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RESEARCH ARTICLE

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Genetic diversity of the Northern Morocco goat population assessed with microsatellite markers

Najat El Moutchou[1,2], Ana M. González-Martínez[2], Mouad Chentouf[3], Khalid Lairini[1] and Evangelina Rodero[2]

[1]University Abdelmalek Essaâdi, Fac. Science and Technology, Km 10 Ziaten, BP 416, Tangier, Morocco [2]University of Cordoba, Department of Animal Production, Campus of Rabanales, ceiA3. 14071. Córdoba, Spain. [3] National Institute of Agricultural Research, Regional Centre of Tangier, 78 Avenue Sidi Mohamed Ben Abdellah, 90010 Tangier, Morocco.

Abstract

The main goal of this work was to study the genetic diversity of the Northern Morocco goat population through the analysis of 19 microsatellites in 144 animals from 61 herds. To detect a possible population structure, three distinct geographic subpopulations were characterized as a function of climate and environmental influences. Most of the markers were highly polymorphic, and the results revealed considerable genetic variation across the studied loci. A total of 204 alleles were detected, with an average number of 10.7 per locus. The PIC average was 0.728, and four microsatellites showed a significant deviation ($p< 0.05$) from Hardy-Weinberg Equilibrium. Analysis of molecular variance (AMOVA) indicated that only 0.5% of the variation corresponded to differences among subpopulations, and 99.5% corresponded to differences among individuals. Factorial correspondence analysis showed intense admixtures across the putative subpopulations, and the subdivision related to geographical or environmental adaptation was undetectable. The Northern Morocco goat population presented high genetic diversity and a lack of population structure. The main reason for these findings is the absence of the breed concept (reproductively closed population), resulting in uncontrolled crossbreeding with exotic breeds and other local goats.

Additional keywords: animal genetic resources; local population; sustainable development.

Abbreviations used: AFC (Factorial correspondence analysis); AMOVA (Analysis of Molecular Variance); An (Number of alleles per locus); FIS (Inbreeding coefficient of an individual relative to the subpopulation); FIT (Inbreeding coefficient of an individual relative to the total population); FST (Effect of subpopulations compared to the total population); He (Expected heterozygosity); Ho (Observed heterozygosity); PIC (Polymorphic Information Content).

Authors' contributions: Conceived, designed, performed the experiments, analyzed the data and wrote the paper: NEM, AMGM, and ER. Contributed reagents/materials/analysis tools: ER and MC. All authors read and approved the final manuscript.

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Correspondence should be addressed to Najat El Moutchou: najatelmoutchou@gmail.com

Introduction

Molecular genetic characterization is the first approach for the sustainable use of animal genetic resources. In the absence of genetic information, development of local populations is often ignored in favour of the introduction of exotic breeds. Therefore, characterization of breeds is essential at both the level of animal phenotypes and genetic variability (FAO, 2007, 2011, 2013). Microsatellite marker analysis is very indicative of the historical progression of breeds by showing the evolution and differentiation of animal populations; this technique has been used in genetic diversity studies of European, African and American goats (Ajmone-Marsan *et al*., 2014).

In Morocco, three major goat populations have been identified according to their geographic location or production system: the Black population (with three subpopulations: Atlas, Barcha, and Ghazalia), the Draa population and the Northern population (Ibnelbachyr *et al*., 2015). The genetic characterization of Moroccan goats using microsatellites has been limited to studies of the Draa (Tadlaoui Ouafi *et al*., 2002), Black Rahalli breeds (Ouragh *et al*., 2012) and the Hamra population (Hilal *et al*., 2016). Previous studies reporting the genetic structure and diversity of Moroccan goat

populations have been achieved using mitochondrial DNA markers (Benjelloun *et al*., 2011) and WGS data (Benjelloun *et al*., 2015).

