Genetic Diversity and Population Structure of the Indigenous Sheep in Kenya Based on Microsatellite Analysis: Implications for their Conservation

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ABSTRACT
Knowledge of the genetic relationship and admixture among neighbouring livestock populations is crucial for conservation efforts. This study analyzed the molecular diversity of fifteen sheep populations (both indigenous and exotic) in Kenya. Blood samples from 582 individuals were genotyped across the 15 microsatellite markers. The expected heterozygosity and Mean number of alleles ranged from 0.596 to 0.807 and 6.67 to 9.33 respectively. Most populations showed significant heterozygote deficiency due to a moderately high level of inbreeding, f_{IS} (0.109). Population genetic differentiation was reasonably high (θ_{ST} = 0.101). Four population clusters majorly based on geographical proximity and interbreeding among populations were detected. These results indicate levels of admixture warranting institution of conservation measures. However, a more encompassing study including all regions in the country as well as more microsatellite markers is necessary to comprehensively understand the dynamics of genetic introgression.

Keywords: Admixture; exotic breeds; gene flow; Sustainable breeding programs

INTRODUCTION

Indigenous and locally developed sheep breeds are an important asset due to the unique combinations of adaptive traits they have developed and thus can respond effectively to the pressures of the local environment (Buduram, 2004). Such adaptive traits include tolerance to various diseases, fluctuations in feed quality, extreme climatic conditions and the ability to survive and reproduce for long periods of time (Hammond, 2000).

African sheep are described as thin-tailed, fat-tailed or fat-rumped (Mason & Maule, 1960) with thin-tailed further segregated into hairy or woolled types (Epstein, 1971). The Eastern African sheep are classified as either fat-tailed or fat-rumped (Rege *et al*., 1996). More production units, mainly pastoralists, in African farming systems own goats and sheep than any other species of domestic livestock except poultry, this is because of their lower feed requirements, rapid reproduction cycles and the ease with which they can be handled, thus they are particularly important for resource-poor households and often are the property of underprivileged groups, such as women and children (Devendra, 2002).

In Kenya, small ruminants are kept both for tangible benefits, such as cash income from animal, milk and meat sales and for home consumption, and intangible benefits including savings, an insurance against emergencies, cultural and ceremonial purposes (Kosgey *et al.,* 2006a, b). Kosgey *et al*., (2006b), ranks regular cash income as the most important purpose of ovicaprids towards both smallholders and pastoral extensive farmers. In Kenya, sheep supply an estimated 15-20 percent of the red meat consumed in the country (Ministry of Livestock and Fisheries Development 2003). According to Gathuka (1986), arid and semi-arid land forms eighty five percent of Kenya's diverse ecological zones which is also home to most of the indigenous sheep genotypes. The indigenous fat-tailed sheep breeds found in Kenya include the Red Maasai and East African Somali Blackhead Persian which are found in virtually all parts of the country (Sheep and Goat Annual Report 2003).

It has become apparent over the past few decades though, that many of these indigenous breeds are at risk of extinction. This has been occasioned by; the advent of artificial insemination and improved transportation which have reduced the number of breeding rams, thus leading to a reduction in the effective population size (N_e) of many breeds. There is as well a change in focus to only a few highly yielding breeds, to the detriment of rare or minority breeds, which are likely to be important genetic resources because of their local adaptive traits (Mendelsohn, 2003). Minority breeds have also been lost by introgression into large commercial populations. Such loss of diversity in domestic species including sheep has far reaching economic, ecological and scientific as well as social implications. An understanding of the evolutionary history of domestic breeds and data on genetic variation within and among breeds is vital to these initiatives to provide critically important data for the decision-making process (Rege and Gibson 2003). Information on both within and among-breed diversity is important as the former provides information for management at the breed level whereas the latter helps identify divergent breeds that may harbour distinct genotypes hence worthy of conservation efforts even if their within-breed diversity is relatively high.

In the present study, a panel of 15 microsatellite markers was used to evaluate the partitioning of genetic diversity within and among a diverse sample of 582 individuals

obtained from 15 populations of domestic sheep. The extent of admixture and population structure among the sheep populations in relation to conservation and management was also examined.

