Small Ruminant Research 227 (2023) 107086

Contents lists available at ScienceDirect

Small Ruminant Research

journal homepage: www.elsevier.com/locate/smallrumres

A homozygosity-based investigation of the South African feral Tankwa goat population

A.S. Kropff [a,b], C. Visser [b,*], A. Kotzé [a,c]

[a] South African National Biodiversity Institute, P.O. Box 754, Pretoria 0001, South Africa
[b] Department of Animal Science, University of Pretoria, Private Bag 20, Hatfield 0028, South Africa
[c] Department of Genetics, University of the Free State, Bloemfontein 9300, South Africa

ARTICLE INFO

Keywords:
Genomics
Inbreeding
Runs of homozygosity
Signatures of selection

ABSTRACT

The Tankwa goat is a known feral goat landrace that originated in the Karoo region of South Africa. These goats are able to thrive with no managerial intervention, and prosper in the harsh, arid conditions that characterizes their natural habitat. This study aimed to use a ROH-approach to describe the Tankwa goat in terms of autozygosity and to identify possible signatures of selection. Genome-wide SNP data for 360 Tankwa goats were used to calculate diversity statistics, detect runs of homozygosity and estimate individual genetic inbreeding coefficients. SNP genotypes of 48 Angora and 40 Dairy individuals were compared using the F_{ST} approach to detect signatures of selection. Relatively low minor allele frequency (0.249), and high linkage disequilibrium (r^2 = 0.469) levels were estimated for the Tankwa population, with moderate levels of heterozygosity (H_E = 0.368; H_O = 0.367). The results for both the detected runs of homozygosity and inbreeding estimate, indicates an ancient origin of inbreeding for the Tankwa goats with low levels of autozygosity. Signatures of selection were identified in 50 SNPs, of which 0.1% was considered significant. A total of 49 genes were identified that may possibly be significant in various biological pathways. Three of these genes, namely *GJB2*, *GJB6* and *GJA3* on CHI12, were previously associated with adaptation to heat and drought resistance in other breeds. Genes *GJB2* and *GJB6* are known to be linked to the sensory perception of sound, while *GJA3* and *OPA3* are linked to visual perception. These genes could play an important role in the survival of an individual existing in a harsh environment in terms of foraging and evading predators. Understanding the genetic background of these genes, as well as the metabolic pathways that they control, could assist in further investigating production efficiency of domesticated species in a climate change environment.

1. Introduction

After its domestication in the Fertile Crescent about 10,000 years ago (Benjelloun et al., 2015; Amills et al., 2017), goats dispersed to surrounding areas following human migration routes, reaching southern Africa approximately 8 000 years later (Amills et al., 2017; Colli et al., 2018). Goat are considered one of the most adaptable domestic species and are mostly found in desert areas, mountains and the tropics (Amills et al., 2017; El-Halawany et al., 2017). Many goat populations gradually adapted to their local environment through natural selection, leading to the development of diverse landraces and unique populations (Benjelloun et al., 2015; Marsoner et al., 2018). These populations were known to interbreed, with limited selection for specific traits and thus maintaining high phenotypic diversity (Benjelloun et al., 2015; Marsoner et al., 2018). Artificial selection on the other hand, gave rise to specialized commercial breeds (Henkel et al., 2019) with specific production purposes (e.g. meat, milk or fibre). There are more than 500 recognised goat breeds worldwide (FAO et al., 2015), with different phenotypic characteristics, reproductive performance, production performance and environmental adaptation (Brito et al., 2017; Bertolini et al., 2018). Many populations still need to be phenotypically and genetically characterized, especially those kept by subsistence farmers with minimal managerial inputs and limited or no artificial selection.

Indigenous goat breeds are generally assumed to be locally adapted goats that underwent no or limited artificial selection, with natural selection playing a significant role in their development (Onzima et al., 2018a). They are considered a valuable genetic resource due to their adaptation to a diverse range of harsh environments, including specific

* Corresponding author.
E-mail address: carina.visser@up.ac.za (C. Visser).

https://doi.org/10.1016/j.smallrumres.2023.107086
Received 31 May 2023; Received in revised form 28 August 2023; Accepted 30 August 2023
Available online 1 September 2023

environmental conditions such as high temperatures, high incidences of disease and a lack of water availability (Webb & Mamabolo, 2004; Ajmone-Marsan et al., 2014; Benjelloun et al., 2015; Onzima et al., 2018a). Indigenous breeds play an important role in maintaining across-breed genetic diversity as a reservoir for rare genetic material (Biscarini et al., 2015). Cosmopolitan breeds, such as the Angora, Boer and Saanen goats in South Africa, are developed breeds that underwent artificial selection for specific traits that include phenotypic and production traits (Brito et al., 2017; Henkel et al., 2019).

The feral Tankwa goat was declared a landrace by the South African National Department of Agriculture and Land Reform (DALRD) in 2019 (personal communication with Deon Kriel - DKriel@ncpg.gov.za). It is believed that the population was formed by individuals from multiple other breeds that escaped from farms in the Karoo area and formed a free roaming, isolated population that was first observed in the Tankwa Karoo National Park (Northern Cape province) about 90 years ago (personal communication with Deon Kriel - DKriel@ncpg.gov.za). The population thus originated from a small founder population relatively recently, with little human interference (Kotzé et al., 2014; Ahmed et al., 2018). These goats have varied in coat colours and appearances, survive in harsh conditions, with temperatures ranging from an annual minimum of 4 °C to a maximum of 30 °C and under dry condition (World Weather Online, 2023). The Tankwa goats were discovered with the proclamation of a new national park in 1986. In 2007 the South African National Parks (SANParks) initiated the removal of these goats from the Tankwa Karoo National Park, as they were considered a threat to the natural and unique succulent Karoo plant diversity (Chynoweth et al., 2013).

The Department of Agriculture, Environmental Affairs, Rural Development and Land Reform (DAERL), Northern Cape moved 60 animals (36 males and 24 females) to a research station in Carnarvon (Northern Cape) in 2009 (Mdladla et al., 2018). The Tankwa goat population, although free roaming, is being maintained on the farm at approximately 300 individuals (Ahmed et al., 2018). The population shows a high degree of phenotypic variation with regards to phenotypic characteristics such as coat colour, coat length, horn shape, head shape and general morphology (Fig. 1). The goats are all horned, and the average adult female weighs between 20 and 40 kg and the average adult male weighs between 25 and 55 kg (personal communication with Deon Kriel - DKriel@ncpg.gov.za). The characterization of breeds is considered a strategic priority for the development of a national plan for the management of animal genetic resources (FAO, 2011; Ajmone-Marsan et al., 2014). In addition, it supports conservation as well as the effective utilization of the indigenous genetic resources (Visser, 2019).

Optimal utilization of indigenous genetic resources is key for effective conservation, possible breed improvement and the management of small populations (Monau et al., 2020a). Small populations, such as the Tankwa goats, are at risk of loss of diversity due to inbreeding, cross-breeding and natural factors such as disease. The conservation of such populations requires continuous genetic monitoring over time to ensure that management decisions will not adversely impact the population by increased inbreeding or reducing population size below the recommended effective population size (FAO, 2011; Meek et al., 2015; Allendorf, 2017; Monau et al., 2020a).

