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Population genomics and gene introgression in goat herds naturally adapted to Brazil[1]

Genômica populacional e introgressão gênica em rebanhos caprino naturalmente adaptado ao Brasil

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ABSTRACT - The aim of this study was to apply the Illumina 50 K goat SNP Chip to analyse population genomic structure in two herds of Marota goats in the State of Piauí, one private and the other an official conservation herd, and to investigate evidence of genetic erosion in these herds caused by the Anglo-Nubian goat. To that end, 86 Marota and 10 Anglo-Nubian animals were genotyped. Genetic diversity was analysed by comparing minor allele frequency (MAF) in the herds. Population structure and genetic differentiation were evaluated using a Bayesian approach, principal component analysis (PCA) and the fixation index (F_{ST}). High genetic differentiation (F_{ST} = 0.16) was seen in the Marota population in relation to the Anglo-Nubian. The private herd shared a greater number of fixed SNPs with the herd of Anglo-Nubians (1024) than did the conservation herd (741). The results of the PCA, together with those from the analysis carried out using the Structure software, showed the presence of Anglo-Nubian genes in the Marota herds. It can therefore be concluded that the high level of polymorphism and high genetic differentiation between Marota and Anglo-Nubian goats characterise these animals as a source of genetic diversity for goat farming in the region; the Illumina 50 K goat SNP Chip is efficient in population structure analysis in Marota goats; microarray technology, analysis using the Structure software, and Principal Component Analysis complement each other in expanding the ability to detect gene introgression in small populations; there is evidence of the introgression of Anglo-Nubian genes in the herds of Marota goats under analysis.

Key words: SNP chip. Population structure. Genetic resources.

RESUMO - Objetivou-se aplicar *Chip* SNP caprinos 50 K da *Illumina* para analisar a estrutura genômica populacional em dois rebanhos de caprinos Marota, um particular e outro de conservação oficial, localizados no Piauí, e na investigação de indícios de erosão genética provocada pela raça Anglonubiana nesses rebanhos. Para isso, 86 animais Marota e 10 Anglonubianos foram genotipados. A diversidade genética foi analisada comparando-se alelos de menor frequência (MAF) nos rebanhos. A estrutura populacional e diferenciação genética foram avaliadas utilizando-se abordagem bayesiana, análise de componentes principais (PCA) e o índice de fixação (F_{ST}). A diferenciação genética alta (F_{ST} = 0,16) foi observada na população Marota em relação à população Anglonubiana. O rebanho particular compartilhou maior número de SNPs fixados com o rebanho Anglonubiano (1024) do que o rebanho de conservação oficial (741). Os resultados da PCA, juntamente com os da análise do *Structure*, mostraram a presença de genes Anglonubianos nos rebanhos Marota. Logo, conclui-se que elevado nível de polimorfismo e diferenciação genética alta entre caprinos Marota e Anglonubianos caracterizam esses animais como fonte de diversidade genética para a caprinocultura da região; o C*hip* SNP caprino 50 K da *Illumina* mostra-se eficiente para análise de estrutura populacional em caprinos Marota; as tecnologias de microarranjos, análises do programa *Structure* e Análise de Componentes Principais se complementam para ampliar a capacidade de detecção de introgressão gênica em pequenas populações; há indício de introgressão gênica da raça Anglonubiana nos rebanhos de caprinos Marota analisados.

Palavras-chave: *Chip* SNP. Estrutura populacional. Recursos genéticos.

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INTRODUCTION

Goats were first brought to Brazil by Portuguese settlers, and were bred with no regard for zootechnical practices or for selection directed at production. Breeding was disorganised and, through a process of natural selection, gave rise to the various ethnic types currently found in the country (BARROS *et al*., 2011). They were mainly concentrated in arid and semi-arid regions, where they play an important social, economic and nutritional role (SILVA *et al*., 2015).