MATERIALS AND METHODS

Sample collection and preparation

Blood samples were collected from 582 genetically unrelated individuals representing 15 populations (Table 1 and Figure 1). Dorper sheep were sampled from a research farm in Kapiti plains, Machakos, affiliated with the International Livestock Research Institute.

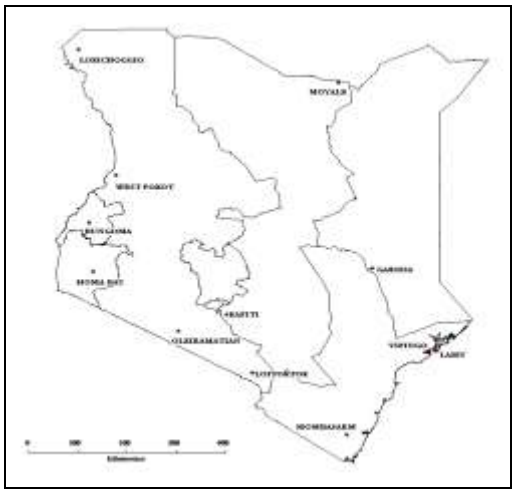

Figure 1. Geographic distribution of the sheep populations used in this study

Table 1: Sampling sites, Population acronyms (in brackets), GPS positions, Breed and number of sheep sampled

Site Name	Latitude	Longitude	Breed	No. of Ewes sampled	No. of Rams sampled
BUNGOMA(BGM)	+0.4592	+34.5163	East African fat-tailed	27	13
GARISSA(GAR)	-0.5458	+39.6831	Blackhead Somali	29	11
WEST POKOT(WP)	+1.4900	+35.0188	East African fat-tailed	31	10
VIPINGO(VIP)	-2.3239	+40.7267	Red Maasai	30	12
LAMU(LAM0	-2.2337	+40.9071	Blackhead Somali	30	10
LOKICHOGGIO(LOK)	+4.1829	+34.3231	Blackhead Somali	24	8
LOITOKTOK(LTK)	-2.5784	+36.9474	Red Maasai	31	12
MOYALE(MOY)	+3.5129	+39.0631	Blackhead Somali	32	11
KAPITI(KAP)	-1.5678	+36.9322	Red Maasai and Dorper	52	20
OKIRAMATIAN(OKM)	-1.8652	+36.1656	Red Maasai and Blackhead Somali	53	23
HOMABAY(HOM)	-0.5873	+34.5941	East African fat-tailed	29	11
SOMALI(SBH)	+7.5800	+47.4400	Blackhead Somali	30	10
MOMBASA(REMA)	- 4.1028	+39.2737	Red Maasai	24	9
Total				**422**	**160**

Total number of sheep sampled = 582

Microsatellite analysis and genotyping

Fifteen microsatellite markers used in this study were from the panel recommended by ISAG/FAO for sheep diversity studies (http://dad.fap.prg/). Forward primers were end-labeled with fluorescent dyes (6-FAM, VIC, PET or NED). PCR was carried out in a total volume of 10 µl system containing 1 µl of template DNA (20 ng/µl), 0.2 µl of each primer, 5 µl of ReddyMix™ PCR Master Mix (ABgene, UK) and 3.6 µl of double distilled water. The cycling conditions included an initial activation step at 95 °C for 5min, 30 cycles of 94 °C for 30 s, annealing at 50-65 °C for 30 s and extension at 72 °C for 30 s, and a final extension at 72 °C for 10 min. PCR was performed on a 9800 GeneAMP®PCR System (Applied Biosystems, USA). PCR products were genotyped using an ABI 3730 (Applied Biosystems, Warrington, UK) automated capillary DNA sequencer. GeneMapper® software (version 3.7, Applied Biosystems, USA), was used to perform allele calling using the third order least squares method for fragment sizing.

Statistical analyses

The exact test in GENEPOP package (Rice, 1989) was used to determine the deviations from Hardy-Weinberg equilibrium (HWE) in the populations studied. To assess within-population genetic diversity, mean number of alleles (MNA), observed (H_O) and expected heterozygosity (H_E, Nei's unbiased gene diversity) were calculated using the Microsatellite Toolkit (available at http://animalgenomics.ucd.ie/sdepark/ms-toolkit/). Allelic richness (r) was estimated using the FSTAT program version 2.9.3 (Goudet, 1995). The BOTTLENECK program (Cornuet and Luikart 1997) was used to test the allele frequency data for heterozygosity excess or deficiency.