Genetic characterisation is required to determine estimates of genetic diversity and breed differentiation (Visser, 2019), however, the genetic characterisation of many goat breeds is still lacking (Brito et al., 2017; Monau et al., 2020a). Investigating the genetic diversity of populations using molecular markers, can also shed light on their breed history (Martínez et al., 2012; Ajmone-Marsan et al., 2014). Genome-wide SNP data can be used to investigate differences within whole genomes of individuals and thus to monitor the genetic components of populations (Colli et al., 2018).

Runs of homozygosity (ROH) are defined as continuous segments of homozygous nucleotide sequences, which can be used to indicate both inbreeding as well as genetic diversity (Purfield et al., 2012; Curik et al., 2014; Peripolli et al., 2016). Inbreeding, specifically in small populations, needs to be monitored to prevent or reduce the potential effects of loss of variation, inbreeding depression and an increase in the expression of deleterious alleles (Zhang et al., 2015; Brito et al., 2017). Another application for ROH is to identify signatures of selection within a population, which can be used to investigate evolutionary history and to identify beneficial mutations (Fariello et al., 2013; Saravanan et al. 2020). Keller et al. (2011) concluded that inbreeding coefficients derived from runs of homozygosity (ROH) are optimal for the estimation of genome-wide autozygosity and for detecting inbreeding effects.

Natural selection plays an essential role in the differentiation of breeds that can survive in specific environments (Brito et al., 2017). Alterations observed across the genome due to selection are more

Fig. 1. Phenotypic variation observed in the Tankwa feral goats from the Carnarvon Research Station (Photo by Anna S. Kropff).

commonly referred to as signatures of selection (Gouveia et al., 2017; Purfield et al., 2017; Saravanan et al., 2020). This includes adaptive traits such as heat tolerance and disease resistance, reproductive traits, production traits and behavioural traits (Moradi et al., 2012; Brito et al., 2017). Signatures of selection are defined as the reduction, loss or change in genetic variation of a genomic region that are next to, or overlaps, the functional gene selected upon (Talenti et al., 2017; Dolebo et al., 2019). Strong positive selection leads to the rapid fixation of a gene under selection as well as neutral genomic regions around the gene. The rapid fixation of a gene under selection will increase the genetic divergence between populations (Ajmone-Marsan et al., 2014; Qanbari & Simianer, 2014). F_{ST}-based analysis identifies regions of the genome where allele frequencies are significantly different between different populations by calculating the pairwise fixation index between populations (Gouveia et al., 2017; Onzima et al., 2018c; Zheng et al., 2020).

This study aimed to 1) describe the autozygosity of the Tankwa goat breed by using a ROH-approach; and 2) identify signatures of selection by comparing the feral Tankwa goat with two highly selected (fibre and dairy producing) goat populations.

2. Materials and methods

Ethical approval for the use of secondary data was granted by the Ethics Committee of the University of Pretoria (NAS446/2019 & NAS350/2020). Research ethical clearance was also granted by the South African National Biodiversity Institute's (SANBI) Research Ethics and Scientific Committee (P2020–33).

2.1. Genomic data and quality control

A total of 448 (360 Tankwa, 48 Angora and 40 Dairy) genotyped animals were included in this study. The Tankwa samples used, were collected from the Carnarvon Research Station population. The Angora goat samples originated from fine-hair producing animals and the Dairy samples consisted of highly selected Saanen and British Alpine individuals. The three populations were analysed separately for diversity parameters. All samples were genotyped using the Illumina GoatSNP50 BeadChip with a total of 53 347 SNPs covering 93% of the genome (Tosser-Klopp et al., 2014) at the Biotechnology Platform of the Agricultural Research Council (ARC). The raw genotype files were converted into PLINK software version 1.07 (Purcell et al., 2007) input files. Sample-based quality control was performed based on a minimum individual call rate of 95%, while marker-based quality control was based on a minimum SNP call rate of 95%, a minor allele frequency of 0.02 and a minimum deviation from Hardy-Weinberg equilibrium of $p = 0.001$.

2.2. Diversity statistics

Within population diversity levels were calculated in PLINK v1.07 (Purcell et al., 2007). Statistical analyses included estimating average observed (H_O) and expected (H_E) heterozygosity, minor allele frequency (MAF), runs of homozygosity (ROH) and linkage disequilibrium (LD), using the r^2 measurement. H_O and H_E was calculated using the –het function in PLINK v1.07 (Purcell et al., 2007). The focus of this study was on the Tankwa population, but the other two populations were included for comparative purposes. The r^2 measurement was used to calculate LD as D′ is sensitive to allele frequency and is affected by small population sizes while the r^2 measurement is independent of allele frequency (Gurgul et al., 2014).

2.3. Runs of homozygosity

PLINK v1.07 (Purcell et al., 2007) uses a sliding window approach to identify stretches of consecutive homozygous SNPs. These ROH was detected using a minimum number of 50 SNPs, with a maximum of one heterozygote and three missing SNPs allowed, respectively and a maximum distance of 1000 kb between SNPs. The proportion of false-positive identifications was set to 0.05. The ROH detected were assigned to different length categories namely, 0.1–2MB; > 2–4MB; > 4–8MB; > 8–16MB and > 16MB.

2.4. Inbreeding coefficients

Inbreeding levels were calculated using both the individual inbreeding coefficient F_{IS} and F_{ROH} in PLINK v1.07 (Purcell et al., 2007). F_{IS} was calculated using the –het function in PLINK v1.07 (Purcell et al., 2007). F_{ROH} was calculated for each ROH size class, as well as overall using the formula:

$F_{ROH} = \sum (L_{ROH} / L_{AUTO})$.

Where L_{ROH} is the total length of ROH in the animal and L_{AUTO} is the total length of the autosome covered by SNPs (Purfield et al., 2012; Peripolli et al., 2016).

2.5. Signatures of selection

2.5.1. Between populations

A fixation index (F_{ST}) approach was used to identify possible signatures of selection between the three populations. F_{ST} values were calculated per SNP using PLINK v1.07 (Purcell et al., 2007) by comparing the allele frequencies in the subset of the Tankwa population with the allele frequencies in the combined dataset, as described by Weir & Cockerham (1984), using the –fst command. The –report-variants command was used to obtain the F_{ST}-values per pair-wise comparison, and the –base command was used to specify the Tankwa population as the population of interest (the other populations were compared to the Tankwa population and not to each other).

All negative F_{ST} values were changed to zero as negative values have no biological meaning (Makina et al., 2015; Zhao et al., 2015). To reduce the effect of a small sample size a moving average F_{ST} (maF_{ST}) approach was used by calculating the average F_{ST} for five adjacent SNPs in a sliding window approach, this ensured only strong signals of selection were identified and reduced background noise (Purfield et al., 2012). The top 0.1% of the F_{ST} values were considered significant, with the two flanking SNP to each side of the significant SNP also considered. The results were visualized on a Manhattan plot using the package ggplot in R-studio (RStudio Team, 2020).

The Ensembl and NCBI databases was used to further investigate the identified significant SNPs as well as the SNPs flanking them. All genes found in the area of the significant SNP were considered possible genes under selection. The main functions of these genes were investigated and then classified according to their main biological function.

