



Runs Of Homozygosity and Effective Population Size from Different Goat Genotypes in Kenya

Subtitle: Analysis of ROHs and Ne in Kenyan Goat Genotypes

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Abstract

Limited genetic information in most goat populations hinders the implementation of better breeding strategies for genetic conservation and improvement. Runs of Homozygosity (ROH) were used to analyse the distribution, inbreeding coefficients and effective population size (N_e) of different goat genotypes in Kenya. This was performed from 48808 Single Nucleotide Polymorphism (SNP) that were detected for analysis after quality control. The SNP data of four goat genotypes were used; Galla ($n = 12$), Alpine ($n = 28$), Saanen ($n = 24$) and Toggenburg ($n = 30$). Across the genotypes, 348 ROHs were detected with the highest number (180) observed in Toggenburg and lowest (22) in Galla. From the ROH length categories, the highest mean length was observed on the long ROHs category (>16 Mb) suggesting a recent inbreeding. The distribution of ROHs per chromosome was breed-specific without a clear pattern across the genotypes. Furthermore, 32 genomic regions with a high frequency of ROHs were detected. Sixteen genes (missense and synonymous) associated with various phenotypic functions were identified. High inbreeding coefficient values of > 0.1 were observed in all exotic genotypes suggesting continuous use of few breeding bucks. Toggenburg was found to be the most inbred genotype with the highest inbreeding coefficient of 0.68. The effective population size decreased over time across the genotypes. Galla, Saanen and Toggenburg at recent generation (13genAgo) recorded N_e of less than the recommended threshold ($N_e = 100$) population indicating a limited genetic diversity. The study outcome emphasize the need to use different lines of exotic goats, improved technologies, and/or sustainable implementation of controlled breeding programs.

Keywords: Goats, Genotype, Inbreeding coefficient, Runs of Homozygosity, Effective population size, Kenya

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Introduction

Farmers at small and large scale practice goat production worldwide. In most African nations including Kenya, goat production helps in improving rural livelihood through the provision of meat, milk and income among other benefits (Monau *et al.* 2020a). Kenya is reported to have a diverse genetic structure of goats for both exotic and local genotypes used for genetic improvement programs (Kivila *et al.* 2018; Waineina *et al.* 2021). The shape of the animal genomic structure depends on factors such as geographical location, production and breeding systems that have the potential to increase or decrease genetic diversity (Bosse *et al.* 2012). Inbreeding leads to reduced genetic diversity and hence reduces the animal fitness. Inbreeding levels can be measured at both individual and population levels. Due to improvement in genomic technologies, the most effective way of measuring inbreeding in a population is through estimation of inbreeding coefficients from Runs of Homozygosity (ROHs) (Peripolli *et al.* 2017; Rebelato *et al.* 2018). The ROHs are continuous homogenous regions of the genome in an individual, which

occurs due to the inheritance of identical alleles from parents (Ceballos *et al.* 2018). Unlimited artificial selection for beneficial alleles in a population can also increase homozygosity in genomic regions.

ROHs are either long or short and they usually follow specific distribution patterns in the animal genome (Zhang *et al.* 2015). Long ROHs indicate recent inbreeding whilst short ROHs, indicate ancient inbreeding implying the mating of closely related individuals which is not easily accounted for due to lack of pedigree information. The presence of ROHs patterns in specific genomic regions in selected individuals provides different information. For instance, ROHs distributional patterns have been used to describe the demographic history, gene mapping or differences between livestock genotypes among other genetic information (Upadhyay *et al.* 2017; Islam *et al.* 2019; Xu *et al.* 2019).

The effective population size (N_e) is defined as the size of an idealized population that undergoes the same genetic drift rate and inbreeding as the actual population under study (Falconer, 1996). N_e is an important genetic parameter that describes the genetic

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diversity level of a population and it is estimated by measuring pairwise Linkage Disequilibrium (LD) as a squared correlation coefficient (r^2). The LD refers to the non-random association of alleles which depends on the evolutionary history and the N_e (Deng *et al.* 2019). Changes in N_e over time in a population helps to measure population genetic diversity and implement conservation of important animal genetic resources.