Using the variance-based method of Weir and Cockerham (1984), F-statistics (F_{IS}, F_{IT} and F_{ST}) for calculating overall genetic differentiation among populations and between pairs of populations were performed and tested using FSTAT with 1000 permutations. Analysis of molecular variance (AMOVA) was computed using the GeneAlex 6.1 package (Peakall and Smouse 2006).

To detect the genetic relationships and population structure among the 15 sheep populations, three approaches were applied. Firstly, Nei's D_A genetic distances (Nei *et al.,* 1983) calculated by Microsatellite Analyzer (Dieringer and Schlötterer 2002) helped in the construction of the phylogenetic relationships of the sheep using PHYLIP package (Felsenstein 2004) and the consensus tree drawn by the SplitsTree program (Huson and Bryant 2006). Tree robustness was evaluated by bootstrapping over loci (1000 replicates). Independent Components Analysis (ICA) analysis was performed as an alternative approach to understanding the genetic relationship amongst the populations. Using the Bayesian clustering-model program STRUCTURE (Pritchard *et al.,* 2000; 2007), population structure and the degree of admixture were determined. The output from STRUCTURE was then sent to STRUCTURE HARVESTER (Earl, 2009) which helped in plotting the graph according to Evanno *et al.,* (2005) and Pritchard et al, (2000) for K estimation as well as assist in the preparation of the input files for CLUMPP (Jakobsson and Rosenberg 2007). The output from CLUMPP was then used an input for DISTRUCT (Rosenberg, 2004) a cluster visualization program.

RESULTS

173 alleles were found in the sheep populations studied across the 15 microsatellite loci. The mean number of alleles per population ranged from 6.67 (OKMRM) to 9.33 (KAPRM) (Table 2).

The various values obtained for heterozygosity and mean number of alleles are shown in Table 2. Majority of the loci had their expected heterozygosity values significantly higher than the observed heterozygosity indicating deviations from Hardy–Weinberg equilibrium. *ILSTS005* had the highest number of deviations (12) and *SRCRSP9* had the least deviations (3). The overall means of F_{IT}, θ_{ST} and f_{IS} obtained from jackknifing over loci were significantly different from zero (Table 3).

When all markers were considered, the highest chord distance (0.852) occurred between the Olkiramatian Red Maasai and the Kapiti Dorper populations with the least (0.143) between the Mombasa Red Maasai and the Loitoktok populations (Table 4).

Based on the consensus phylogenetic tree (Fig. 2) populations mainly clustered as per their geographical locations and population identity. The bootstrap support across the phylogenetic tree was low signifying the instability of the topology observed in the tree.
From the population structure analysis the true *K* value = 4 as shown in Figure 3.
Further genetic structure was revealed in each of the clusters obtained at *K*= 4 (Figure 3).

Independent Component Analysis clustered populations in a manner similar to both STRUCTURE and the phylogenetic tree (Figure 4). The first three components (IC1, IC2 and IC3) accounted for 0.3791, 0.3192 and 0.3017 of the total variation respectively.

The tests for heterozygosity excess and deficit under the two phase mutation model (TPM) at $p<0.001$, provided evidence for a recent genetic bottleneck in the Kapiti Dorper population (Table 5).

Table 2: Number of Animals Sampled, Mean heterozygosity, Mean number of Alleles and standard deviations for each of the fifteen populations studied

