat breeds compared with wild goat mtDNA sequences.

Table 2. Result of AMOVA among Nigerian goat breeds base on mtDNA HVR1 sequence.

Source of variation	Variance components	Percentage variation
Among breeds	1.346	22.749
Within breeds	4.573	77.251
Total	5.920	

goats as expected. However, clear differences were observed within the domestic goats of India and the Nigerian goat populations. In the Nigerian goat populations, WAD clearly separated from RSO and SAH goats. Further, genetic analysis based on AMOVA (Table 2) demonstrated that the largest genetic variation (77.25 percent) in all of these goat breeds is accounted for by within-group variation, while among-group variation accounted for approximately a quarter (22.75 percent) of the total genetic variation. Genetic distances between breeds were calculated taking into account the molecular distances between haplotypes, and the resulting F_{ST} values were positively correlated (Figure 3). Mismatch distributions (Figure 4) showed smooth and predominantly unimodal curves but not for WAD (Figure 4, No. 3). This breed appeared to have had a different demographic history from the other two studied breeds.

The results of DnaSP analysis indicated that the selected region (1–620) of the 291 sequences from the three Nigerian goat breeds have sites excluding sequences with gaps (35). The number of polymorphic sites, singleton variable sites and parsimony informative sites for individual breed sequences are higher than those for the entire sequences. SAH goat sequences had the highest value of haplotype diversity and average number of nucleotide difference (0.982 and 6.203), respectively followed by WAD goats. WAD had highest haplotype number (58) and nucleotide diversity (0.259) followed by SAH (40 and 0.204), respectively. Synonymous nucleotide diversity is less than non-synonymous nucleotide diversity in WAD and RSO goats (Table 1). The ratio of d*N*/d*S* was greater than 1.0 in WAD and RSO goats while less than 1.0 in SAH goats. The pictures of the three breeds of Nigerian goats used in this study are presented in Figure 5.

Discussion

The present work is the first substantial diversity study of Nigerian goats based on mtDNA HVR1 sequences. Nigerian goat mtDNA sequences showed some degree of diversity in the HVR1 region. The total number of haplotypes generated in this study for Nigerian goats was similar to the results reported in the literature, which supports a high degree of diversity in goat populations (Joshi *et al.*, 2004; Çinarkul and Ertugrul, 2011; Zhong *et al.*, 2013; Akis *et al.*, 2014; Zhao *et al.*, 2014). In Indian goats, Joshi *et al.* (2004) reported 200 haplotypes in 363 sequences from ten populations. Çinarkul and Ertugrul

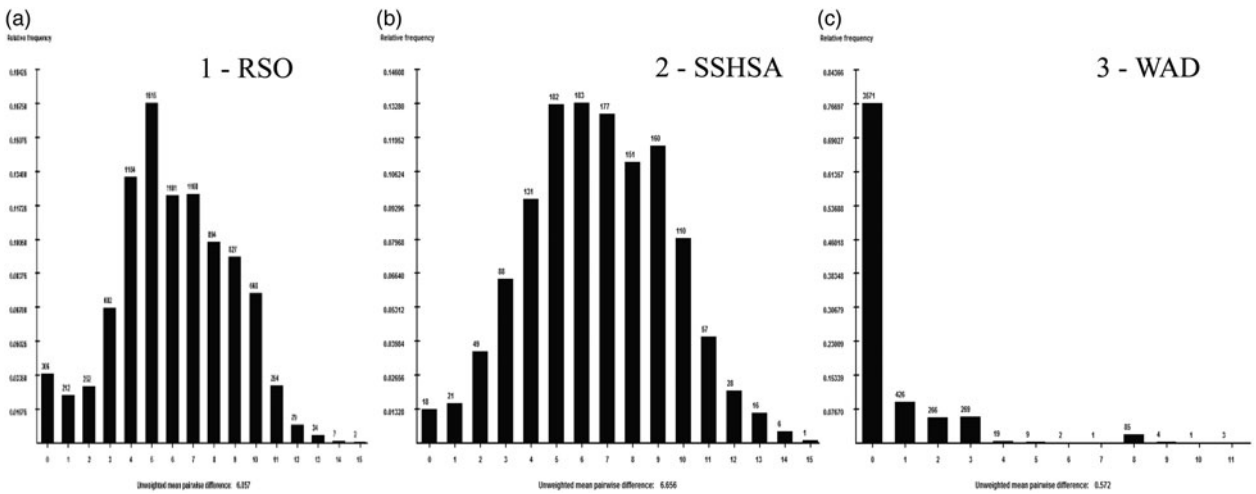


Figure 4. Mismatch distributions for mtDNA types of Nigerian goat breeds. (a) Red Sokoto, (b) Sahel, (c) WAD.