Using Single Nucleotide Polymorphism (SNP) data, this study focused on genomic characterization of ROH distribution, inbreeding coefficients and the N_e among the exotic and local goat genotypes found in Kenya. Despite the genetic diversity and structure of Kenyan goat genotypes being known, information on various genetic parameters such as ROHs within the genotypes is still limited. This study information will enable farmers and livestock breeders to know the accumulated ROHs and inbreeding levels of goat populations in Kenya. Therefore, effective breeding strategies will be easily implemented to improve goat productivity and conservation of unique traits.

Materials and Methods

Sampling

A total of 96 goats from four goat genotypes obtained from 53 farms and one government breeding station in Kenya was used in this study. The goats were purposively selected in different ecological zones of Kenya, namely; Nyeri (Mukurweini Sub-County), Meru (Central Imenti Sub-County) and Homa Bay (Homa Bay town) located in the Central (wet-dry), Eastern (wet) and Western regions (wet area) respectively. The selected areas are some of the entry points of exotic breeds in the country. The goat genotypes that were investigated included; Saanen ($n = 24$), Alpine ($n = 29$) and Toggenburg ($n = 31$) sampled from members of goat farmer associations across the selected Counties and Galla ($n = 12$) from Naivasha, Sheep and Goat government station. Number of goats varied between the breeds and within the sampled households which led to variations in sample size across the genotypes. Blood samples were collected at each selected farm. A member with two does only one doe was used and where there were more, the relationship of the does was confirmed by the farmer to avoid selecting full and half

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siblings. For Galla goat, pedigree information was used to ensure sampling of unrelated goats.

DNA extraction and genotyping

Blood samples were collected at each selected household by a qualified veterinary officer. The animals were constrained during blood collection and all FAO protocols for sampling of blood for DNA were observed. The blood were collected into Ethylenediaminetetraacetic acid (EDTA) tubes from the Jugular vein and stored at -20°C for two months before genomic extraction. Blood sample duplicates were also collected and kept separately.

DNA extraction was done using the Qiagen DNeasy Blood and Tissue Kits. Purified DNA quality and quantity were validated using the Qubit dsDNA BR (Broad-Range) Assay Kit on the Qubit 2.0 and Nanodrop Spectrophotometer (Nanodrop ND-1000). Genotyping was conducted using the Illumina goat SNP50 Bead chip developed by International Goat Genome Consortium (IGGC). Quality control procedures of SNPs were done in PLINK v 1.9 (Chang *et al.* 2015). Standard parameters of SNP filtering were applied: all SNPs $< 95\%$ call rate, < 0.05

Minor Allele Frequency (MAF < 0.05), Hardy-Weinberg Equilibrium (< 0.001) and more than 10% missing genotypes were removed. The study protocol was approved by the Egerton University Research Ethics committee and it occurred in strict accordance with the recommendations of the institute of Primate Research (IPR) Ethical guidelines on Animal care and use of Laboratory Animals.

Statistical analysis

Distribution of runs of homozygosity

Total number, frequency and length distribution of ROHs (Mb) were identified per individual and per genotype in PLINK v1.9 (Chang *et al.* 2015). Homozygosity in this study was defined based on the following parameters; having a minimum number of 15 consecutive homozygous SNPs, a minimum physical length of 1 Mb, 1 maximum missing genotype and 1 heterozygous call were allowed within the ROHs for genotyping errors (Kumar *et al.* 2018; Islam *et al.* 2019). For the chromosomes, the percentage of chromosomes covered by ROHs was calculated by dividing the mean ROH length of chromosome by their respective chromosome length multiply by 100 (Al-Mamun *et al.* 2015). ROHs length was

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categorized into four classes; 2–4 Mb, 4–8 Mb, 8–16 Mb and > 16 Mb.

Estimation of inbreeding coefficient

The inbreeding coefficient was estimated per individual and genotype. Runs of Homozygosity inbreeding coefficients (F_{ROH}) was determined by dividing the total length of ROHs (L_{ROH}) in an individual genome with the autosomal genome length (L_{AUTO}) of goats (2399.4 Mb), (Islam *et al.* 2019).

Genomic Regions with high ROH frequency

The percentage of SNP occurrence was determined by calculating the number of times each SNP occurred in the ROHs throughout the populations. The top 10% of ROHs observed in each genotype were identified as genomic regions with high-frequency ROHs which were extracted using vcftools. The ROHs were then uploaded in the ENSEMBL goat *Capra hircus* using the Variant Effect Predictor (VEP) for functional annotation.