Population	Sample size	Loci typed	H_E	H_E SD	H_O	H_O SD	MNA	MNA SD
BGM	40	15	0.6861	0.0288	0.6186	0.0199	7.53	2.00
SBH	40	15	0.7021	0.0248	0.6373	0.0200	7.13	2.42
GAR	40	15	0.7089	0.0491	0.5641	0.0203	7.80	3.34
KAPD	30	15	0.8068	0.0159	0.8519	0.0168	7.80	2.27
KAPRM	42	15	0.8045	0.0131	0.7713	0.0167	9.33	2.55
VIP	42	15	0.7100	0.0293	0.6286	0.0193	6.93	1.98
LAM	40	15	0.6728	0.0335	0.6150	0.0199	8.00	3.09
LOK	32	15	0.7941	0.0204	0.7051	0.0208	8.60	2.29
LTK	43	15	0.7020	0.0380	0.6217	0.0191	7.80	2.46
MOY	43	15	0.7555	0.0240	0.6717	0.0185	8.20	2.43
OKMBHS	38	15	0.7230	0.0236	0.6415	0.0201	7.20	2.46
OKMRM	38	15	0.5956	0.0645	0.5120	0.0210	6.67	2.94
REMA	33	15	0.7580	0.0240	0.6626	0.0213	7.67	2.35
WP	41	15	0.7058	0.0227	0.5911	0.0198	7.47	1.77
HOM	40	15	0.7254	0.0307	0.6206	0.0198	7.40	1.96
Mean	**38.8**	**15**	**0.7230**	**0.0300**	**0.6480**	**0.0200**	**7.70**	**2.42**

NOTE: BGM- Bungoma, **SBH**-Somali Blackhead, **GAR**- Garissa, **KAPD**- Kapiti Dorper, **KAPRM**- Kapiti Red Maasai, **VIP**-Vipingo, **LAM**- Lamu, **LOK**- Lokichoggio, **LTK**- Loitoktok, **MOY**- Moyale, **OKMBHS**-Olkiramatian Blackhead Somali, **OKMRM**- Olkiramatian Red Maasai, **REMA**- Mombasa Red Maasai, **WP**- West Pokot, **HOM**- Homa Bay.

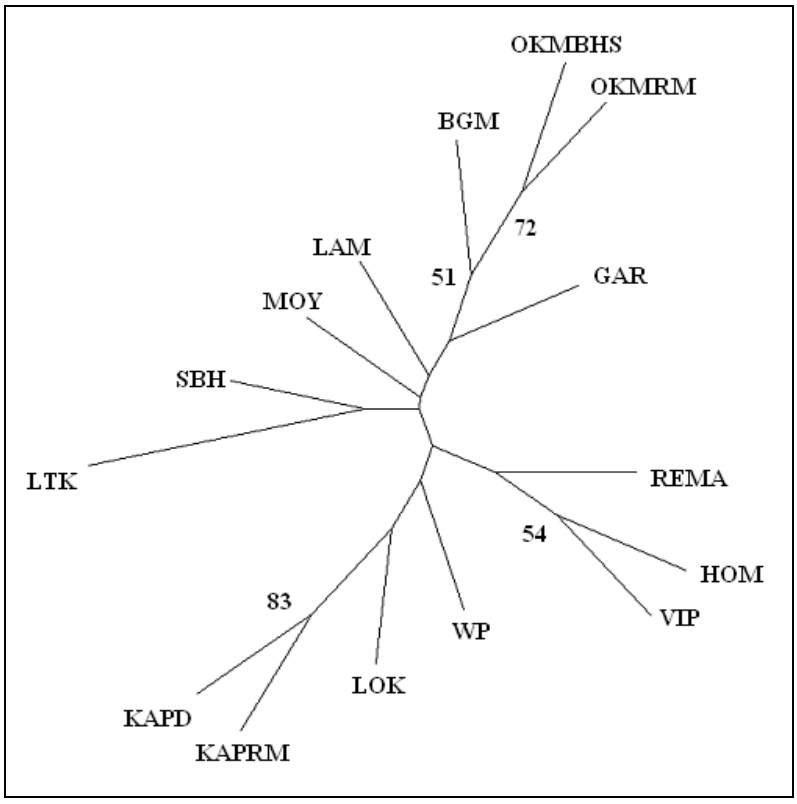

Figure 2: An unrooted neighbour joining phylogenetic tree showing the relationship among the fifteen Kenyan sheep populations studied (only values showing >50 % bootstrap support are reported). For population acronyms see Table 1.