2.5.2. Within population (only Tankwa)

Overlapping ROH were analysed using the package detectRUNS in R-Studio (RStudio Team, 2020). The number of times a SNP falls within a ROH in the population was visualized on a Manhattan plot. The top 10 ROH with a frequency of at least 40% were identified as possibly significant sites. The significant ROH regions as well as a ± 2 MB region on either side of the ROH was investigated to identify possible genes under selection using the Ensembl and NCBI databases.

Table 1
A summary of the number of SNPs that passed quality control (N SNP), average Heterozygosity (H_E and H_O), Minor Allele Frequency (MAF) and Linkage Disequilibrium (r^2) for the Tankwa, Angora and dairy goat populations.

Breed	N SNP	H_E	H_O	MAF	r^2
Tankwa	42 238	0.368	0.367	0.249	0.469
Angora	46 236	0.353	0.349	0.253	0.392
Dairy	48 221	0.406	0.388	0.315	0.332

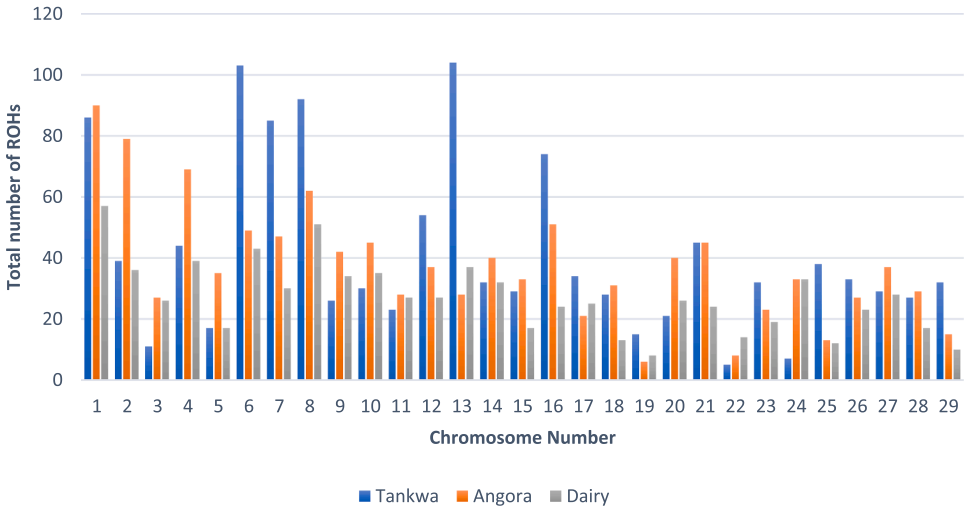

Fig. 2. The total number of detected ROH per chromosome measured in three goat populations.

3. Results

3.1. Quality control

Through sample-based quality control, 36 animals, namely 35 Tankwa and 1 Dairy individual(s) were removed. Marker-based quality control removed 7 703 SNPs for the Tankwa, 3 705 SNPs for the Angora and 1 720 SNPs from the Dairy datasets. The final individual datasets included 325 Tankwa individuals with 42 238 SNPs, 48 Angora individuals with 46 236 SNPs and 39 Dairy individuals with 48 221 SNPs. In the merged dataset, 39 017 common SNPs remained.

3.2. Diversity statistics

A summary of the average diversity values for the three populations is shown in Table 1. The average observed (H_O) ranged from 0.349 (Angora) to 0.388 (Dairy) and the range for expected (H_E) heterozygosity was 0.353 (Angora) to 0.406 (Dairy).

The average MAF, prior to the removal of all SNPs with a MAF below 0.02, ranged from 0.205 for the Tankwa goat to 0.315 for the dairy goats. After pruning based on MAF, the range was between 0.249 (Tankwa) and 0.315 (Angora). The dairy population displayed the highest average MAF across all chromosomes.

Chromosome-specific linkage disequilibrium (LD) estimates using r^2 ranged from 0.316 on CHI9 for the dairy goats to 0.525 on CHI24 for the Tankwa goats. The average LD across the genome ranged from a r^2 value of 0.332 for the Angora goats to 0.469 for the Tankwa goats.

Table 2
Summary statistics calculated for the runs of homozygosity (ROH) identified for the Tankwa, Angora and Dairy populations.

	***n*ROH**[a]	**Mean** Total length[2]	**Median**Total Length[3]	**Mean** ROH length[4]	**Min** ROH length[5]	**Max** ROH length[6]
Tankwa	1225	14.875	13.455	3.946	1.514	19.874
Angora	1090	118.697	115.109	5.227	1.642	32.923
Dairy	784	143.327	118.045	7.130	2.003	62.854

[a] *n*ROH=number of ROH identified, [2]MeanTotal length (MB)=the mean of the summed ROH length per individual, [3]MedianTotal Length (MB)=the median of the summed ROH length per individual, [4]MeanROH length (MB)=the mean ROH length considering all ROH, [5]MinROH length (MB)=the minimum ROH length, [6]MaxROH length (MB)=the maximum ROH length

3.3. Runs of homozygosity

Analysis of homozygous fragments identified 1225 runs of homozygosity (ROH) in the Tankwa goats, 1090 ROH in the Angora goats and 784 ROH in the dairy goats. The average number of ROH observed per goat was 3.7, 20.1 and 22.7 for the Tankwa, dairy and Angora goat populations, respectively. The least and most observed ROH for a single animal were 0 and 11 in the Tankwa goat; 4 and 39 in the dairy goat; and 6 and 40 in the Angora goat populations. The total number of ROH per chromosome for each population is illustrated in Fig. 2. The most (104) ROH were detected on CHI13 and the least (five) on CHI22 in the Tankwa population. All the ROH shorter than 2MB were detected on CHI6 while all the ROH above 16MB were detected on CHI29 in the Tankwa population. For both the Angora and the Dairy populations the most ROH were detected on CHI1 (90 and 57 respectively), while the least were detected on CHI19 (6 and 8 respectively).

Summary statistics for the various ROHs was calculated (Table 2). The largest proportion of the ROHs were between > 2 and 4MB long in all the populations. In the > 8–16MB and > 16MB categories combined, fewer ROH were observed for the Tankwa goat population (40), compared to the Angora (173) and Dairy goats (198). The shortest ROH of 1.51MB was identified in the Tankwa goat population on CHI6, while the longest ROH of 62.85MB was observed in the Dairy goats on CHI20.

3.4. Inbreeding

The individual inbreeding coefficients (F_{IS} and F_{ROH}) were calculated per individual and as an average across each population. The average inbreeding coefficients (both F_{IS} and F_{ROH}) for the population was the lowest in the Tankwa and the highest in the Dairy populations. The individual with the lowest F_{IS} estimate was observed in the Angora population (−0.108) and the highest in the Dairy population (0.259). F_{ROH} was also calculated for the different ROH sizes (1–2 MB, >2–4 MB, >4–8 MB, >8–16MB and >16MB) as shown in Table 3. The lowest F_{ROH} per size category was mostly estimated in the Tankwa population, while the highest F_{ROH} per size category was estimated in the Angora population for the < 2MB and 2.1–4MB size categories and in the Dairy population for the 8.1–16MB and > 16MB size categories.

3.5. Signatures of selection

3.5.1. Between populations

The calculated *ma*F_{ST}-values per chromosome is shown in a Manhattan plot (Fig. 3). This study identified 50 potentially significant SNP

Table 3
Individual inbreeding coefficients for the Tankwa, Angora and Dairy datasets.

