

## Genetic structure of goat breeds from Brazil and the United States: Implications for conservation and breeding programs<sup>1</sup>

G. M. C. Carvalho,\* S. R. Paiva,† A. M. Araújo,\* A. Mariante,‡ and H. D. Blackburn§<sup>2</sup>

\*Embrapa Meio Norte, Teresina, PI, Brazil, 64006-220; †Embrapa Sede – Secretaria de Relações Internacionais, Brasília, DF, Brazil, 70770-901; ‡Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF, Brazil, 70770-917; and §National Animal Germplasm Program, Agricultural Research Service, USDA, Fort Collins, CO 80521

**ABSTRACT:** The objective of this study was to assess genetic diversity among 5 Brazilian (155 animals) and 5 U.S. goat (120 animals) breeds using 23 microsatellite markers. Samples from the United States represented a broad geographic distribution whereas Brazilian samples were from the northeast region. Samples from Boer were common to each country's breed count. Expected and observed heterozygosity among breeds ranged from 0.55 to 0.72, suggesting ample genetic diversity in the breeds evaluated. United States Angora, U.S. Spanish, and Brazilian Nambi ranked highest for allelic richness, averaging 6.1, 7.1, and 6.5 alleles per locus, respectively. Angora and Spanish also ranked highest in private alleles (7 and 9, respectively). Using STRUCTURE,

the U.S. Spanish were also found to share a common cluster assignment with Brazilian Nambi, suggesting that progenitor breeds may have been the same and passed through the Canary Islands or Cape Verde in route to the New World. When non-Boer breeds were pooled by country, the effect of the subpopulation compared with total population ( $F_{st}$ ) = 0.05, suggesting minor genetic differences exist between countries. The lack of genetic structure among goat breeds when compared with other species (e.g., *Bos taurus* vs. *Bos indicus*) suggests goat breeds may exhibit a plasticity that facilitates productivity across a wide range of countries and environments. Taken a step further, the concept of breed for meat goats may not be as relevant for goat production.

**Key words:** breeding strategies, *Capra hircus*, conservation genetics, genetic diversity, goat

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### INTRODUCTION

The long substantial gene flow among livestock throughout the Western Hemisphere suggests that this

region contains a wide variety of genetic diversity for use across ecozones and production systems. This has been demonstrated with sheep (Blackburn et al., 2011), goats (Huson et al., 2014), and pigs (Ibeka et al., 2014). Brazil and the United States have imported a variety of goat breeds from various parts of Europe, Africa, and Central Asia. Both countries produce goats in a variety of ecosystems. However, substantial numbers and types of goats, and particularly meat- and fiber-producing breeds, are raised in semiarid regions with minimal production inputs. In these countries, the meat goat industry has not had sustained and consistent selection programs, similar to many other parts of the world. The genetic structure of New World goat breeds and their origin has not been clearly defined (Oliveira et al., 2010; Ribeiro et al., 2012).

Brazil and the United States have active conservation programs for livestock. Cross-country comparisons of genetic diversity have already been performed

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<sup>2</sup>Corresponding author: harvey.blackburn@ars.usda.gov

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**Table 1.** Breeds, populations, and phenotypic descriptions of the analyzed goats from United States and Brazil

Population	Place	No.	Number of breeders sampled	Number of locations sampled	Breed origin	Use	Status
Marota	Brazil	31	1	1	Portugal	Meat	Endangered
Azul	Brazil	20	1	1	Portugal	Meat	Endangered
Brazilian Boer	Brazil	30	2	1	South Africa	Meat	Commercial
Anglo Nubian	Brazil	35	2	1	United Kingdom	Meat/milk	Commercial
Nambi	Brazil	39	2	1	Portugal	Meat	Endangered
U.S. Boer	United States	24	10	7	South Africa	Meat	Commercial
Lamancha	United States	19	11	8	United States	Milk	Commercial
Myotonic	United States	22	5	4	United States	Meat	Commercial
Spanish	United States	27	7	3	Spain	Meat	Watch
Angora	United States	28	14	2	Turkey	Fiber	Commercial

for sheep (Paiva et al., 2011) and pigs (Ibeka et al., 2014). This evaluation is a continuation of the cross-country evaluation, principally for meat-producing goats. The goal of this effort is to better quantify the genetic diversity within and between the 2 countries and increase the knowledge for future exchange of animal genetic resources. Previous comparisons between Iberian and Brazilian goats were unable to trace the origin of New World goat breeds by microsatellite analysis (Ribeiro et al., 2012; Oliveira et al., 2010). The objective of this study was to assess genetic diversity among 5 Brazilian (155 animals) and 5 U.S. goat (120 animals) breeds using 23 microsatellite markers, thereby adding more information concerning the origin of American goat breeds and how those results might be used in breeding and conservation programs.