Among these animals, the Marota genetic group should be mentioned; naturally adapted to the semi-arid region of Brazil, and a source of genes that favour adaptation to the hardships of this ecosystem (ARAÚJO *et al*., 2009), the group is now being replaced by more-productive breeds, and is at risk of extinction.

Animal genetic resources developed in the semi-arid environment may present possibly unique combinations of genes (BARROS *et al*., 2011) which are related to hardiness, as they have been shaped by nature in response to inclement environmental conditions. These animals can contribute important characteristics (TORO; FERNÁNDEZ; CABALLERO, 2009), thereby justifying the need to maintain their identity as genetic groups in this environment; genetic erosion caused by mixing with other breeds should therefore be avoided.

Genetic erosion is a threat to groups at risk of extinction, such as the Marota group of goats, and is a high risk imposed by the introgression of standardised commercial breeds, like the Anglo-Nubian, a breed that is present in most of the herds of the northeast, demonstrating its regional importance (OLIVEIRA *et al*., 2009; SILVESTRE *et al.*, 2015) and capacity to adapt to the hot environment.

The conservation of animal genetic resources includes the maintenance of genetic diversity for those characteristics allowing adaptation to the Brazilian semi-arid environment (ARAÚJO *et al*., 2009; CARVALHO *et al*., 2015); molecular tools permit the levels of genetic variation in the population to be monitored, allowing management activities to be planned that aim to avoid a decline in the genetic variability of conservation herds (BRITO *et al*., 2017).

It was with the aim of facilitating the genetic study of goats that in 2010 the IGGC (International Goat Genome Consortium) proposed the creation of an SNP chip specific to goats, of moderate density (50-60 K), segregating with high to moderate frequency in the Alpine, Boer, Crioulo, Katjang, Saanen and Savanna breeds (TOSSER-KLOPP *et al*., 2014). This had a positive effect on the genetic research of the species (LASHMAR; VISSER; VAN MARLE-KÖSTER, 2015).

This technology has been useful, from characterising the level of genetic diversity (KIJAS *et al*., 2013), to the identification of genes associated with specific and important biological functions (ARAÚJO; CAETANO, 2016; KIJAS *et al*., 2013; RESENDE *et al*., 2008).

The aim of this work, therefore, was to apply the Illumina 50 K goat SNP Chip to the study of population genomic structure in two herds of Marota goats in the State of Piauí, one an official conservation herd *in situ* and the other a private herd, and to investigate evidence of genetic erosion in these herds caused by the Anglo-Nubian goat.

MATERIAL AND METHODS

Ethics Statement

All procedures carried out on the animals are in accordance with the norms of the Ethics and Research Committee of the Federal University of Piauí, registration number 058/14.

Analysed herds

A sample of 86 goats of the Marota genetic group were used in the analysis. Of these, 76 were sampled *in situ* from the conservation herd maintained by Embrapa Meio Norte in the district of Castelo de Piauí, in the State of Piauí (PI) (05º19’20” S and 41º33’09” W); a further 10 animals were sampled from a private herd, located in the district of Elesbão Veloso, PI (06º12’07” S and 42º08’25” W). The animals comprising the samples were chosen at random, with around 31% of the animals from each herd being genotyped.

Given the large participation of the Anglo-Nubian breed in the herds of Piauí, 10 Anglo-Nubian animals from the UFPI herd in Teresina, PI (05º02‟39,95” S, 42º47‟03,70” W) were genotyped, in order to investigate the possibility of gene introgression from this breed to the populations under study.

Collecting blood, extracting DNA and genotyping

Three ml of blood were collected from each animal by vacuum puncture of the jugular vein. The tube used contained the glycolytic inhibitor sodium fluoride and EDTA to preserve cell morphology and maintain the quality of the sample.

The DNA isolation procedure was carried out using the AxyPrep Blood Genomic DNA Miniprep Extraction Kit (Code AP-MN-BL-GDNA-50).