In Northern Morocco, the goat herding sector plays a vital role in the socioeconomic development of the region, providing more than 70% of the revenue in rural communities (Chentouf *et al*., 2011) and includes approximately 788,000 goats; these goats represent 13% of the total census in Morocco and 43% of the total small ruminants in the region (Chentouf, 2014). In a previous study, morphological differentiation was conducted in this goat population based on measurable and qualitative morphological traits, considering that this population was likely subdivided into three subpopulations according to geographic location, origin and breed influences (El Moutchou *et al*., 2014, 2017). The results showed high phenotypic variability, very heterogeneous subpopulations and undetectable differences among the groups. In the literature, the goats of Northern Morocco are related to Spanish and French breeds such as Murciana, Malagueña and Serrana Andaluza (Benlekhal & Tazi, 1996; Analla & Serradilla, 1997). However, management practice improvement and breeding plans in this unstudied goat population are very challenging and difficult to achieve due to a lack of genetic information.

The aim of the present research was to study the genetic diversity of the Northern Morocco goat population using microsatellite markers. To detect a possible population structure, three distinct geographic subpopulations were characterized as a function of climate and environmental influences because the genetic diversity among breeds or populations has been shown to be related to geographical location (Iamartino *et al*., 2005). This work was developed as part of a comprehensive international project oriented towards cataloguing and conserving animal genetic resources as a basis for rural development in Morocco according to FAO directives (El Moutchou, 2016). The results obtained from this characterization provided useful information that may contribute to the improvement of management practices and productivity in this population.

Material and methods

DNA sampling

Blood samples were collected from 144 unrelated goats in the north and northwest of Morocco (Fig. 1). Animals were selected according to the following criteria. First, individuals with unique phenotypes that clearly resembled well-known breeds were excluded. Second, based on the geographic distribution of the goats, the sampled territory was divided into three main geographical zones according to climate conditions and environmental influences: Dual (42 goats from 15 herds), Mediterranean (55 goats from 22 herds) and Atlantic (47 goats from 24 herds). To make the geographical sampling more representative and to avoid possible herd bias, the terrain was divided into cells; in each cell, 1 to 4 herds were selected. From each herd, 1 to 3 animals were sampled. Blood samples were collected by jugular venepuncture in Vacutainer EDTA-containing tubes. A commercial extraction kit (Qiagen® Mini Blood) was used to isolate DNA from whole blood according to the manufacturer's protocol.

Microsatellite amplification and analysis

A panel of nineteen microsatellites recommended by ISAG/FAO (FAO, 2011) for the genetic analysis of goats was used, including BM1258, BM1329, CSRD247, ETH10, FCB20, HSC, ILSTS11, ILSTS19, ILSTS030, ILSTS87, INRA005, INRA006, INRA023, INRA063, INRA172, MAF65, SRCRSP5, SRCRSP8, and TGLA53 (Table 1). Genotypes for all 19 microsatellites were determined via four multiplex fluorescent PCR reactions, and fragment lengths were determined in a single semi-automated multiplex electrophoresis run in an ABI Prism® 3130xl Genetic Analyzer using Gene Mapper ™ software from Applied Biosystems. Each reaction was performed in a total volume of 20 µL containing 50 ng of template DNA, 1× Qiagen Multiplex PCR Master Mix, 1× PCR Master Mix, primer mix, and nuclease-free water. The PCR programme consisted of an initial denaturation at 95°C for 15 min, followed by 32 cycles of 45 s at 95°C, 1 min 50 s at 58°C, and 1

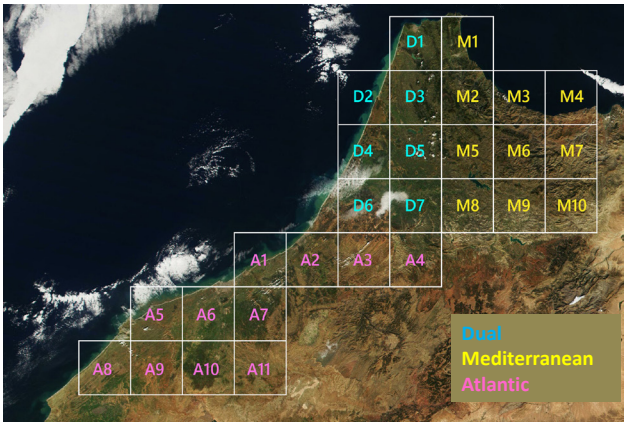

Figure 1. Geographic map illustrating the distribution of the cells in the sampled area. Different colours illustrate the limits of the main three zones in the north of Morocco [7 cells in Dual, 10 cells in Mediterranean and 11 in Atlantic].