## MATERIALS AND METHODS

A total of 275 blood or semen samples were collected from 5 Brazilian and 5 U.S. breeds for the study (Table 1). All Brazilian goats were sampled from the semiarid northeastern region of Brazil in the Piauí State. Samples originated from herds kept by the Embrapa Mid-West Center (Marota, Azul, Nambi, and Anglo Nubian) or from private farms (Anglo Nubian, Nambi, and Boer). The Marota, Azul, Nambi, and Anglo Nubian at Embrapa were formed by widely sampling various herds of these breeds. Three of the Brazilian breeds originated from Portuguese breeds imported during the colonial period (Marota, Azul, and Nambi). Later importations of Anglo Nubian (from Britain) and most recently the Boer (from South Africa) were also sampled. All Brazilian breeds are used for meat production and vegetation control.

The 5 U.S. breeds included Spanish, Angora, Myotonic, Lamancha, and Boer. Spanish and Lamancha are believed to have originated from the Iberian Peninsula whereas Myotonic was developed in the United States but with limited information about the breeds used in the formation. The Myotonic and

Spanish are used for meat production and vegetation control. Myotonic goats exhibit the recessively inherited condition of myotonia congenital, which results in the side effect of increasing the animals muscle mass (Dzakuma et al., 2002). The Lamancha was developed into a dairy breed. Angora, a breed originating in Turkey, was sampled. Angora are phenotypically distinct from other breeds in they have undergone intensive selection for fiber production in the United States and South Africa. The U.S. Boer has contributed to goat meat production but with variable results as environment and management change (Blackburn, 1995). Boer were sampled from varying environments (Table 1) and represent a breed with no known genetic ties to other U.S. breeds. It is unknown if any common ancestors exist between the U.S. and Brazilian Boers; therefore, it is assumed both were independent importations.

Genotyping was performed by the Veterinary Genetics Laboratory at the University of California, Davis. Twenty-six microsatellite markers were evaluated; of these, 12 were members of the Food and Agriculture Organization of the United Nations (2004) microsatellite panel (Appendix I). No microsatellites or animals were dropped from the analysis due to missing data. The software package LOSITAN (Antão et al., 2008) was run to test for microsatellites that may have been influenced by selection. Of the 26 microsatellites, 3 (INRA23, RM006, and SRCRSP23) were found to be under the influence of selection and dropped from the analysis.

The GENALEX 6 program (Peakall and Smouse, 2006) was used to compute the average and effective numbers of alleles, allele frequency per locus, observed and expected heterozygosity, private alleles of a breed or group of breeds, principal coordinate (PC) analysis, and the analysis of molecular variance. STRUCTURE (Pritchard et al., 2000) was run using a burn-in of 50,000 and 300,000 iterations per cluster ( $K$ ) and with 3 replicates per  $K$ . Delta  $K$  (Evanno et al., 2005) computed from the change in log-likelihood was computed and it was determined that the number of  $K$  to evaluate this set of breeds was 7. The software package DISTRICT (Rosenburg, 2004) was used

**Table 2.** Measures of allelic richness and genetic diversity<sup>1</sup>

Population	$N_a$	$N_e$	$H_o$	$H_e$	$UH_e$	$F_{is}$
Marota	4.04	2.723	0.581	0.559	0.568	0.022
Azul	5.30	2.962	0.611	0.605	0.621	0.016
Brazilian Boer	4.17	2.659	0.639	0.580	0.590	0.085
Anglo Nubian	4.96	2.656	0.586	0.547	0.555	0.057
Nambi	6.48	3.773	0.647	0.664	0.672	0.038
U.S. Boer	5.00	2.936	0.611	0.602	0.615	0.007
Lamancha	4.30	2.949	0.602	0.592	0.608	0.011
Myotonic	5.70	3.193	0.654	0.635	0.649	0.007
Spanish	7.13	4.267	0.720	0.708	0.721	0.000
Angora	6.09	3.603	0.650	0.658	0.670	0.030