Table 3: Weir and Cockerham 1984 multilocus estimates for diploid data based on Jackknife resampling over all loci (the number in the parenthesis indicates the standard error)

Locus	f_{IS}	θ_{ST}	F_{IT}	G_{ST}	G_{ST}'	H_T	H_S	A
BM8125	0.0744*	0.1559**	0.2187**	0.149	0.158	0.687	0.585	7
DYMS1	0.1207**	0.1275**	0.2328**	0.114	0.121	0.762	0.675	13
HSC	0.0352*	0.0363**	0.0703**	0.034	0.037	0.862	0.832	12
HUJ616	0.1163**	0.1065**	0.2104**	0.10	0.106	0.84	0.756	17
ILSTS005	0.3123**	0.0730**	0.3625**	0.073	0.078	0.837	0.776	10
MAF209	0.1042**	0.1354**	0.2255**	0.125	0.133	0.86	0.752	10
MCM42	0.1212**	0.1067**	0.2150**	0.10	0.107	0.68	0.612	8
OARFCB11	0.0952**	0.1950**	0.2716**	0.184	0.194	0.861	0.703	12
OARFCB20	0.0683**	0.1088**	0.1696**	0.102	0.109	0.866	0.778	13
OARFCB226	0.1004**	0.0844**	0.1763**	0.08	0.085	0.824	0.758	16
OARHH47	0.1201**	0.1057**	0.2131**	0.10	0.107	0.873	0.785	17
OARJMP29	0.0719*	0.0668**	0.1339**	0.072	0.077	0.742	0.688	10
OARVH72	0.1116**	0.1460**	0.2413**	0.136	0.144	0.773	0.668	10
SRCRSP9	0.0098^{ns}	0.0473**	0.0566^{ns}	0.047	0.051	0.73	0.696	8
TGLA53	0.1516**	0.0256**	0.1733**	0.025	0.027	0.821	0.8	10
Overall:	**0.109 (0.019)****	**0.101(0.012)****	**0.199 (0.02)****	**0.096**	**0.102**	**0.801**	**0.724**	**173**

f_{IS}, within-population inbreeding estimate; F_{IT}, total inbreeding estimate; θ_{ST}, measure of population differentiation;

A, the number of Alleles

Statistical significance: *- p<0.05, ** - p<0.01, ***- p<0.001 ^{ns}- non-significant based on 10 000 randomisations (after Bonferroni corrections)

Table 4: Pairwise population matrix of Nei's chord distances (D_A) for the fifteen Kenyan sheep populations studied

POPLN	BGM	SBH	GAR	KAPD	KAPRM	VIP	LAM	LOK	LTK	MOY	OKMBHS	OKMRM	REMA	WP	HOM
BGM	0.000														
SBH	0.378	0.000													
GAR	0.319	0.232	0.000												
KAPD	0.557	0.419	0.419	0.000											
KAPRM	0.405	0.305	0.402	0.285	0.000										
VIP	0.339	0.316	0.348	0.506	0.361	0.000									
LAM	0.270	0.206	0.209	0.521	0.391	0.297	0.000								
LOK	0.577	0.465	0.665	0.618	0.497	0.704	0.655	0.000							
LTK	0.192	0.161	0.214	0.449	0.331	0.278	0.179	0.543	0.000						
MOY	0.243	0.193	0.224	0.396	0.334	0.368	0.175	0.509	0.152	0.000					
OKMBHS	0.323	0.357	0.302	0.617	0.521	0.620	0.357	0.536	0.333	0.296	0.000				
OKMRM	0.386	0.551	0.389	0.852	0.755	0.741	0.521	0.796	0.439	0.533	0.315	0.000			
MOMBRM	0.255	0.177	0.226	0.456	0.281	0.196	0.251	0.513	0.143	0.226	0.419	0.533	0.000		
WP	0.274	0.254	0.327	0.378	0.234	0.313	0.358	0.538	0.208	0.266	0.473	0.625	0.206	0.000	
HOM	0.418	0.446	0.513	0.608	0.426	0.276	0.504	0.617	0.363	0.439	0.630	0.651	0.346	0.293	0.000

NOTE: **BGM**- Bungoma, **SBH**-Somali Blackhead, **GAR**- Garissa, **KAPD**- Kapiti Dorper, **KAPRM**- Kapiti Red Maasai, **VIP**-Vipingo, **LAM**- Lamu,

LOK- Lokichoggio, **LTK**- Loitoktok, **MOY**- Moyale, **OKMBHS**- Olkiramatian Blackhead Somali, **OKMRM**- Olkiramatian Red Maasai,

MOMBRM- Mombasa Red Maasai, **WP**- West Pokot, **HOM**- Homa Bay.