Table 1. Description of amplification conditions used in this study.

Microsatellites	Primer sequence (forward and reverse)	Chromosome	Size range (bp)	Annealing temperature (°C)
Multiplex 1				
BM1258	GTATGTATTTTTCCCACCCTGC GAGTCAGACATGACTGAGCCTG	OAR 23	110-120	50
BM1329	TTGTTTAGGCAAGTCCAAAGTC AACACCGCAGCTTCATCC	OAR 6	145-161	50
Multiplex 2				
HSC	CTGCCAATGCAGAGACACAAGAGTC TGTCTCCTGTCTTGTCATC		271 - 304	55
ILSTS19	CTGCAGTTCTGCATATGTGG CTTAGACAACAGGGGTTTGG	2q(2)	144-158	55
INRA005	CAATCTGCATGAAGTATAAATAT CTTCAGGCATACCCTACACC	12	118-126	55
INRA063	GACCACAAAGGGATTTGCACAAGC AAACCACAGAAATGCTTGGAAG	CHI18	171-181	55
SRCRSP5	GGACTCTACCAACTGAGCTACAAG TGAAATGAAGCTAAAGCAATGC	CHI21	158-180	55
SRCRSP8	TGCGGTCTGGTTCTGATTTCAC GTTTCTTCCTGCATGAGAAAGTCGATGCTTAG	Unknown	209-235	55
INRA023	GAGTAGAGCTACAAGATAAACTTC TAACTACAGGGTGTTAGATGAACT	BTA3	197-215	55
Multiplex 3				
ETH10	GTTCAGGACTGGCCCTGCTAACA CCTCCAGCCCACTTTCTCTTCTC	CHI5	200-210	55
ILSTS030	CTGCAGTTCTGCATATGTGG CTTAGACAACAGGGGTTTGG	2q(2)	146-158	55
INRA006	AGG AAT ATC TGT ATC AAC CTC AGT C CTG AGC TGG GGT GGG AGC TAT AAA TA	3	109-123	55
TGLA53	GCTTTCAGAAATAGTTTGCATTCA ATCTTCACATGATATTACAGCAGA	BTA16	126-160	55
Multiplex 4				
CSRD247	GGACTTGCCAGAACTCTGCAAT CACTGTGGTTTGTATTAGTCAGG	OAR14	220-247	58
FCB20	AAATGTGTTTAAGATTCCATACAGTG GGAAAACCCCCATATATACCTATAC	OAR 2	93-117	58
ILSTS87	AGCAGACATGATGACTCAGC CTGCCTCTTTTCTTGAGAG	BTA6	137-155	58
ILSTS11	GCTTGCTACATGGAAAGTGC CTAAAATGCAGAGCCCTACC	BTA14	230-300	58
INRA172	CCACTTCCCTGTATCCTCCT GGTGCTCCCATTGTGTAGAC	BTA26	135-153	58
MAF65	AAAGGCCAGAGTATGCAATTAGGAG CCACTCCTCCTGAGAATATAACATG	OAR15	116-158	58

min 20 s at 72ºC, with a final extension at 60°C for 30 min. The analysis of the amplified fragments was carried out by regression analysis with GeneScan v.3.7 software using standard size fragments and presented with GeneMapper 3.7 software.

Statistical analysis

The Cervus 3.0 program (Kalinowski *et al*., 2007) was used to calculate the number of alleles (An), the allele frequencies, the polymorphic information content

(PIC) (Botstein *et al*., 1980), the genetic diversity (GD), the allelic richness (AR) and the private alleles for each locus (PA). The observed (Ho) and expected (He) heterozygosity (Nei, 1978) for each locus in each subpopulation, as well as deviations from Hardy-Weinberg equilibrium (HWE), were calculated using GENEPOP v.3.4 (Raymond & Rousset, 1995). FSTAT v.2.9.3 software (Goudet, 1995) was used to estimate the genetic structure of the population with pairwise distance (FST) (Wright, 1965). Fixation indices (FIS, FST and FIT) per locus were obtained using the variance-base method of Weir & Cockerham (1984) by applying a Jackknifing procedure over the loci and taking a 95% confidence interval computed with 1000 bootstraps. Analysis of molecular variance (AMOVA) was implemented in Arlequin v.3.1 to test the partition of genetic variance among and within geographic areas. Factorial Correspondence Analysis (AFC) (Lebart *et al*., 1984) was performed to test the possible admixtures using the "AFC subpopulations" module of GENETIX software (Belkhir *et al*., 1996-2004).