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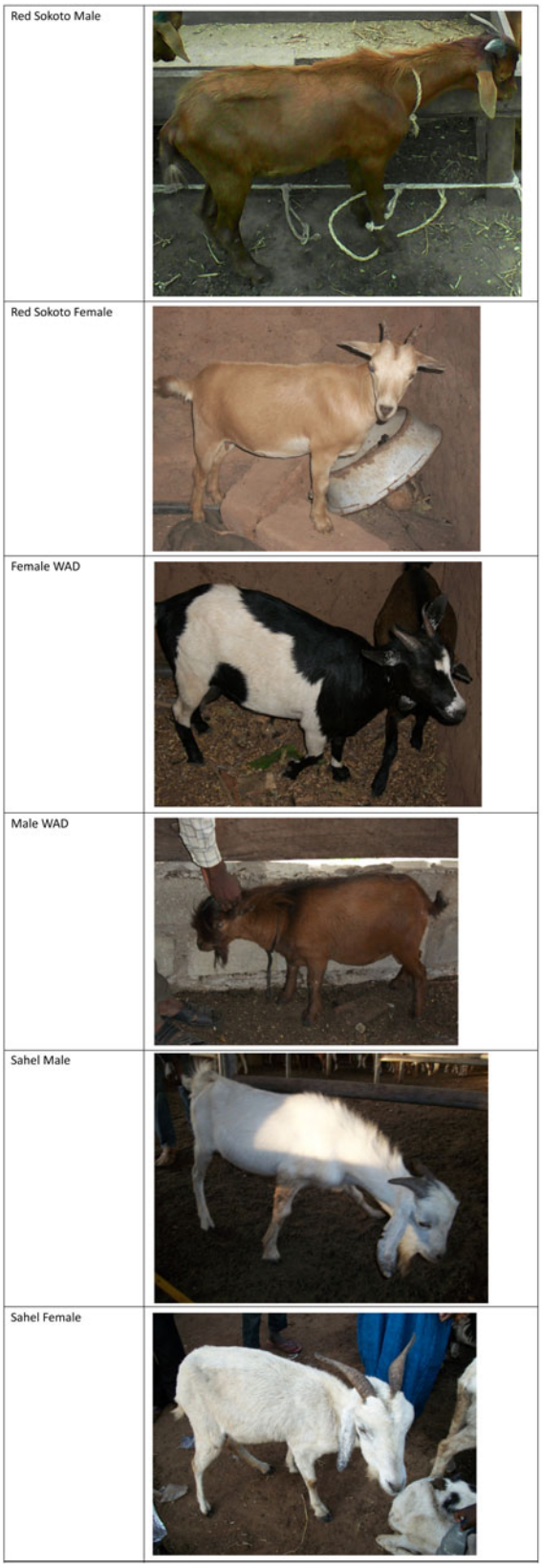


Figure 5. Pictures of the three breeds of Nigerian goats.

(2011) reported 208 haplotypes in Turkish goat populations. These results also compare well with a recent study in Chinese goats, which observed a total of 192 haplotypes with 141 variable sites with haplotype and nucleotide diversities based on 481-bp segment of the mtDNA D-loop region, indicating a relatively high genetic diversity in Chinese black goats (Zhong *et al.*, 2013). Median joining network constructed from transition and transversion data revealed considerable diversity and interrelatedness among the different Nigerian goat's breeds in the present study. Okpeku *et al.* (2011a, 2011b) working with microsatellites reported interrelatedness in Nigerian goat breeds, which could be attributed to uncontrolled breeding among different breeds and a subsequent reduction in heterozygosity. This heterozygote deficiency have been reported to arise due to population sub-structure from pooling together different populations resulting in genetic admixture (Cerda-Flores *et al.*, 2002; Muema *et al.*, 2009; Rout *et al.*, 2012), overlapping generations, mixing of populations from different geographical locations and natural selection favouring heterozygotes or subdivision accompanied by genetic drift (Agha *et al.*, 2008). Similar results of high genetic diversity resulting from average expected heterozygosity (0.671 across loci, 10.7 alleles per locus) in Iranian goats accounting for the within-breed component (G_{ST} = 5.9 percent) have recently been reported using microsatellite DNA markers (Vahidi *et al.*, 2014). In addition, positive and highly significant F_{IS} values in the Naini, Turki-Ghashghaei, Abadeh and Markhoz breeds indicate some level of inbreeding in these populations (Vahidi *et al.*, 2014). Some studies indicate poor genetic diversity and low differentiation in Chinese domestic goat breeds (Li *et al.*, 1997; Jia *et al.*, 1999; Li and Valentini, 2004) in contrast to Nigerian goats.