The 96 samples were then genotyped using the Illumina 50 K goat SNP Chip, containing 53,347 SNPs

evenly spaced on the chromosomes. The Chip was produced as per Illumina™ Infinium technology, using the iScan platform.

The genotyping protocol established by the manufacturer (ILLUMINA, 2013) was followed, carrying out respectively: 1) Isothermal DNA amplification; 2) Overnight incubation of the samples; 3) Fragmentation of the samples; 4) Precipitation and resuspension of the fragmented DNA; 5) Preparation of the BeadChip, 6) Overnight hybridisation, 7) Single-base enzyme extension, 8) Image visualisation using the iScan platform, and 9) Generation of results stored in spreadsheets.

Data Quality Control

The Plink v 1.9 software (PURCELL *et al*., 2007) was used for quality control during genotyping, the use of quality control procedures in studies with SNP Chips having the function of removing laboratory errors in genotyping and genotype calling (ANDERSON *et al*., 2010).

Samples with a Call Rate lower than 80% were eliminated from the analysis, and the following criteria were applied to identify informative molecular markers for each goat group: SNPs with a Call Rate greater than 90% were used in the analysis of genetic diversity; in analysing population genetic structure, SNPs common to these two genetic groups were used which had a Call Rate greater than 90%, a Minor Allele Frequency (MAF) greater than 1% and that were in Hardy-Weinberg Equilibrium (HWE), as determined by Fisher's exact test with 1,000 permutations, at a probability of over 5%.

Diversity Analysis and Population Genetic Structure

The basic indices of genetic diversity, including the percentage of polymorphic markers and allele frequencies, were calculated using the Hierfstat package (v 0.04-22, 2005) of the R platform (The R Project for Statistical Computing, v 3.2.3) (GOUDET, 2005).

The allele frequencies were obtained for each group. Based on the MAF, rare alleles (MAF less than 0.01) and fixed alleles (MAF equal to zero) were then identified in the herds. Polymorphic alleles were defined as those with an MAF between 0.01 and 0.50. In addition to this classification, the alleles were further defined as highly polymorphic when they presented MAF values between 0.30 and 0.50. Comparative analysis was used to identify fixed, rare or polymorphic SNPs in the genome of each genetic group. These analyses were carried out using the Plink v 1.9 software (PURCELL *et al*., 2007).

Genetic differentiation between the groups was calculated using the inbreeding coefficient between subpopulations (F_{ST}), obtained using the Hierfstat package of the R software (GOUDET, 2005).

In order to identify a subdivision between and within populations, and evidence of genetic erosion caused by the Anglo-Nubian breed, the Structure v 2.3.3 software (PRITCHARD; STEPHENS; DONNELLY, 2000) was used, with the number of groups (K) ranging from two to nine. Ten runs of 10,000 iterations, after one run of 10,000 iterations, were performed for each K. The Admixture sample model was used in the program, with no *a priori* population information. The most probable number of genetic groups formed by the reulting data was estimated using the ΔK method (EVANNO; REGNAUT; GOUDET, 2005).

In order to complement the results of the Structure software regarding the quantification of genetic erosion, the relationship between the herds was assessed by Principal Component Analysis (PCA), estimated from the Euclidean distance matrix, and obtained with the Plink v 1.9 software (PURCELL *et al*., 2007).

RESULTS AND DISCUSSION

Quality control and diversity analysis

It was found that each sample had a Call Rate greater than 80%, thus not violating the criterion established for quality control; therefore, no sample was excluded from the analysis, and all 96 animals were used in the study. In relation to the markers, the number of SNPs with a Call Rate greater than 90% was high in both the Marota goats and the Anglo-Nubian samples, showing that 98.97% and 97.79% respectively of the 53,347 SNPs that comprise the Chip being used did not violate the established quality criteria.

Despite the Marota and Anglo-Nubian goats not being included in those genotyped to construct the 50 K Goat SNP BeadChip launched by Illumina, the high Call Rate values of the samples and markers showed that this Chip displayed good genotyping quality, confirming its use for characterising genetic diversity in goats.