Results

Nineteen microsatellite markers were successfully amplified, and a total of 204 alleles were observed from the 144 samples analysed in the studied population (Table 2). The number of alleles per locus (An) ranged from 5 (ETH10, INRA005) to 23 (HSC), with a global average of 10.7 alleles per locus. Most of the markers were highly polymorphic: 8 of the 19 loci analysed exhibited more than 10 alleles. The PIC values ranged from 0.457 (ILSTS19) to 0.867 (HSC), and the average value was 0.728. Four microsatellites (ETH10, ILSTS11, INRA023, and MAF65) showed significant ($p< 0.05$) deviations from Hardy-Weinberg Equilibrium.

Genetic variability within the three geographical groups was relatively high and very similar, as indicated in Table 3. The mean values over all loci for allelic richness, allele number, private alleles, and observed and expected heterozygosity were very close in the three geographical groups. The Dual goats had the highest PIC, heterozygosity and gene diversity values (0.729, 0.773 and 0.767, respectively), while the Atlantic animals presented a high AR and An (8.989 and 9.05, respectively). The FIS, FST and FIT obtained by Jackknifing over loci showed a small deficit of heterozygosity FIS of 1.9%, and the total goat population FIT exhibited 2.4%. The Pairwise FST ($p < 0.001$) values were close to zero: 0.0038 between the Mediterranean and Atlantic areas, and 0.0069 between the Dual and Atlantic areas. The AFC required over 20 components to explain more than 50% of the total variation. The first three components explained only 6.82% of the total variation (Fig. 2). The analysis of molecular variance (AMOVA) (Table 4) indicated only 0.5% of variation between subpopulations, and 99.5% of the variation corresponded to differences among individuals.

Discussion

Genetic diversity findings concur with the high variation previously observed in phenotypic traits of the studied population (El Moutchou *et al*., 2014, 2017). The genetic variability estimated by the various studied parameters was very high. The An (10.7) and He (0.758) values obtained here were higher than those reported by other authors examining other Moroccan goats. Tadlaoui *et al*. (2002), with five microsatellite markers, obtained mean values for An (7.83 and 8.33) and He (0.673 and 0.670) for Black Rahali and Draa goats, respectively. Using 12 microsatellite markers and a highly polymorphic milk protein gene, Ouragh *et al*. (2012) studied three Moroccan goat populations and reported An mean values of 8.53, 8.23, and 7.92, and He values of 0.746, 0.783 and 0.726 for the Black, Draa, and Northern goat populations, respectively. In their work, Ouragh *et al*. used a small sample size located only in the Dual area of our study. Hilal *et al*. (2016) obtained an An value of 8.67 for Beni Arouss and a value of 8.07 for Rommani. Our results are in agreement with those obtained by Benjelloun *et al*. (2011) in the analysis of mitochondrial DNA. These authors attributed the high level of variability observed in Moroccan goats to the high heterogeneity of the founder population and the influence of Spanish breeds across the Strait of Gibraltar. Genetic differentiation (FST) among the populations was not detected (2%), and 98% of the genetic variability of the studied subpopulations was due to differences among individuals of the total population and not to differences among the geographical subpopulations. Our FST values are notably inferior to those reported by Ouragh *et al*. (2012) but are similar to those obtained with SNPs for other Moroccan goats (Black of the Atlas, Draa and Northern populations) by Benjelloun *et al*. (2015).