Effective population size

The SNeP v1.1 was used to estimate N_e among the genotypes based on LD (Barbato

et al. 2015). This followed the formula described by (Sved, 1971);

$$E(r^2) = \frac{1}{1 + 4N_e c}$$

Where;

N_e is the effective population size,

c is the genetic distance between SNPs in Morgans

$E(r^2)$ is the expected correlation between allele frequencies of two loci.

The estimated N_e were plotted against the past 1000 generations to determine its trend.

Results

Detection of ROH and ROH patterns

348 ROHs were detected across the goat genotype with a mean of 4.703 per individual. Table 1 shows the descriptive statistics of ROHs per genotype among the studied populations. The number of ROH per genotype according to length category shows more short ROHs than long ROHs (Table 2). Additionally, ROHs detected per chromosome vary according to genotype in all the 28 chromosomes (Fig 1).

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Table 1. ROH Descriptive statistics per genotype

| Genotype | No. Of ROHs Detected | No. Of individuals with ROH | Mean No. Of ROH | Stdev. of ROH | ROH length (Mb) | Mean ROH length |
|-----------------|-----------------------------|------------------------------------|------------------------|----------------------|------------------------|------------------------|
| Alpine | 54 | 20 | 2.7 | 29.77 | 554.92 | 27.75 |
| Gala | 22 | 5 | 4.4 | 14.9 | 211.17 | 42.23 |
| Saanen | 92 | 22 | 4.2 | 29.41 | 846.67 | 38.49 |
| Toggenburg | 180 | 27 | 6.7 | 36.86 | 1631.53 | 60.43 |

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Table 2. Total number of ROH, Total number of individuals with ROH and mean sum of ROH length (Mb) according to ROH categories across the genotypes.

| ROH length category | Gala | | | Toggenburg | | | ALP | | | SAA | | |
|---------------------|---------|--------------|-------------|------------|-------------|-------------|---------|-------------|-------------|---------|-------------|-------------|
| | ROH No. | No. Of Indv. | Mean Length | ROH No. | No. Of Indv | Mean Length | ROH No. | No. Of Indv | Mean Length | ROH No. | No. Of Indv | Mean Length |
| 2-4Mb | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4-8Mb | 12 | 5 | 6.13 | 102 | 27 | 5.99 | 30 | 17 | 6.33 | 50 | 22 | 5.91 |
| 8-16Mb | 8 | 5 | 12.02 | 59 | 22 | 10.45 | 16 | 12 | 12.02 | 32 | 14 | 10.68 |
| >16Mb | 2 | 2 | 20.76 | 19 | 13 | 21.25 | 8 | 4 | 24.84 | 10 | 8 | 20.95 |