	F_{IS}	F_{ROH}[a]	$F_{ROH}\leq$ 2MB[2]	$F_{ROH>}$2–4MB[3]	$F_{ROH>}$4–8MB[4]	$F_{ROH>}$8–16MB[5]	$F_{ROH}>$ 16MB[6]
Tankwa	0.001	0.006	< 0.001	0.003	0.002	< 0.001	< 0.001
Angora	0.011	0.052	< 0.001	0.015	0.018	0.010	0.005
Dairy	0.044	0.062	< 0.001	0.010	0.016	0.017	0.016

[a] F_{ROH}=inbreeding coefficient based on all runs of homozygosity (ROH), [2]F_{ROH}< 2 Mb= inbreeding coefficient based on all ROH smaller than 2 Mb, [3]F_{ROH}2.1–4 Mb=inbreeding coefficient based on all ROH between 2.1 and 4 Mb, [4]F_{ROH}4.1–8 Mb=inbreeding coefficient based on all ROH between 4.1 and 8 Mb, [5]F_{ROH}8.1–16 Mb=inbreeding coefficient based on all ROH between 8.1 and 16 Mb, [6]F_{ROH}> 16 Mb=inbreeding coefficient based on all ROH larger than 16 Mb

with the most found on CHI18 (9 SNPs). For 18 of these SNPs no associated genes were previously annotated in the Ensembl or NCBI databases. For the remaining SNPs, 49 possible genes were identified and a sub-set of these genes that affect behaviour, the organs or the senses are listed in Table 4.

3.5.2. *Within population (only Tankwa)*

The incidence at which each SNP occurred within a specific ROH was visualised in a Manhattan plot (Fig. 4). This study identified 10 potentially significant ROH in the Tankwa population. The longest region spanning 115 SNPs was identified on CHI24, while CHI16 harboured the highest number of significant ROH regions (Table 5). The 10 regions contained many possible genes under selection that affect cellular processes, behaviour, organs, reproduction and the senses.

4. Discussion

4.1. *Quality control*

During quality control the largest number of SNPs were filtered out based on minor allele frequency (MAF) with approximately double the number removed for the Tankwa goats (5681) when compared to the Angora goats (2796); and close to eight times the amount compared to the dairy goats (667), due to ascertainment bias. Ascertainment bias is defined as a deviation of the population genetic statistics from the theoretical true value due to non-random selection of individuals (Malomane et al., 2018). It is common during the development of a SNP array when rare (and requisite) SNPs remain undiscovered (Clark et al., 2005), or due to the unintentional exclusion of breed or population-specific SNPs (Kijas et al., 2012). The population sample used in the original caprine SNP discovery process was limited in that there was no breed representation for the African continent nor were there any fibre-producing (e.g. mohair, or cashmere) breeds included to develop the Illumina CaprineSNP50 BeadChip (Tosser-Klopp et al., 2014). In this study ascertainment bias was predicted, as not all SNPs included on the commercial chip were expected to be informative in the indigenous populations for the breeds that were not used in the development of the SNP array. The detection of variants common in those breeds that were included in the development of the array, are thus more likely to detect rare or unique variants, which may skew the MAF (Willing et al., 2012) and influence downstream analyses.

4.2. *Diversity statistics*

Heterozygosity is an important diversity parameter in population genetics, as an increase in inbreeding will lead to a decrease in heterozygosity and a possible decrease in fitness (Hansson & Westerberg, 2002; Monau et al., 2020b). In this study all three populations showed an observed heterozygosity (Tankwa=0.367, Angora=0.349, Dairy=0.388) comparable to other goat breeds (both indigenous and commercial) (Nicoloso et al., 2015; Onzima et al., 2018c; Paim et al., 2019; Monau et al., 2020b). These moderate values indicate that there is no reduction in the fitness of Tankwa goats when compared to other goat populations, even though the population size is small. A previous genetic variation study on 20 individuals from the original Tankwa goats reported observed and expected heterozygosity levels of 0.35 and 0.33 respectively (Mdladla et al., 2016), which are marginally lower than the results obtained in this study (H_E =0.368 and H_O=0.367). The small difference between the two studies is most probably due to the small sample size in the 2016 study.

The MAF reported in this study (Tankwa=0.249, Angora=0.253, Dairy=0.315) corresponds to the values reported in previous studies on other goats. Onzima et al. (2018a) reported MAF ranging from 0.257 to 0.280 for six Ugandan goat breeds, while Mdladla et al. (2016) estimated the MAF for SA Tankwa goats at 0.24. The lower MAF estimated for the Tankwa population relative to the Dairy goat population, can be attributed to ascertainment bias as the breeds in the dairy dataset were used in the development of the SNP array used in this study.

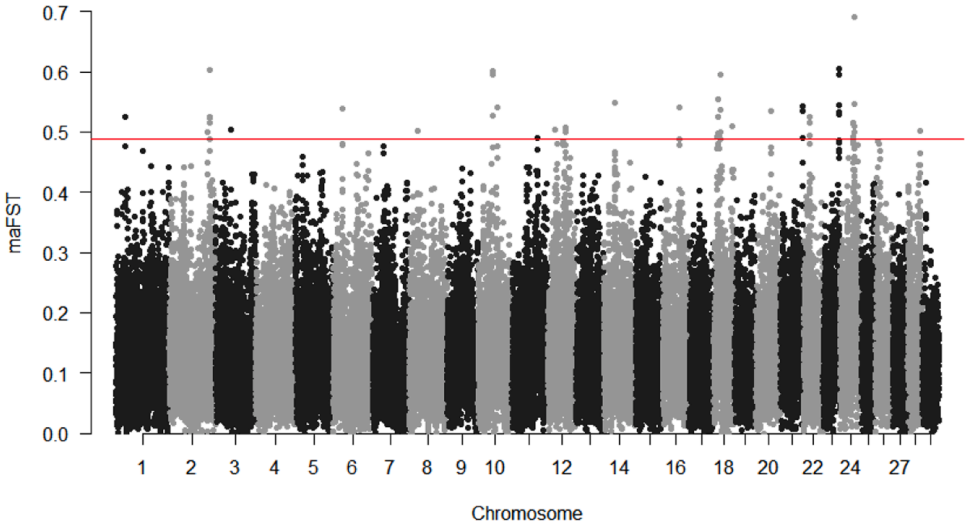

Fig. 3. Manhattan plot of the *ma*F_{ST}-values plotted per chromosome.

Table 4
A sub-set of the identified genes and their functions by chromosome number (Ensembl; UniProt; NCBI).