As such, these animals join other goat groups that are also not at the heart of its construction, but whose genotyping was considered of good quality, helping to reduce the scarcity of genomic information for this species. By way of example are the results of Tosser-Klopp *et al*. (2014), who validated the same Chip for goats of the Angora, Jinlan and Skopelos breeds. Similarly, Kijas *et al*. (2013), who successfully used the same Chip for studies on diversity in goats of the Boer, Cashmere and Rangelang breeds. The same Chip was also validated in Angora goats

from southern Africa by Lashmar, Visser and Van Marle-Köster (2015).

The percentage of polymorphic SNPs (0.01<AMF<0.5) presented by the Marota and Anglo-Nubian animals was 97.8% and 99.4% respectively. In broad-perspective analysis, the high level of polymorphism (Table 1) is within the range of variation presented in the literature by Kijas *et al*. (2013) in Australian populations of Boer (97.1%), Cashmere (98%) and Rangeland (99.6%) goats; and by Lashmar, Visser and Van Marle-Köster (2015), who tested the efficiency of the Chip in South-African Angora goats, and found 88.1% polymorphic SNP.

When only highly polymorphic SNPs (0.3<MAF<0.5) are considered, the Anglo-Nubian goats stand out in relation to the Marota goats, with 53.7% of their SNPs being highly polymorphic compared to 39.2% found in the Marota goats (Table 1). Changing the breeding stock every two years in the Anglo-Nubian herd, and mating without favouring inbreeding may have influenced the result.

It can be seen that only the Marota goats presented SNPs with rare alleles (MAF<0.01) (Table 1), which can be explained by the smaller sample of Anglo-Nubians used in the analysis, since it is more difficult to find rare alleles in a smaller sample. To complement this discussion, the fixed SNPs that are unique and common to both groups of animals are shown in the Venn diagram (Figure 1).

The large number of fixed and exclusive genes found in the Marota animals (587) and the Anglo-Nubian animals (1513) (Figure 1A), may also have influenced the process of selection to which they were subjected, since according to McManus, Paiva and Louvandini (2010), the response to natural selection in the Marota goat was to sacrifice productive performance for adaptation to the breeding environment.

According to Silvestre *et al*. (2015), the use of breeding stock from the herd itself, with replacement giving priority to those of well-defined racial standard, is a procedure that leads to the fixing of alleles, especially in small herds. Such management occurs in the Marota herds under analysis, helping to increase genetic uniformity and making the herd vulnerable; genetic variability is a guarantee of species survival, which allows it to adapt to changes in the environment.

The number of fixed SNPs in the private Marota herd (3,817) (Figure 1B) was greater than seen in the official Marota herd (1,811) (Figure 1C). Disregarding the difference in size between the samples, this result can also be attributed to the private herd having only one reproductive animal, while the official herd had 18.

There is also the possibility of gene introgression from the Anglo-Nubian breed, which is prevalent in the herds of northeastern Brazil (MALHADO *et al*., 2008). This was mainly seen in the private herd, which shared 1024 fixed SNPs with the Anglo-Nubian herd (Figure 1B), greater than the number of fixed SNPs shared between the official herd and the Anglo-Nubian herd (741) (Figure 1C).

An F_{ST} of 0.16 indicates significant genetic differentiation between the Marota animals and the Anglo-Nubians, showing that the Marota goats retain their identity and are genetic material that should continue to be preserved.