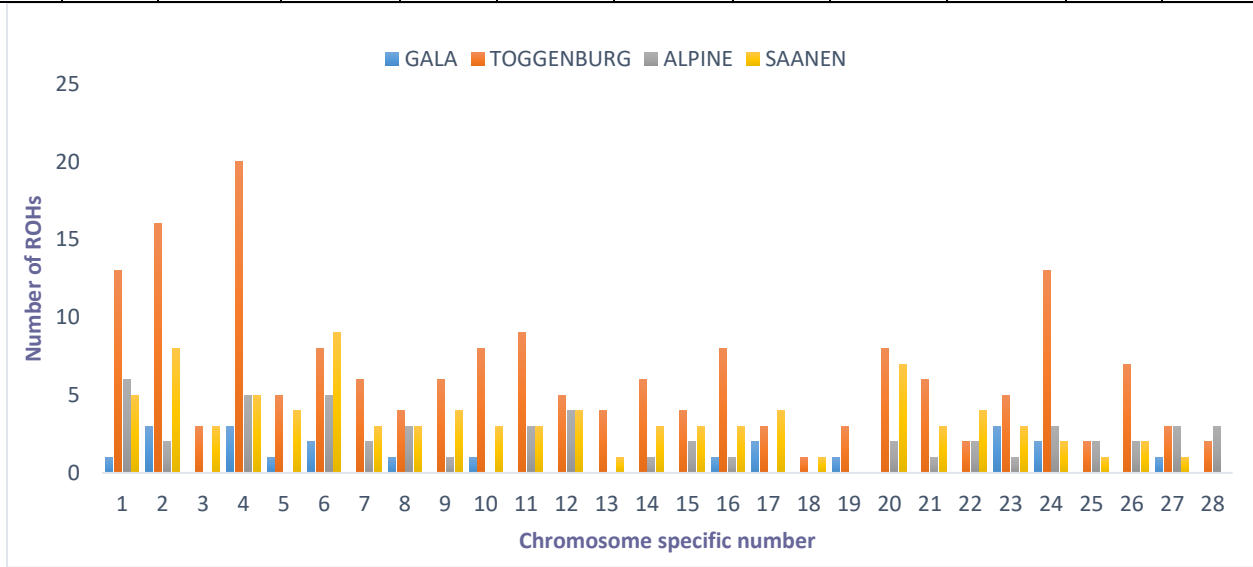


Figure 1. ROHs identified per chromosome per genotype

Inbreeding coefficients

The overall inbreeding coefficients calculated from runs of homozygosity in this study were 1.35. The variations of inbreeding

per genotype are presented in table 3 where Tottenburg shows the highest inbreeding levels (0.68) compared to other genotypes in the study.

Table 3. Inbreeding coefficients per genotype

| GENOTYPE | GALA | TOGGENBURG | ALPINE | SAANEN | TOTALS |
|-------------------------------------|--------|------------|--------|--------|-------------|
| Inbreeding coefficient per genotype | 0.09 | 0.68 | 0.23 | 0.35 | 1.35 |
| Mean Range | 0.02 | 0.03 | 0.01 | 0.02 | |
| Total ROH length | 211.17 | 1631.53 | 554.92 | 846.67 | |
| Mean ROH length | 42.234 | 60.427 | 27.746 | 38.485 | |

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Genomic regions with high frequencies of ROH

Runs of homozygosity islands and SNP percentage were evaluated in all the four goat

genotypes where 34 genomic regions were identified. Sixteen genes were identified from the genomic regions with missense and synonymous effects.

Table 4. Genomic regions with the high frequency of Runs of Homozygosity (ROH), genes identified and their consequences

| Genotype | CHR | START | END | GENES | CONSEQUENCES |
|----------|-----|-----------|-----------|--------------------|-----------------------|
| TOT | 2 | 121194945 | 127160014 | ZSWIM2, FSIP2, | Missense |
| TOT | 2 | 122540040 | 127934583 | ZSWIM2 | Missense |
| TOT | 2 | 29975669 | 35490029 | ABCA12 | Missense |
| SAA | 8 | 103492446 | 112591777 | MYT1L, MEGF9 | Missense |
| GAL | 17 | 50496599 | 55334347 | NAA15 | Synonymous |
| SAA | 17 | 24404597 | 28958842 | PIWIL1 | Missense |
| TOT | 17 | 23941309 | 28606126 | PIWIL1 | Missense |
| TOT | 21 | 39316366 | 46004536 | EAPP, AKAP6 | Missense & Synonymous |
| TOT | 21 | 40245597 | 47248076 | EAPP, AKAP6 | Missense & Synonymous |
| SAA | 23 | 35428109 | 40516154 | PNPLA1, ZNF76, | Synonymous |
| SAA | 24 | 56109867 | 61291762 | ATP8B1 | Missense |
| ALP | 27 | 3855715 | 10045474 | RARB, TOP2B | Missense |
| SAA | 27 | 1051338 | 7735492 | RARB, TOP2B | Missense |
| TOT | 27 | 600400 | 10512553 | KAT6A, RARB, TOP2B | Missense |
| ALP | 28 | 39181 | 5758953 | C10orf71 | Missense |

CHR = Chromosome

Effective population size (Ne)

The estimates of ancestral effective population size (Ne) over past generations obtained in this analysis are presented in fig 2. As the number of generations increases, effective population size across the genotypes also increased at a different increasing rate. Effective population size for Alpine tends to increase rapidly compared to

all other genotypes in this study. At the most recent 13th generation, the Ne for Alpine, Gala, Saanen and Toggenburg was 109, 49, 81 and 93 respectively indicating little genetic pool for all the genotypes except Alpine. The Ne for the furthest distant generation was 3709, 2428, 7515 and 2548 for ALP, GAL, SAA and TOT respectively, Supplementary file 1.