CHI	Gene	Molecular Function	Biological Process
6	*MTTP*	• Ceramide 1-phosphate transfer activity • Cholesterol transfer activity • Lipid binding • Phosphatidylcholine transfer activity • Phosphatidylethanolamine transfer activity • Protein heterodimerization activity • Triglyceride transfer activity	• Cholesterol homeostasis • Circadian rhythm • Lipoprotein transport • Low-density lipoprotein particle remodelling • Plasma lipoprotein particle assembly • Protein lipidation • Protein secretion • Triglyceride metabolic process • Triglyceride transport
11	*DRC1*	• None	• Axonemal dynein complex assembly • Cilium-dependent cell motility • Determination of left/right symmetry • Heart development
12	*GJA3*	• Gap junction hemi-channel activity	• Cell communication • Gap junction-mediated intercellular transport • **Visual perception**
12	*GJB2*	• Calcium ion binding • Gap junction channel activity involved in cell communication by electrical coupling • Identical protein binding	• Cell-cell signalling • Gap junction assembly • Gap junction-mediated intercellular transport • **Sensory perception of sound**
12	*GJB6*	• Actin filament binding • Beta-tubulin binding • Gap junction channel activity involved in cell communication by electrical coupling • Microtubule binding	• **Ear morphogenesis** • Gap junction assembly • Gap junction-mediated intercellular transport • **Sensory perception of sound**
18	*JPH3*	• None	• **Exploration behaviour** • Learning • Locomotion • Memory • Neuromuscular process controlling balance • Regulation of neuronal synaptic plasticity • Regulation of ryanodine-sensitive calcium-release channel activity
18	*OPA3*	• None	• **Visual perception**
22	*GRM7*	• Adenylate cyclase inhibitor activity • Group III metabotropic glutamate receptor activity • Protein dimerization activity • Serine binding	• Axon development • Chemical synaptic transmission • Glycosylation • **Sensory perception of sound**
24	*ZBTB14*	• DNA-binding transcription repressor activity, RNA polymerase II-specific • RNA polymerase II cis-regulatory region sequence-specific DNA binding	• Cardiac septum development • Coronary vasculature development • Heart valve development • Kidney development
24	*PTPRM*	• Cadherin binding • Identical protein binding • Transmembrane receptor protein tyrosine phosphatase activity	• Homophilic cell adhesion via plasma membrane adhesion molecules • Negative regulation of angiogenesis • Negative regulation of endothelial cell migration • Negative regulation of endothelial cell proliferation • Response to xenobiotic stimulus • **Retina layer formation** • **Retinal ganglion cell axon guidance** • Signal transduction

*Ensembl (https://www.ensembl.org/index.html, accessed 11 May 2022; Zerbino et al., 2018); UniProt (https://www.uniprot.org/, accessed 11 May 2022); NCBI Genome data viewer (https://www.ncbi.nlm.nih.gov/genome/gdv/, accessed 11 May 2022)
Biological functions in bold are directly associated with adaptation and survival.

Ascertainment bias was observed in previous studies on both commercial and indigenous goats (Brito et al., 2017; Tarekegn et al., 2019).

The Tankwa goats showed a higher average linkage disequilibrium (0.469) than the other two populations. Mdladla et al. (2016) also reported a higher r^2 for Tankwa goats than for veld type goats. This is most probably due to the founder effect and population history of the Tankwa goats. The Tankwa goat is a relatively recently formed population that originated from a very limited number of founders.

4.3. Runs of homozygosity and inbreeding

ROH can be used as a measure of inbreeding, with the length of the ROH indicating when the inbreeding occurred (Cardoso et al., 2018). The Tankwa population had a large number of short ROH (<4MB) and very few long ROH (>16MB). This indicates more ancient inbreeding, probably due to the founder effect when the population was formed. This also indicates low levels of recent inbreeding as supported by the inbreeding analysis. The Angora and dairy populations had a higher number of longer ROHs (>16MB) than the Tankwa goats indicating more recent inbreeding. This can probably be explained by the selection emphasis on economically-important traits, as well as the use of a limited number of males with high genetic merit in the management of commercial breeds.

Inbreeding was calculated using both F_{IS} and F_{ROH}. For both measures, the Tankwa goats had lower values (F_{IS}=0.001, F_{ROH}=0.006) compared to the other two populations. The average F_{ROH} values were higher than the F_{IS} values, which can be ascribed to the differences between the two measurements. The F_{IS} value can be negative for an individual or population while the F_{ROH} value is always positive, leading to a higher average (Onzima et al., 2018b). Various commercial breeds were previously studied, with reported F_{IS} values ranging from − 0.05–0.23 (Nicoloso et al., 2015; Visser et al., 2016; Paim et al., 2019). The study by Paim et al. (2019) included indigenous breeds with F_{IS} values ranging from 0.05 to 0.125. This was consistently lower than the commercial breeds in the same study and higher than the Tankwa goats. Cardoso et al. (2018) studied 25 indigenous breeds and used F_{ROH}

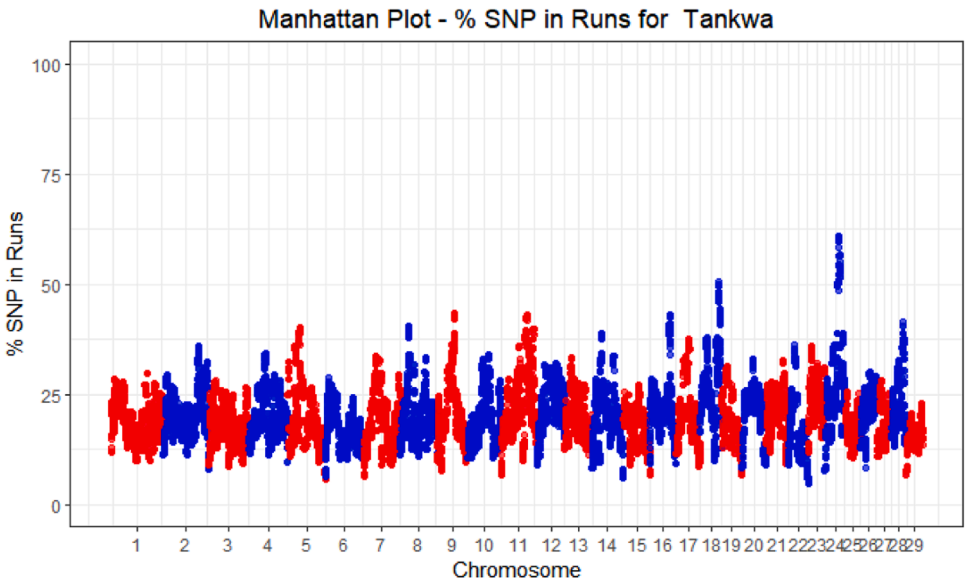

Fig. 4. Manhattan plot of the incidence (in %) that each SNP occur within a specific ROH, plotted per chromosome.

as an estimator of inbreeding. The F_{ROH} values ranged from 0.02 to 0.66 for these 25 breeds, with most breeds (16) having F_{ROH} values below 0.2. Mdladla et al. (2016) also calculated inbreeding for the Tankwa goats and reported a much higher F_{IS} value (0.15). This could probably be attributed to the small sample size (20) or the unintentional inclusion of closely related animals in that study, as no relatedness information was available for selected individuals. In this study a much larger sample size was used.

4.4. Signatures of selection

Of the forty-nine genes identified using the F_{ST} approach, eight genes had no known function with thirty-five of the genes being part of intracellular transport, signalling pathways, organelle structuring and cellular organization. These genes could affect a variety of processes and would need to be studied further to identify and verify specific association with environmental adaptation.