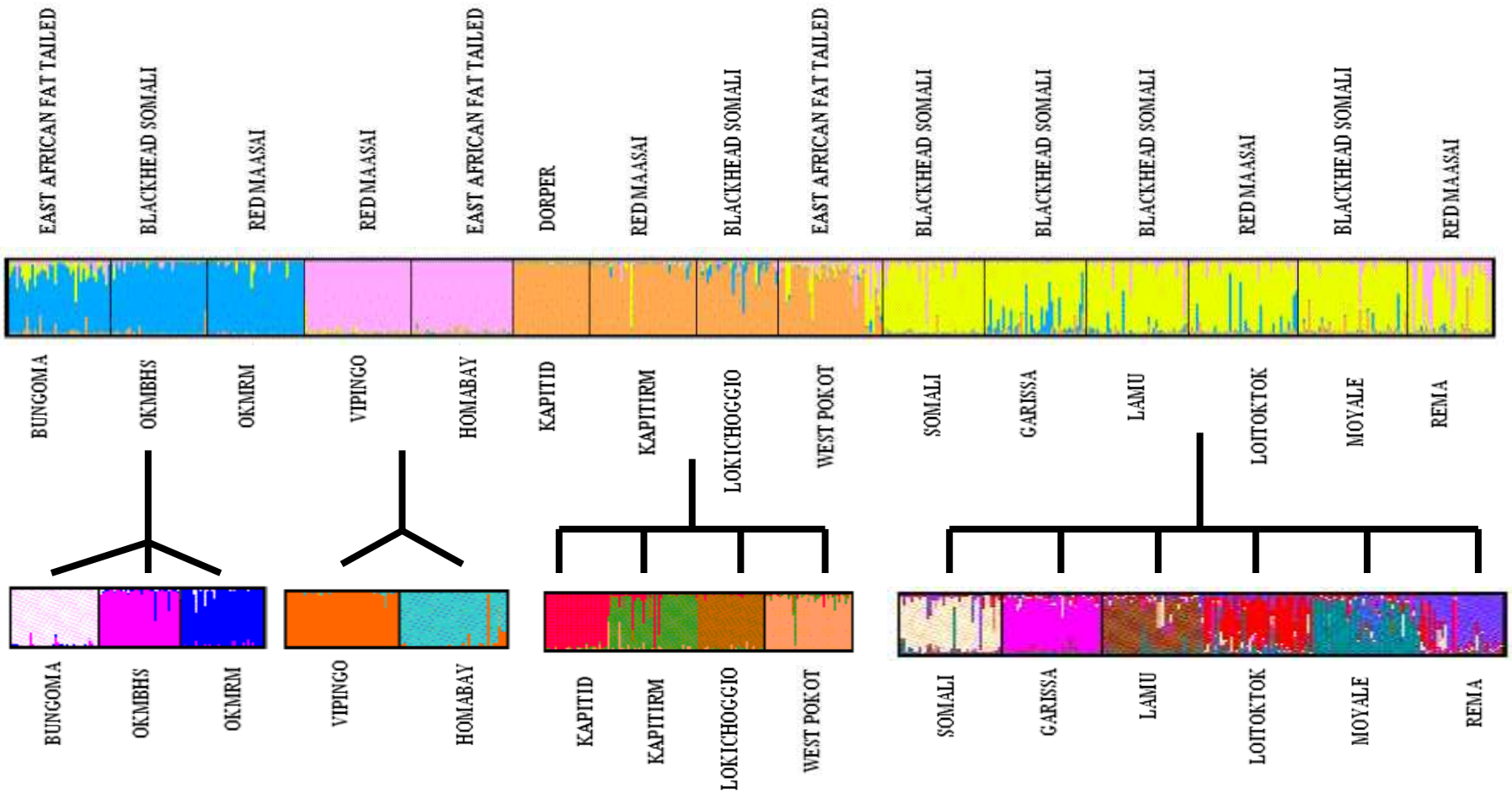

Figure 3. Population partitioning of the sheep populations as suggested by STRUCTURE based on 15 microsatellite markers using individual Q matrices. Junctions show where the data was split into *K* populations and re-run on the sub-data. Black lines separate the individuals of different populations. Population names are indicated below and phenotypic breed identities above the diagram. For population acronyms see Table 1.