Our results contrast somewhat with a recent study of HVR1 in Anatolian goats using 295 individuals that observed high genetic diversity values and a weak phylogeographical structure (Akis *et al.*, 2014), although it is consistent with overall findings of (Luikart *et al.*, 2001; Naderi *et al.*, 2007). Recent re-analysis of a consensus fragment of 481 bp in the D-loop region from 339 individuals of indigenous Chinese goat mtDNA showed high diversity but poor geographic specificity (Zhao *et al.*, 2014), although the network and NJ tree revealed three divergent maternal haplogroups (A, B1 and B2) in 17 local breeds captured in 198 different haplotypes. The discrepancies between published reports can be partially explained to differences in methodologies the investigators used in those aforementioned reports (Liu *et al.*, 2006). The NJ tree placed Nigerian goats into two distinct breeds or groups; the Northern (SAH and RSO) and Southern (WAD). Generally, similar classifications based on microsatellite markers obtained in earlier studies (Okpeku *et al.*, 2011a, 2011b) support our findings.

Within group variation was far higher and accounted for 77.25 percent of the genetic diversity observed in this study. High genetic diversity observed within breeds from mtDNA analysis can be attributed to maternal effect of multiple ancestors (Naderi *et al.*, 2007; Rout *et al.*, 2012; Akis *et al.*, 2014). In an analysis involving 2 430 individuals from all over the world, Naderi *et al.* (2007)

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also reported that 77 percent of mtDNA variation is distributed within breeds. Similarly, in Indian goats, 83 percent of the total molecular variance was observed in the within-breed component (Joshi *et al.*, 2004), and more than 75 percent of the variations in Anatolian goats have been found between haplotypes. The higher within-breed variation observed has favoured genetic exchange, as goats are portable food resources that often accompany humans through migratory movements and trade routes (Azor *et al.*, 2005; Amills *et al.*, 2009; Liu *et al.*, 2009).

Mismatch distributions (pairwise comparisons) of mtDNA have also been widely used to explore demography (Rogers and Harpending, 1992). In the present study, mismatch analysis was done to evaluate population expansion among the different breeds, vital for predicting breeds with more population growth potentials. Populations with a constant size usually demonstrate ragged multimodal distribution, whereas a smooth, unimodal distribution is observed in expanding populations. The match of a real data set to these models can be assessed by the "raggedness" (Joshi *et al.*, 2004). In this study, the WAD goat breed showed a higher raggedness in this regard while the Northern breeds showed more uniform curves. These differences suggest a greater population expansion in the Northern population (SAH and RSO) than in the South (WAD). This suggests that the Northern goat breeds may have demographic origins different from WAD. However, distinctive demarcation of the breeds could also be attributed to the high genetic diversity of mtDNA HVR1 sequences. High polymorphic sites, singleton variable sites and nucleotide diversity were found in WAD, indicating that WAD exhibited the highest genetic diversity potentially more useful for selection. The higher genetic diversity of HVR1 in WAD may be related to its extensive adaptability and survival across the Southern Nigeria. In terms of nucleotide and haplotype diversities, SAH and WAD showed high values compared with other goat breeds worldwide (Luikart *et al.*, 2001; Pereira *et al.*, 2005; Naderi *et al.*, 2007). Higher non-synonymous nucleotide diversity relative to synonymous nucleotide diversity in WAD and RSO may be due to direct selection and a ratio of d*N*/d*S* greater than 1 suggests that variation at the mtDNA HVR1 is under positive selection (Kryazhimskiy and Plotkin, 2008).

In conclusion, a clear genetic structure was found among Nigerian goat breeds with appreciable variation in mtDNA HVR1 region. This study grouped Nigerian goat breeds into two major groups with higher within-breed variation than variation among breeds. Results suggest two different demographic origins for northern and southern breeds within goat populations in Nigerian. The present study suggests a high degree of genetic admixing among Nigerian goats arising from possibly different maternal origins, which is in contrast to evidence from goats in the Levant and Central Asia, where goats where originally domesticated.

Acknowledgements

We thank the International Foundation for Science (IFS), Stockholm, Sweden and the Indian Government through the Indian National Science Academy Junior Research Development Tata fellowship for financial support to Moses Okpeku. Additional support from the College of Agriculture and Life Sciences, Cornell University, Ithaca, NY is gratefully acknowledged.

Statement of interest

The authors declare that we do not have any conflicting interest during and after this research.

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