The Dual goats were different from the other goats and had greater variability and introgression from the Mediterranean than the Atlantic goats, probably because they are not affected by the north-south movements following the Rif valleys and the Atlas Mountains. Furthermore, due to the geographic

Table 2. Diversity parameter estimates in the goat population of Northern Morocco. Total number of alleles detected per locus (An), total number of private alleles (PA), index of polymorphic information content (PIC), observed heterozygosity (Ho), expected heterozygosity (HE), significance of Hardy-Weinberg Equilibrium test (HWE) and F-statistics (FIS, FST, FIT) according to Weir and Cockerham (1984) values for 19 microsatellites markers analysed in the goat population of Northern Morocco (N=144).

Locus	An	PA	PIC	Ho	He	HWE[a]	FIT[b]	FST[b]	FIS[b]
BM1258	12	1	0.820	0.847	0.841	n.s	-0.006	0.004	-0.010
BM1329	10	1	0.794	0.785	0.820	n.s	0.042	-0.003	0.045
CSRD247	10	2	0.838	0.875	0.858	n.s	-0.018	0.006	-0.025
ETH10	5	0	0.601	0.618	0.665	*	0.079	0.028	0.053
FCB20	9	2	0.736	0.757	0.767	n.s	0.012	-0.004	0.016
HSC	23	7	0.876	0.875	0.888	n.s	0.017	0.005	0.012
ILSTS11	8	0	0.680	0.688	0.709	*	0.031	0.002	0.029
ILSTS19	7	1	0.457	0.479	0.482	n.s	0.007	0.002	0.004
ILSTS30	17	4	0.836	0.889	0.855	n.s	-0.041	-0.002	-0.038
ILSTS87	10	1	0.572	0.604	0.598	n.s	-0.010	0.002	-0.012
INRA005	5	1	0.585	0.604	0.633	n.s	0.047	0.004	0.044
INRA006	13	4	0.849	0.819	0.867	n.s	0.055	-0.001	0.055
INRA023	12	1	0.800	0.792	0.823	*	0.037	-0.002	0.040
INRA063	6	1	0.599	0.618	0.664	n.s	0.068	-0.006	0.073
INRA172	9	2	0.756	0.750	0.788	n.s	0.057	0.025	0.032
MAF65	14	2	0.817	0.792	0.838	*	0.058	0.007	0.051
SRCRSP5	10	3	0.755	0.813	0.787	n.s	-0.029	0.011	-0.040
SRCRSP8	12	2	0.767	0.771	0.799	n.s	0.034	-0.002	0.036
TGLA53	12	3	0.698	0.708	0.725	n.s	0.029	0.018	0.011
Mean	10.7		0.728	0.741	0.758		0.024	0.005	0.019
Total	204	38							

[a]* $p \leq 0.05$, ** $p \leq 0.01$,*** $p \leq 0.001$, n.s>0.05; [b]Jackknifing estimate over the loci.

Table 3. Mean values over all loci for diversity parameter estimates in Northern Morocco goats. Total number of alleles (An), number of private alleles (PA), allelic richness (AR), polymorphic information content (PIC), observed (Ho) and expected (He) heterozygosity.

	N	An	PA	AR	PIC	Ho	He
Dual	42	8.842	12	8.842	0.729	0.773	0.767
Mediterranean	55	8.789	15	8.456	0.718	0.737	0.753
Atlantic	47	9.053	11	8.893	0.710	0.718	0.748
Population total	144	10.7	38	8.043	0.728	0.741	0.758

Table 4. Partitioning of genetic variation by the fixation indices (FST, FIS, FIT) and the analysis of molecular variance (AMOVA) based on 19 microsatellite loci for the Northern Morocco goat populations.