Table 5: The Wilcoxon test for genetic bottlenecks

Population	Sample Size	One Tail P-value (TPM) H.deficit	H.excess
Bungoma	40	0.10388	0.90619
Somali Blackhead	40	0.55481	0.46704
Garissa	40	0.91559	0.09381
Kapiti Dorper	30	0.99997	0.00005***
Kapiti Red Maasai	42	0.97232	0.03186
Vipingo	42	0.88535	0.12619
Lamu	40	0.17957	0.83487
Lokichoggio	32	0.99377	0.00754
Loitoktok	43	0.70026	0.31934
Moyale	43	0.87381	0.13843
Olkiramatian Blackhead Somali	38	0.64014	0.38077
Olkiramatian Red Maasai	38	0.07571	0.93231
Mombasa Red Maasai	33	0.97937	0.02396
West Pokot	41	0.26224	0.75565
Homa Bay	40	0.84860	0.16513

***- statistically significant at p<0.001 based on 10 000 replications (after Bonferroni corrections)

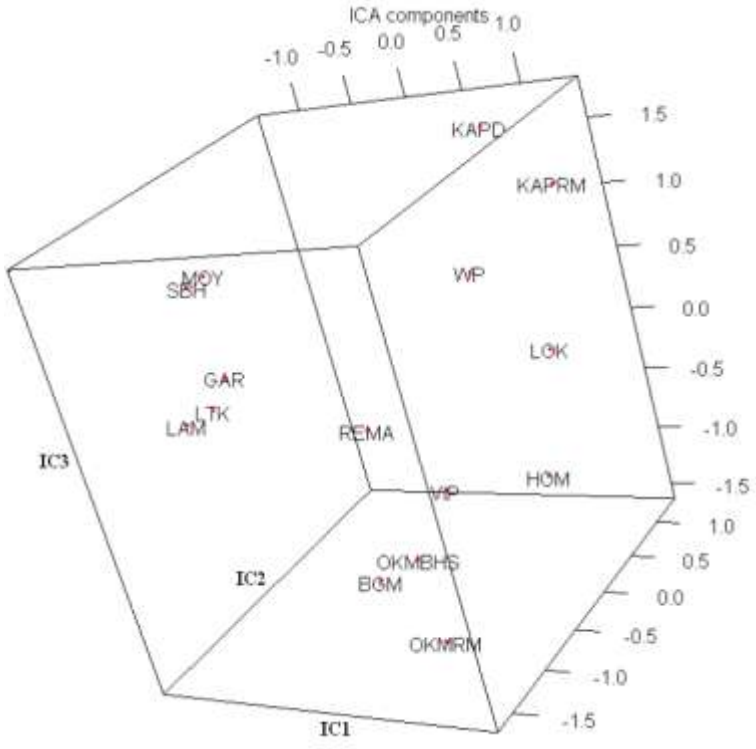

Figure 4: The Independent Component Analysis plot for the fifteen sheep populations.
For population acronyms see Table 1.

DISCUSSION

This study yielded 7.70, 0.723 and 0.648 as the mean number of alleles (MNA), expected and observed heterozygosities respectively, a testimony to the high genetic diversity in these populations. These are comparable to the ones reported by Muigai (2003) MNA, H_E and H_O of 7.24, 0.74 and 0.69 respectively for the sub-Saharan sheep as well as Ligda *et al.,* (2009) with MNA, H_E and H_O as 8.34, 0.74 and 0.696 respectively for Greek sheep breeds. The MNA is an appropriate measure of genetic variation compared to heterozygosity for it's expected to be proportional to the extent of polymorphism whereas the heterozygosity is hardly affected by low frequency alleles (Nei, 1987).

Throughout the study, the farmers' maintained populations had a comparatively lower variability to the ones kept and maintained in nucleus herds with the exception of the Kijipwa Red Maasai population kept and maintained by the Lafarge Ecosystems in Mombasa. The Kapiti population, a nucleus herd kept and maintained by the International Livestock Research Institute as opposed to the farmer herds has its animals sourced from different source flocks and kept separately based on their sex with mating done in a way to reduce consanguineous matings by using properly kept animal records. This is quite unlike the farmers' flocks where animals are grazed and housed together in the 'bomas' irrespective of their sex thus increasing the chances of closely related animals mating. Lack of meticulously kept records for the Kijipwa Red Maasai prospectively explicates their reduced variability since efficient control of siblings from mating might not be possible. The animals in Kijipwa are kept for the sole purpose of grazing under the Lafarge Ecosystems' trees thus the chances of bringing new animals into the flock are slim. The probability that animals held in the flock at any one time are the ones likely to be 'parents' of future populations is high.