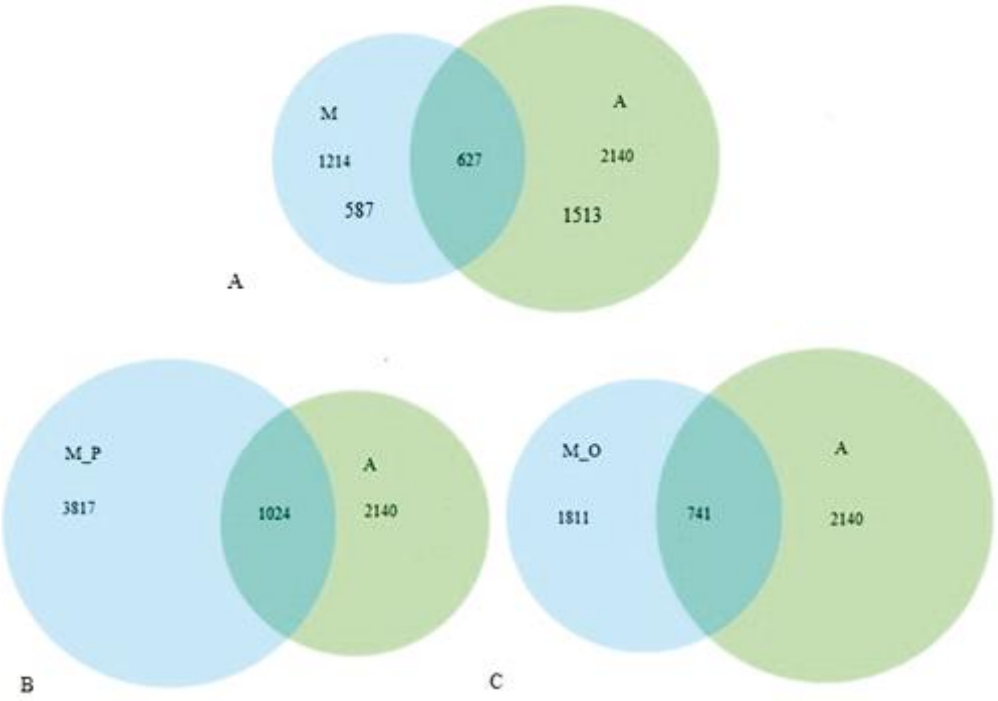
Similar considerations were presented by Grasso *et al*. (2014), who compared Creole sheep with animals from the commercial Corriedale and Merino breeds, and found F_{ST} values of 0.16 and 0.1 respectively. Between

Table 1 - Minor Allele Frequency (MAF) in the conservation herd of Marota goats and the herd of Anglo-Nubian goats, determined with the 50K goat SNP Chip

Goat	Minor Allele Frequency - MAF							
	Allele	Min	Max	Median	Mean	Variance	SD	SNPs
Marota	All	0.000	0.500	0.244	0.242	0.023	0.151	53.040
	Rare	0.006	0.007	0.000	0.002	0.000	0.000	865
	Polimorphic	0.012	0.500	0.256	0.254	0.021	0.145	52.175
	Highly Polimorphic	0.300	0.500	0.401	0.401	0.003	0.055	20.893
Anglo-Nubian	All	0.000	0.500	0.300	0.279	0.020	0.143	53.040
	Rare	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Polimorphic	0.050	0.500	0.300	0.294	0.017	0.131	53.040
	Highly Polimorphic	0.300	0.500	0.400	0.391	0.004	0.063	28.672

Min and Max are the minimum and maximum values of the MAF respectively. SD - Standard Deviation

Figure 1 - Venn diagrams showing fixed SNPs (MAF = 0) and common SNPs between Marota and Anglo-Nubian goats. Joint and individual analysis of the private Marota Herd (M_P) and the Official Marota Herd (M_O)



the commercial breeds, the F_{ST} value was only 0.08, showing that the commercial breeds are more related to each other than to the Creole breed, a result attributed by the authors to the long period of natural selection to which the Creole animals were subjected.

Evaluating population structure and genetic erosion

For a more detailed evaluation of the variability of the Marota goats, the population structure was analysed using 47,398 SNPs present in the two sampled groups that presented an MAF>1% and CR>90%, and were in HWE.