Source of variation	Degrees of freedom	Variance components	Percentage of variation	Fixation indices	*p* value
Among subpopulations	2	0.03502	0.49	F_{ST}= 0.005	0.650
Among individuals within subpopulations	141	0.13904	1.93	F_{IS} = 0.019	0.042
Among individuals within total population	144	7.04167	97.59	F_{IT} = 0.024	0.020
Total	287	7.21573			

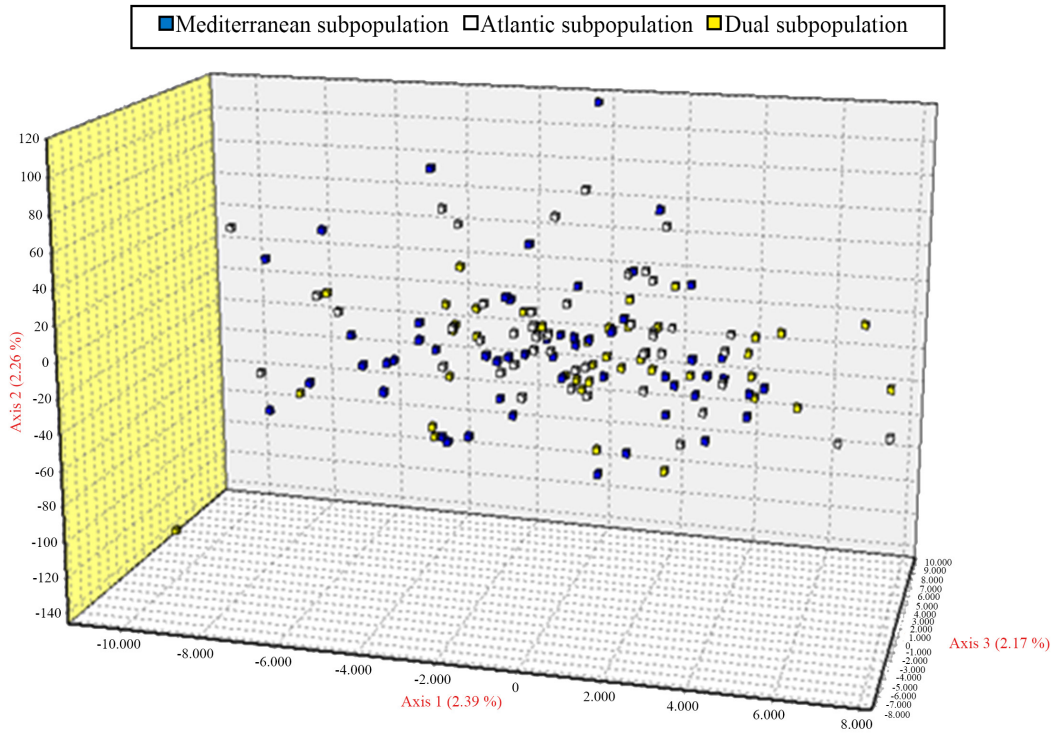

Figure 2. Spatial representation of the three goat subpopulations of Northern Morocco as defined by factorial correspondence analysis. The values shown in each axis are the percent of variance explained by each one of the first three components.

proximity, it is more probable that the influence of local Black goat breeds occurs more on goats from the Mediterranean and Atlantic areas than on Dual goats. The Draa breed in southern Morocco could have influenced the Atlantic goats more than the goats in the other two areas. Additional studies are necessary for a better understanding of Moroccan genetic resources.

The AFC analysis showed a lack of population structure in the 144 studied goats, and the high admixture in the three groups confirms their high similarity, as indicated by genetic parameters. This could be a result of high goat mobility across different regions, providing the opportunity for introgression and resulting in reduced differentiation (Luikart *et al*., 2001; Naderi *et al*., 2007).

These findings are very similar to those examining other Moroccan goat populations, *i.e.*, Black, Draa and Northern (Benjelloun *et al*., 2015), for which three principal components explained only 5.8% of the variance among the three populations. Hilal *et al*. (2016) reported weak differentiation in the Hamra goat population in two different locations of Morocco. In general, this result could be due to the absence of a breed concept in North Africa (reproductively closed population), resulting in uncontrolled crossbreeding with exotic breeds and other local goats.

In summary, the Northern Morocco goat population presented high genetic diversity and an absence of population structure. This population may be considered valuable in order to meet current production needs while preserving its purity and avoiding uncontrolled crossbreeding. These findings reinforce the need for improved management practices and implemented breeding plans based on genetic data, to avoid inbreeding and preserve genetic and allelic diversity. We recommend adopting a goat sector approach and orienting the traditional production system towards labelling using local skills, which would allow these genetic resources to be integrated into the economic and social development of Morocco.

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