Populations deviating from mutation-drift equilibrium while exhibiting a significant heterozygosity excess for selectively neutral markers can be considered to have experienced a recent genetic bottleneck (Cornuet and Luikart 1996); this was the case with the dorper population from Kapiti. Being a nucleus herd, the animals used to establish it were obtained from several source populations The mating of such genetically diverse animals, obtained from many flocks but with very little or none-representative rare alleles from the source populations, will more often than not lead to significant elevation in heterozygosity but reduced MNA. There is however need to assess if the genetic bottleneck observed will have any impact on this dorper population.

The genetic distances observed among the populations were varied with the highest population pairwise distances occurring between the Kapiti Dorper and the Lokichoggio populations relative to the rest of the sheep populations. The distance between the Kapiti Dorper and the other populations was rather expected since this is an exotic breed whereas the rest are indigenous. The only surprising exception was between the two Kapiti populations (Dorper and Red Maasai). This being a nucleus herd one would have expected that the two populations be rather genetically distinct, but the observed relationship could be as a result of the animals used to establish the flocks especially the Red Maasai were not pure since they were acquired locally from farmers or other nucleus herds. A revelation by Kwallah (2007) 8% dorper in the Red Maasai genetic constitution that in the Olmagogo nucleus herd in Naivasha plausibly explains the Kapiti case since some animals used to establish the Kapiti Red Maasai flock were

sourced from Olmagogo. A more important observation however is that the Kapiti Red Masaai does not represent the whole Kenyan Red Maasai population and one should consider expanding their genetic base using other still existing Red Maasai populations. The high genetic distances between the Lokichoggio and other populations can be attributed to the physical geographical barrier given the long distance between Lokichoggio and other sites from which other populations were sampled from. The close relationship between the Garissa, Moyale, Lamu and Somali Blackhead populations is in line with their geographical locations, the pastoral-nomadic way of life as well as the raiding practices of the occupants of these places. This can as well suggest the presence of common markets or the sharing of pastures and watering points thus enhancing gene flow among the populations. Also, the frequent droughts and disease outbreaks in most of these areas often results in massive animal deaths with follow-up restocking exercises mostly done using animals bought from neighbouring areas. The close relationship of the Somali Blackhead populations to the Loitoktok population in Kajiado, the heart of Maasai land is a sure sign of the high rate of gene flow from indiscriminate crossbreeding by the farmers ostensibly in an effort to improve on the size of their Red Maasai animals.
The average within population inbreeding coefficient for all the sheep studied was 0.109 suggesting a rather high level of inbreeding since most of the populations had open breeding structures. The high f_{IS} value obtained could as well emanate from the sub-structuring among the sheep since different farmers' populations are relatively isolated and the local parental individuals contribute to the majority of the next sheep generation. The θ_{ST} and G_{ST} values as well as AMOVA analysis indicate that most of the genetic variation (89.8%) is within populations with the pairwise between-population test indicating that most populations were significantly different from each other with an overall θ_{ST} of 10.1%.

Implications of this study for the conservation of indigenous sheep in Kenya

With how genetically diverse the indigenous sheep in Kenya are, the biggest challenge is how the observed diversity can be maintained, conserved and or even improved upon. The inbreeding observed within the populations will likely compromise their existence and productiveness due to the dangers associated with inbreeding depression thus proper and sustainable breeding programs should be designed to help deal with it. The admixture levels especially between the Red Maasai and other breeds is worrying since the genetic qualities suitable for the unfavorable conditions in which the indigenous sheep thrive are likely to be diluted and polluted. There is urgent need therefore to set up proper conservation programs but given the limited resources the greatest challenge is actually what to conserve?

Given the population structure observed, conserving one or a few populations will not be enough to tap the wide genetic diversity resident in the indigenous sheep in Kenya. The option would be therefore to determine those populations that contribute more to the observed genetic diversity and prioritize them for conservation.

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