The groupings provided by the Structure software, based on the Bayesian method, are shown in Figure 2B; assuming that there are two populations (K=2), which are determined by Δk (EVANNO; REGNAUT; GOUDET, 2005). For K=2, the Marota and Anglo-Nubian genetic groups were clearly differentiated (Figure 2A).

It could be seen that the observed variability might have been associated with a specific genetic origin: in the case under study, with the introgression of Anglo-Nubian genes to the Marota herds under analysis (Figure 2B). Introgression of Anglo-Nubian genes was seen in both the official Marota herd and in the private herd, which increases the risk of genetic erosion and, according to Núñez-Domínguez *et al*. (2016), is included as a factor to be considered in the conservation and sustainable use of animal genetic resources.

Figure 3 demonstrates that the spread of the animals on a Cartesian plane formed by the first two principal components showed a distinct separation of the two genetic groups, which together explained 13.25% of the variation (9.71% and 3.52% respectively).

The complementarity of the techniques in better explaining the variability becomes evident when the results shown in Figures 2B and 3 are superimposed. It can be seen that despite the *in situ* official conservation herd being closed, some animals have spread, indicating a herd with a certain degree of genetic diversity. However, when evaluating this result with those obtained by the Structure software, one of the causes of this spread becomes obvious - the presence of Anglo-Nubian genes.

By way of illustration, it can be seen that one Marota goat from the private herd was closer to the Anglo-Nubian goats (Figure 3), indicating a large participation of the Anglo-Nubian breed in its composition.

The possible introgression of genes from other breeds to the private herd should also be considered, since the herd is under development, including the probable introduction of animals from other herds, generally without

Figure 2 - A) Delta K, showing the peak of highest probability for K=2; B) Population structure analysis estimated from 47,398 SNPs, considering two groups (K=2). Each individual is represented by a vertical line divided by coloured segments K, representing the estimated fraction belonging to each group (C is the official herd and F the private herd)