The six remaining genes were associated with vision, hearing, development and learning. Of the possible genes identified *GJB2*, *GJB6* and *GJA3* on CHI12 were the only ones previously associated with adaptation to heat and drought (Kim et al., 2016; Onzima et al., 2018b; Sejian et al., 2019). Genes *GJB2* and *GJB6* are involved in ear morphogenesis and the sensory perception of sound, while *GJA3* is involved in visual perception. These genes were previously identified as genes involved in adaptation to heat stress (Sejian et al., 2019). In addition to *GJA3*, the gene *OPA3* is also involved in visual perception, while *GRM7* on CHI22 is associated with sound perception. The genes associated with vision and hearing could lead to better foraging, however, further studies would be needed to support this. The genes associated with vision and hearing could also be under selection for survival against predators such as jackal and caracal as these goats are free roaming. The *DRC1* gene is associated with development functions of the heart and the determination of left/right symmetry. This gene could probably assist in maintaining the relatively constant heart rate and cardiac output which assist goats to survive and perform better than sheep during heat stress (Sejian et al., 2019). The gene *JPH3* is associated with learning, movement, memory and exploratory behaviour. These aspects are all essential to survival and thus of importance for the Tankwa goat.

Of the forty-nine genes identified using the F_{ST} approach, only nine genes were also identified using the ROH approach. These common genes were associated with general biological functions, such as reproduction and growth. It is significant that the genes associated with adaptation and survival, did not differentiate within the Tankwa population and is possibly conserved within these individuals. The between-population approach compared the Tankwa goat to two breeds that are highly selected and thus highlighted genes that are of importance to the Tankwa goats' survival in their specific environment.

Table 5
Summary statistics of the ROH identified in at least 40% of the Tankwa goat population.

CHI	nSNP	Start bp	End bp
5	3	35345962	35542479
8	12	26161259	26844990
9	40	48288603	50982469
11	16	74026374	74916962
16	25	56384422	57721312
16	4	59316248	59614934
16	6	59846364	60236704
18	74	53294459	57813057
24	115	37378363	45305169
28	3	34575629	34819324

5. Conclusion

This study aimed at investigating the feral Tankwa goat population, with a specific focus on ROH. Results indicate that the Tankwa goat population is currently not at risk of losing genetic diversity as low levels of inbreeding were observed. Continuous monitoring of population parameters is key to ensure that any management decisions do not adversely affect the population. Three genes that have previously been associated with tolerance to heat stress, were identified in the Tankwa population. As these goats have the ability to thrive in challenging environments with no managerial interventions, it would be worthwhile to further explore the metabolic pathways associated with these genes. A deeper understanding of their functions, as well as their interaction with genes associated with behaviour, could prove to be important in a harsh, climate-change environment.

Funding

This work was supported by the Department of Agriculture, Environmental Affairs, Rural Development and Land Reform (DAERL), Northern Cape.

CRediT authorship contribution statement

CV conceptualized the manuscript. CV and SK prepared the first draft. SK performed the statistical analyses. All authors contributed to writing the discussion and editing the final manuscript.

Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Ahmed, S., Kropff, A.S., Jonker, T., Kotze, A., 2018. Can we source the origin of the feral Tankwa goat of South Africa? J. Phylogenetics Evol. Biol. 6, 2. https://doi.org/10.4172/2329-9002.100020.

Ajmone-Marsan, P., Colli, L., Han, J.L., Achilli, A., Lancioni, H., Joost, S., Lenstra, J.A., Italian Goat Consortium, Econogene Consortium, & Globaldiv Consortium., 2014. The characterization of goat genetic diversity: Towards a genomic approach. Small Rumin. Res 121, 58–72 https://doi.org/10.1016/j.smallrumres. 2014.06.010.

Allendorf, F.W., 2017. Genetics and the conservation of natural populations: allozymes to genomes. Mol. Ecol. 26, 420–430. https://doi.org/10.1111/mec.13948.

Amills, M., Capote, J., Tosser-Klopp, G., 2017. Goat domestication and breeding: a jigsaw of historical, biological and molecular data with missing pieces. Anim. Genet 631–644. https://doi.org/10.1111/age.12598.

Benjelloun, B., Alberto, F.J., Streeter, I., Boyer, F., Coissac, E., Stucki, S., BenBati, M., Ibnelbachyr, M., Chentouf, M., Bechchari, A., Leempoel, K., Alberti, A., et al., 2015. Characterizing neutral genomic diversity and selection signatures in indigenous populations of Moroccan goats (*Capra hircus*) using WGS data. Front. Genet 6. https://doi.org/10.3389/fgene.2015.00107.

Bertolini, F., Servin, B., Talenti, A., Rochat, E., Kim, E.S., Oget, C., Palhière, I., Crisà, A., Catillo, G., Steri, R., Amills, M., Colli, L., et al., 2018. Signatures of selection and environmental adaptation across the goat genome post-domestication. Genet. Sel. Evol. 50, 1–24. https://doi.org/10.1186/s12711-018-0421-y.

Biscarini, F., Nicolazzi, E.L., Stella, A., Boettcher, P.J., Gandini, G., 2015. Challenges and opportunities in genetic improvement of local livestock breeds. Front. Genet. 6, 1–7. https://doi.org/10.3389/fgene.2015.00033.

Brito, L.F., Kijas, J.W., Ventura, R.V., Sargolzaei, M., Porto-Neto, L.R., Cánovas, A., Feng, Z., Jafarikia, M., Schenkel, F.S., 2017. Genetic diversity and signatures of selection in various goat breeds revealed by genome-wide SNP markers. BMC Genom. 18, 1–20. https://doi.org/10.1186/s12864-017-3610-0.

Cardoso, T.F., Amills, M., Bertolini, F., Rothschild, M., Marras, G., Boink, G., Jordana, J., Capote, J., Carolan, S., Hallsson, J.H., Kantanen, J., Pons, A., et al., 2018. Patterns of homozygosity in insular and continental goat breeds. Genet. Sel. Evol. 50, 1–11. https://doi.org/10.1186/s12711-018-0425-7.

Chynoweth, M.W., Litton, C.M., Lepczyk, C.A., Hess, S.C., Cordell, S., 2013. Biology and Impacts of Pacific Island Invasive Species. 9. *Capra hircus*, the Feral Goat (Mammalia: Bovidae). Pac. Sci. 67, 141–156 https://doi.org/10.2984/ 67.2.1.

Clark, A.G., Hubisz, M.J., Bustamante, C.D., Williamson, S.H., Nielsen, R., 2005. Ascertainment bias in studies of human genome-wide polymorphism. Genome Res 15 (11), 1496–1502.

Colli, L., Milanesi, M., Talenti, A., Bertolini, F., Chen, M., Crisà, A., Daly, K.G., del Corvo, M., Guldbrandtsen, B., Lenstra, J.A., Rosen, B.D., Vajana, E., et al., 2018. Genome-wide SNP profiling of worldwide goat populations reveals strong partitioning of diversity and highlights post-domestication migration routes. Genet. Sel. Evol. 50, 1–20. https://doi.org/10.1186/s12711-018-0422-x.

Curik, I., Ferenčaković, M., Sölkner, J., 2014. Inbreeding and runs of homozygosity: a possible solution to an old problem. Livest. Sci. 166, 26–34. https://doi.org/10.1016/j.livsci.2014.05.034.