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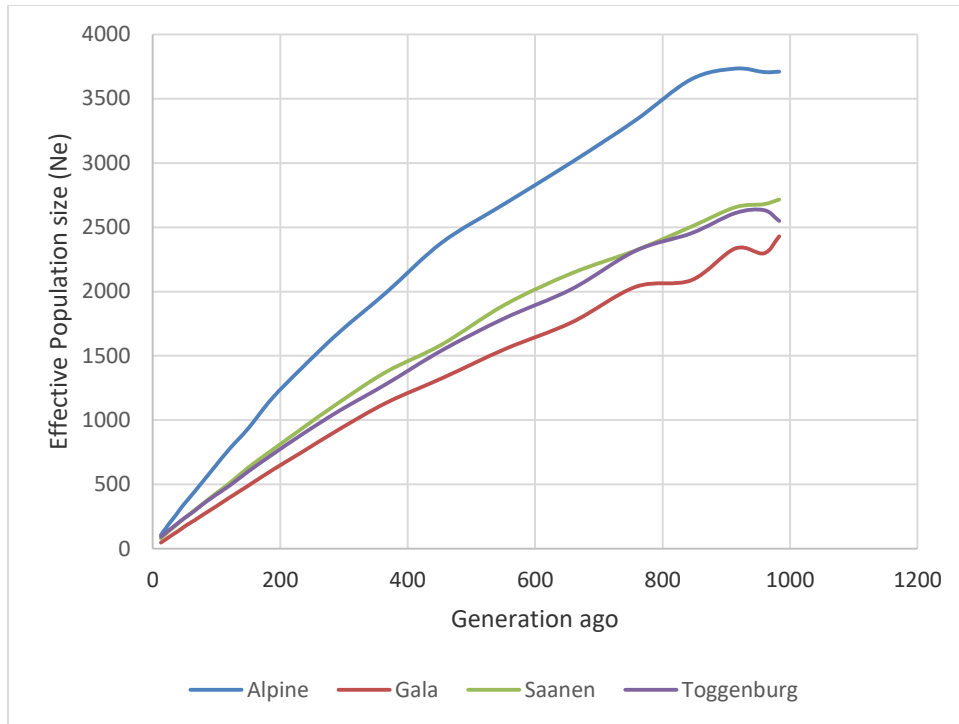


Figure 2. The effective population size of Kenyan goat genotypes

Discussion

Runs of homozygosity

The descriptive statistics of ROHs per genotype (Table 1) show differences among the studied populations. Generally, all genotypes in this study have ROHs in their genome whose presence varies in terms of the total number, length and distributions. These findings are similar to the distribution of ROHs observed in Italian goat populations and cattle breeds of Poland (Szmatola *et al.* 2019; Mastrangelo *et al.* 2021). According to Bosse *et al.* (2012), the formation of ROH in a population is a factor of demographic

events and recombination rate. The mean ROH length tends to be higher in Galla compared to Alpine and Saanen which recorded low numbers of ROHs. A similar trend was also observed in domestic Greek goat breeds (Michailidou *et al.* 2019).

Results for the analysis of ROHs per different length categories varied across the genotypes as indicated in table 2. Xu *et al.* (2019), reported that different length categories of ROHs provide information on genetic variations between genotypes. The highest mean length of ROH coverage across genotypes was observed in long ROHs > 16

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Mb which suggests recent inbreeding. Similar observations were made in Asian pig and Italian goat populations (Bosse *et al.* 2012; Mastrangelo *et al.* 2021). This result can be attributed to management and breeding systems applied in these populations such as uncontrolled breeding, artificial selection of best breeding bucks or the presence of few replacement stocks for breeding in the population. Furthermore, ROHs were more common in short ROHs (4 – 8 Mb) than in long ROHs (> 16Mb) contrary to what was observed in related ROH studies of goats and sheep (Purfield *et al.* 2017; Onzima *et al.* 2018). Generally, the majority of the mean ROH coverage was reported at the length of >16Mb suggesting recent inbreeding across the genotypes. This information is important for planning better breeding programs since most deleterious variants are reported to be carried in the long ROHs (Szpiech *et al.* 2013). The ROHs detected per chromosome varied according to genotype in all the 28 chromosomes (Fig 1). The distribution pattern of ROH per chromosome across the genotypes was non-specific concurring with the fact that the distribution of ROH per chromosome is breed-specific (Mastrangelo *et al.* 2017). The

highest number of ROHs in chromosome 4 of Toggenburg suggested continuous transfer of ancestral genes specific for chromosome 4.