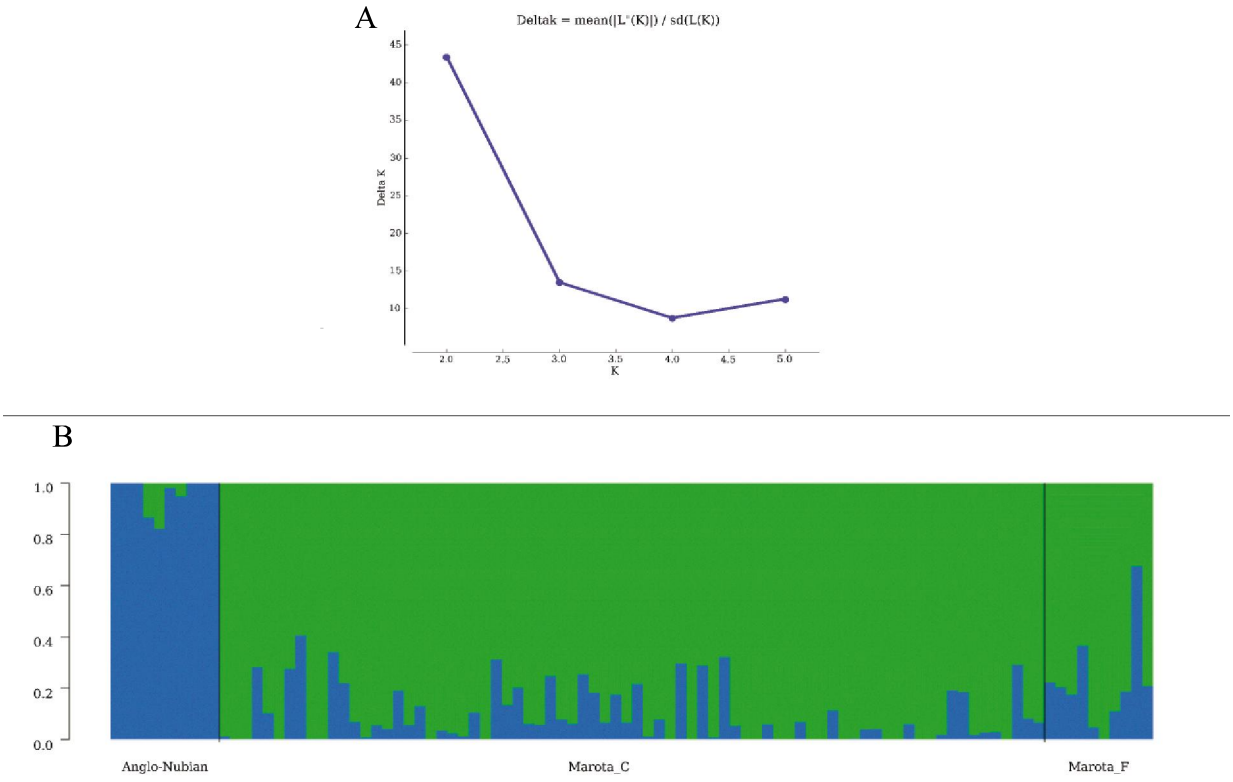
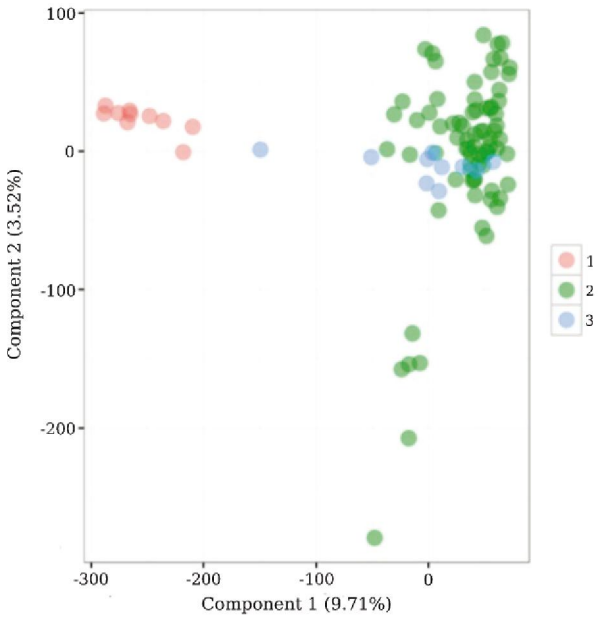


Figure 3 - Population structure analysis estimated from 47,398 SNPs by Principal Component Analysis: (1 - Anglo-Nubian goats, 2-Marota goats from the official herd, 3 – Marota goats from the private herd)



accurate genetic analysis, and sometimes only requiring that the animal exhibit standard phenotypic characteristics of the Marota goat.

The two analyses obtained with the data from the microarrays proved to be applicable for verifying gene introgression in populations at risk of extinction. PCA complements the results of the Structure software in detecting gene introgression, and can be recommended as a suitable technological package for monitoring conservation herds.

Furthermore, with precise knowledge of the participation of commercial breeds in the animals of the *in situ* conservation herd, it is possible to identify individually those most suitable for breeding in order to maintain breed purity and variability, and guide the disposal of animals of no conservational interest.

CONCLUSIONS

1. The high level of polymorphism and high genetic differentiation between Marota and Anglo-Nubian

goats characterise these animals as a source of genetic diversity for goat farming in the region;

2. The Illumina 50 K goat SNP Chip is efficient in population structure analysis in Marota goats, a genetic group naturally adapted to the semi-arid environment of Brazil;

3. Microarray technology, analysis using the Structure software, and Principal Component Analysis complement each other in expanding the ability to detect gene introgression in small populations;

4. There is evidence of the introgression of Anglo-Nubian genes in the herds of Marota goats under analysis, which shows the importance of institutionalising conservation programs in Brazil and of monitoring genetic erosion in herds of those breeds at risk of extinction.

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