Dolebo, A.T., Khayatzadeh, N., Melesse, A., Wragg, D., Rekik, M., Haile, A., Rischkowsky, B., Rothschild, M.F., Mwacharo, J.M., 2019. Genome-wide scans identify known and novel regions associated with prolificacy and reproduction traits in a sub-Saharan African indigenous sheep (*Ovis aries*). Mamm. Genome 30, 339–352.

El-Halawany, N.K., Abd-El-Razek, F.M., El-Sayed, Y.A., Shawky, A.A., Al-Tohamy, A.F., Abdel-Shafy, H., 2017. Genetic polymorphisms in Exon-3 region of growth hormone gene in the Egyptian goat breeds. Egypt. Acad. J. Biol. Sci. 9, 1–8. https://doi.org/10.21608/eajbsc.2017.13662.

FAO, 2011. Molecular genetic characterization of animal genetic resources. FAO Animal Production and Health Guidelines. No. 9. Rome.

FAO, 2015. The Second Report on the State of the World's Animal Genetic Resources for Food and Agriculture, edited by B.D. Scherf & D. Pilling. FAO Commission on Genetic Resources for Food and Agriculture Assessments. Rome (available at http://www.fao.org/3/a-i4787e/index.html).

Fariello, M.I., Boitard, S., Naya, H., SanCristobal, M., Servin, B., 2013. Detecting signatures of selection through haplotype differentiation among hierarchically structured populations. Genet 193, 929–941. https://doi.org/10.1534/genetics.112.147231.

Gouveia, J.J., de, S., Paiva, S.R., McManus, C.M., Caetano, A.R., Kijas, J.W., Faco, O., Azevedo, H.C., de Araujo, A.M., de Souza, C.J.H., Yamagishi, M.E.B., Carneiro, P.L. S., Lôbo, R.N.B., et al., 2017. Genome-wide search for signatures of selection in three major Brazilian locally adapted sheep breeds. Livest. Sci. J. 197, 36–45. https://doi.org/10.1016/j.livsci.2017.01.006.

Gurgul, A., Semik, E., Pawlina, K., Szmatoła, T., Jasielczuk, I., Bugno-Poniewierska, M., 2014. The application of genome-wide SNP genotyping methods in studies on livestock genomes. J. Appl. Genet 55, 197–208. https://doi.org/10.1007/s13353-014-0202-4.

Hansson, B., Westerberg, L., 2002. On the correlation between heterozygosity and fitness in natural populations. Mol. Ecol. 11 (12), 2467–2474.

Henkel, J., Saif, R., Jagannathan, V., Schmocker, C., Zeindler, F., Bangerter, E., Herren, U., Posantzis, D., Bulut, Z., Ammann, P., Drögemüller, C., Flury, C., et al., 2019. Selection signatures in goats reveal copy number variants underlying breed-defining coat color phenotypes. PLOS Genet 15, 1–18 https://doi.org/10. 1371/journal.pgen.1008536.

Keller, M.C., Visscher, P.M., Goddard, M.E., 2011. Quantification of inbreeding due to distant ancestors and its detection using dense single nucleotide polymorphism data. Genet 189 (1), 237–249.

Kijas, J.W., Lenstra, J.A., Hayes, B., Boitard, S., Porto Neto, L.R., San Cristobal, M., Servin, B., McCulloch, R., Whan, V., Gietzen, K., Paiva, S., 2012. Genome-wide analysis of the world's sheep breeds reveals high levels of historic mixture and strong recent selection. PLoS Biol. 10 (2), e1001258.

Kim, E.S., Elbeltagy, A.R., Aboul-Naga, A.M., Rischkowsky, B., Sayre, B., Mwacharo, J. M., Rothschild, M.F., 2016. Multiple genomic signatures of selection in goats and sheep indigenous to a hot arid environment. Hered. (Edinb.) 116, 255–264. https://doi.org/10.1038/hdy.2015.94.

Kotzé, A., Grobler, J.P., Jonker, T., Dalton, D.L., 2014. The Tankwa Karoo National Park feral goat population: a unique genetic resource. S. Afr. J. Anim. Sci. 44, 43–48. https://doi.org/10.4314/sajas.v44i1.6.

Makina, S.O., Taylor, J.F., Van Marle-Köster, E., Muchadeyi, F.C., Makgahlela, M.L., Macneil, M.D., Maiwashe, A., 2015. Extent of linkage disequilibrium and effective population size in four South African Sanga cattle breeds. Front. Genet 6. https://doi.org/10.3389/fgene.2015.00337.

Malomane, D.K., Reimer, C., Weigend, S., Weigend, A., Sharifi, A.R., 2018. Efficiency of different strategies to mitigate ascertainment bias when using SNP panels in diversity studies. BMC Genom. 19, 22 https://doi.org/10.1186/ s12864-017-4416-9.

Marsoner, T., Egarter, L., Manck, F., Jaritz, G., Tappeiner, U., Tasser, E., 2018. Indigenous livestock breeds as indicators for cultural ecosystem services: a spatial analysis within the Alpine Space. Ecol. Indic. 94, 55–63 https://doi.org/10. 1016/j.ecolind.2017.06.046.

Martínez, A., Ferrando, A., Manunza, A., Gómez, M., Landi, V., Jordana, J., Capote, J., Badaoui, B., Vidal, O., Delgado, J.V., Amills, M., 2012. Inferring the demographic history of a highly endangered goat breed through the analysis of nuclear and mitochondrial genetic signatures. Small Rumin. Res. 104, 78–84. https://doi.org/10.1016/j.smallrumres.2011.11.012.

Mdladla, K., Dzomba, E.F., Huson, H.J., Muchadeyi, F.C., 2016. Population genomic structure and linkage disequilibrium analysis of South African goat breeds using genome-wide SNP data. Anim. Genet. 47, 471–482. https://doi.org/10.1111/age.12442.

Mdladla, K., Dzomba, E.F., Muchadeyi, F.C., 2018. Landscape genomics and pathway analysis to understand genetic adaptation of South African indigenous goat populations. Heredity 120, 369–378. https://doi.org/10.1038/s41437-017-0044-z.

Meek, M.H., Wells, C., Tomalty, K.M., Ashander, J., Cole, E.M., Gille, D.A., Putman, B.J., Rose, J.P., Savoca, M.S., Yamane, L., Hull, J.M., Rogers, D.L., et al., 2015. Fear of failure in conservation: the problem and potential solutions to aid conservation of extremely small populations. Biol. Conserv. 184, 209–217. https://doi.org/10.1016/j.biocon.2015.01.025.

Monau, P., Raphaka, K., Zvinorova-Chimboza, P., Gondwe, T., 2020a. Sustainable utilization of indigenous goats in Southern Africa. Diversity 12, 1–9 https://doi. org/10.3390/d12010020.

Monau, P.I., Visser, C., Muchadeyi, F.C., Okpeku, M., Nsoso, S.J., Van Marle-Köster, E., 2020b. Population structure of indigenous southern African goats based on the Illumina Goat50K SNP panel. Trop. Anim. Health Prod. 52, 1795–1802.

Moradi, M.H., Nejati-Javaremi, A., Moradi-Shahrbabak, M., Dodds, K.G., McEwan, J.C., 2012. Genomic scan of selective sweeps in thin and fat tail sheep breeds for identifying of candidate regions associated with fat deposition. BMC Genet 13. https://doi.org/10.1186/1471-2156-13-10.