Inbreeding coefficient

The observed individual genomic inbreeding coefficients calculated from ROHs were generally low (0.00 to 0.07) indicating non-inbred individuals. For instance, the inbreeding levels per individual for Alpine goats were below 0.05. This concurs with the findings of other scholars in related studies who concluded that Kenyan Alpine goats are not inbred and they suggested the implementation of a controlled breeding system to avoid future inbred populations (Marete *et al.* 2011). A population with low inbreeding levels must have inbreeding coefficient levels of less than 0.1. In this study, only local Gala recorded F_{ROH} value of 0.09 which corresponds with the observed low numbers of ROHs. This suggests that the genetic material for this genotype is at least well managed in the government farm but measures must be implemented to maintain recommended inbreeding levels at both at the controlled farms and farmer levels. The variations of inbreeding per genotype show that exotic genotypes were most inbred with

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inbreeding levels of 0.68, 0.39 and 0.23 for Toggenburg, Saanen and Alpine, respectively, as presented in table 3. This observation is in agreement with the inbreeding coefficient values of goats observed from different geographical locations by Bertolini *et al.* (2018). It can therefore be eluded to the extensive use of exotic bucks for breeding in goat populations since these genotypes were brought in Kenya to improve local goat productivity.

Genomic regions with the high frequency of ROH

From the genomic regions associated with the high frequency of ROHs, more missense genes (12) were identified compared to synonymous genes (4) as shown in table 4. This observed missense and synonymous genes were reported to be associated with genetic disorders or diseases, reproduction and general body immunity. However, evaluation of the identified genes in the goat population is limited compared to other mammal species.

Effective population size

The N_e for all the genotypes at the very distant past (983 generations ago) was high with N_e values of above 2000 across the

genotypes. Over time until the recent present, a decrease in the N_e was observed (Fig 2). This trend was also observed in local swiss sheep (Bertolini *et al.* 2018), Australian and Canadian boar goat (Brito *et al.* 2015), Buffalo populations (Deng *et al.* 2019) and local South African goats (Monau *et al.* 2020b). To ensure the long-term viability of any livestock population, the effective population size must reach a threshold of $N_e = 100$ (Meuwissen *et al.* 2009). However, at the 13th generation, ago recent N_e for all the genotypes except Alpine did not meet the required N_e threshold ($N_e = 100$) indicating limited genetic diversity. Similar results were also obtained at 13th generation ago in two goat populations of china (Islam *et al.* 2019). Measures such as exchange of breeding bucks or use of artificial insemination can be implemented in Gala, Saanen and Toggenburg to ensure the required levels of diversity are sustained. It is important to ensure that populations of local genotypes have high genetic variations at all times since they are a source of many genetic materials adaptable to the local environment (Monau *et al.* 2020b). In the 20th generation ago, the N_e for all exotic genotypes was above the threshold of $N_e = 100$ with 156, 113 and 122

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for Alpine, Saanen and Toggenburg. These results are comparable with N_e observed in the same goat breeds at 20th generation ago (Brito *et al.* 2015).

Conclusion

Accumulations of ROHs have been confirmed in the goat population of Kenya with high numbers of ROHs and inbreeding levels observed in exotic goat genotypes compared to the local genotype. This indicates uncontrolled breeding among the studied goat population, which causes an increase in homozygosity and affects the effective population size. Therefore, strategic breeding should be a priority in these populations to avoid a reduction in genetic diversity which can lead to loss of important genetic materials and accumulation of undesirable genes. Therefore, special considerations should be made to have different lines of exotic goat genotypes, use of improved technologies such as Artificial Insemination and/or implementation of controlled breeding programs to ensure effective genetic improvement and conservation.

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