Nicoloso, L., Bomba, L., Colli, L., Negrini, R., Milanesi, M., Mazza, R., Sechi, T., Frattini, S., Talenti, A., Coizet, B., Chessa, S., Marletta, D., et al., 2015. Genetic diversity of Italian goat breeds assessed with a medium-density SNP chip. Genet. Sel. Evol. 47. https://doi.org/10.1186/s12711-015-0140-6.

Onzima, R.B., Upadhyay, M.R., Doekes, H.P., Brito, L.F., Bosse, M., Kanis, E., Groenen, M.A.M., Crooijmans, R.P.M.A., 2018a. Genome-wide characterization of selection signatures and runs of homozygosity in Ugandan goat breeds. Front. Genet. 9, 1–13. https://doi.org/10.3389/fgene.2018.00318.

Onzima, R.B., Gizaw, S., Kugonza, D.R., Van Arendonk, J.A.M., Kanis, E., 2018b. Production system and participatory identification of breeding objective traits for indigenous goat breeds of Uganda. Small Rumin. Res. 163, 51–59. https://doi.org/10.1016/j.smallrumres.2017.07.007.

Onzima, R.B., Upadhyay, M.R., Mukiibi, R., Kanis, E., Groenen, M.A.M., Crooijmans, R.P. M.A., 2018c. Genome-wide population structure and admixture analysis reveals weak differentiation among Ugandan goat breeds. Anim. Genet. 49, 59–70. https://doi.org/10.1111/age.12631.

Paim, T., do, P., Faria, D.A., Hay, E.H., McManus, C., Lanari, M.R., Esquivel, L.C., Cascante, M.I., Alfaro, E.J., Mendez, A., Faco, O., Silva, K., de, M., Mezzadra, C., et al., 2019. New world goat populations are a genetically diverse reservoir for future use. Sci. Rep. 9. https://doi.org/10.1038/s41598-019-38812-3.

Peripolli, E., Munari, D.P., Silva, M.V.G.B., Lima, A.L.F., Irgang, R., Baldi, F., 2016. Runs of homozygosity: current knowledge and applications in livestock. Anim. Genet. 48, 255–271. https://doi.org/10.1111/age.12526.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M.A.R., Bender, D., Maller, J., Sklar, P., De Bakker, P.I.W., Daly, M.J., Sham, P.C., 2007. REPORT PLINK: A Tool Set for Whole-Genome Association and Population-Based Linkage Analyses. Am. J. Hum. Genet 81, 559–575. https://doi.org/10.1086/519795.

Purfield, D.C., Berry, D.P., McParland, S., Bradley, D.G., 2012. Runs of homozygosity and population history in cattle. BMC Genet 13, 70. https://doi.org/10.1186/1471-2156-13-70.

Purfield, D.C., McParland, S., Wall, E., Berry, D.P., 2017. The distribution of runs of homozygosity and selection signatures in six commercial meat sheep breeds. PLoS One 12. https://doi.org/10.1371/journal.pone.0176780.

Qanbari, S., Simianer, H., 2014. Mapping signatures of positive selection in the genome of livestock. Livest. Sci. 166, 133–143. https://doi.org/10.1016/j.livsci.2014.05.003.

R.Studio Team. 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

Saravanan, K.A., Panigrahi, M., Kumar, H., Bhushan, B., Dutt, T., Mishra, B.P., 2020. Selection signatures in livestock genome: a review of concepts, approaches and applications. Livest. Sci., 104257 https://doi.org/10.1016/j.livsci.2020.104257.

Sejian, V., Bagath, M., Krishnan, G., Rashamol, V.P., Pragna, P., Devaraj, C., Bhatta, R., 2019. Genes for resilience to heat stress in small ruminants: a review. Small Rumin. Res. 173, 42–53. https://doi.org/10.1016/j.smallrumres.2019.02.009.

Talenti, A., Bertolini, F., Pagnacco, G., Pilla, F., Ajmone-Marsan, P., Rothschild, M.F., Crepaldi, P., The Italian Goat Consortium., 2017. The Valdostana goat: a genome-wide investigation of the distinctiveness of its selective sweep regions. Mamm. Genome 28, 114–128. https://doi.org/10.1007/s00335-017-9678-7.

Tarekegn, G.M., Wouobeng, P., Jaures, K.S., Mrode, R., Edea, Z., Liu, B., Zhang, W., Mwai, O.A., Dessie, T., Tesfaye, K., Strandberg, E., 2019. Genome-wide diversity and demographic dynamics of Cameroon goats and their divergence from east African, north African, and Asian conspecifics. Plos One 14 (4), e0214843.

Tosser-Klopp, G., Bardou, P., Bouchez, O., Cabau, C., Crooijmans, R., Dong, Y., Donnadieu-Tonon, C., Eggen, A., Heuven, H.C.M., Jamli, S., Jiken, A.J., Klopp, C., et al., 2014. Design and characterization of a 52K SNP chip for goats. PLoS One 9, 1–8. https://doi.org/10.1371/journal.pone.0086227.

Visser, C., 2019. A review on goats in southern Africa: an untapped genetic resource. Small Rumin. Res 176, 11–16 https://doi.org/10.1016/j.smallrumres.2019.05. 009.

Visser, C., Lashmar, S.F., Van Marle-Köster, E., Poli, M.A., Allain, D., 2016. Genetic diversity and population structure in South African. Fr. Argent. Angora goats Genome-wide SNP data. PLoS One 11 https://doi.org/10. 1371/journal.pone.0154353.

Webb, E.C., Mamabolo, M.J., 2004. Production and reproduction characteristics of South African indigenous goats in communal farming systems. S. Afr. J. Anim. Sci. 34, 236–239.

Weir, B.S., Cockerham, C.C., 1984. Statistics for the analysis of population structure. Evol. (N. Y) 1358–1370. https://doi.org/10.1111/j.1558-5646.1984.tb05657.x.

Willing, E.M., Dreyer, C., van Oosterhout, C., 2012. Estimates of genetic differentiation measured by F_{ST} do not necessarily require large sample sizes when using many SNP markers. PLoS One 7, 1–7. https://doi.org/10.1371/journal.pone.0042649.

World Weather Online. ⟨https://www.worldweatheronline.com/kompromise-weather-averages/northern-cape/za.aspx⟩ (accessed 10 July 2023).

Zhang, Q., Calus, M.P.L., Guldbrandtsen, B., Lund, M.S., Sahana, G., 2015. Estimation of inbreeding using pedigree, 50k SNP chip genotypes and full sequence data in three cattle breeds. BMC Genet 16. https://doi.org/10.1186/s12863-015-0227-7.

Zhao, F., McParland, S., Kearney, F., Du, L., Berry, D.P., 2015. Detection of selection signatures in dairy and beef cattle using high-density genomic information. Genet. Sel. Evol. 47. https://doi.org/10.1186/s12711-015-0127-3.

Zheng, Z., Wang, X., Li, M., Li, Y., Yang, Z., Wang, X., Pan, X., Gong, M., Zhang, Y., Guo, Y., Wang, Y., Liu, J., Cai, Y., et al., 2020. The origin of domestication genes in goats. Sci. Adv. 6. https://doi.org/10.1126/sciadv.aaz5216.