<sup>1</sup> $N_a$  = number of alleles;  $N_e$  = number of effective alleles;  $H_o$  = observed heterozygosity;  $H_e$  = expected heterozygosity;  $UH_e$  = unbiased expected heterozygosity;  $F_{is}$  = inbreeding of the individual relative to the subpopulation (computed with FSTAT; <http://www2.unil.ch/popgen/softwares/fstat.htm>).

to graph STRUCTURE results. Allele frequencies of 23 microsatellite loci can be found at [http://nrrc.ars.usda.gov/A-GRIN/tax\\_inv\\_drilldown\\_page/index\\_by\\_tax?comefrom=FirstSearch&germplasm\\_type=&original\\_common\\_name=Goat&original\\_species=Bovidae+Capra+hircus&original\\_sublevel=&record\\_source=US&species\\_id=1092&sublevel\\_id=&views=Table+Only&web\\_class\\_id=4](http://nrrc.ars.usda.gov/A-GRIN/tax_inv_drilldown_page/index_by_tax?comefrom=FirstSearch&germplasm_type=&original_common_name=Goat&original_species=Bovidae+Capra+hircus&original_sublevel=&record_source=US&species_id=1092&sublevel_id=&views=Table+Only&web_class_id=4); Accessed August 12, 2015).

## RESULTS

### Within-Breed Analysis

All breeds exhibited high levels of observed and expected heterozygosity, suggesting substantial variability exists within and among the evaluated breeds. The Spanish, Angora, and Nambi ranked the highest for measures of heterozygosity. Observed and expected heterozygosity for Azul and Marota were similar to the values presented by Ribeiro et al. (2012). For this set of breeds and microsatellites, the average number of alleles per loci (Table 2) was 5.32 with a range of 4.04 (Marota) to 7.13 (Spanish). Within-breed inbreeding of the individual relative to the subpopulation ( $F_{is}$ ) was low and suggests population with limited inbreeding. Given the substantial selection among Angora goats, we importantly note that  $F_{is}$  of 0.03 was computed, suggesting little accumulation of inbreeding, and is in the range previously reported (Ağaoğlu and Ertuğrul, 2012). Brazilian Boer had the highest  $F_{is}$  but for the other measures of genetic variability, there is little difference between the Boer populations of the 2 countries.

Breeds with the highest number of private alleles (Appendix II) were Angora, Spanish, and Nambi. Across breeds, only 4 loci had private alleles with a frequency greater than 0.05: Angora (SPS113), Nambi

(F65), U.S. Boer (ETH10 and SPS113), and Brazilian Boer (SRCRSP5). The private alleles for Boer populations are due to sampling either within a country or in the original importation.

### Intra- and Interbreed Evaluation

Nei's genetic distance (Nei, 1973) was calculated (Table 3) and ranged from 0.073 (Brazilian Boer vs. U.S. Boer) to 0.579 (Anglo Nubian vs. Brazilian Boer). The computed genetic distances are similar in range to those reported for cattle and sheep (Paiva et al., 2011; Cronin et al., 2013). The largest distances were between both countries Boer vs. Anglo Nubian followed by Boer vs. Lamancha. The Azul and Nambi had a small genetic distance (0.10). Both Lamancha and Nambi express the earless mutation (Epstein, 1946) but the genetic distance between these breeds is large (0.25). United States breeds had a large range of values for genetic distances (ranging from 0.17 to 0.50).

The Angora is phenotypically unique due in part to relatively intense levels of selection and origin. Genetic distances (Table 3) computed in this study were relatively large when compared with the levels computed by Ağaoğlu and Ertuğrul (2012), who compared Angora to other Turkish breeds.

A neighbor joining tree (Fig. 1) was constructed with bootstrapping. Bootstrapping values ranged from 19 to 100. Four primary branches (with bootstrap values) were evident for Boer (100), Angora (62), the United States–developed Lamancha and Myotonic (19), and the branch containing the remainder of the Brazilian breeds, Spanish and Anglo Nubian (32).

STRUCTURE (Pritchard et al., 2000) results inferred 7 clusters for the 10 populations tested (Fig. 2A). Six clusters had a proportional assignment for a breed that was greater than 0.90. These were Angora (0.96), Lamancha (0.97), Boer (0.92 for U.S. Boer and 0.98 for Brazilian Boer), Myotonic (0.91), Marota (0.97), and Anglo Nubian (0.93). The seventh cluster was for Nambi, but its proportional assignment was 0.79. Breed assignments that were admixed and of interest included Marota–Azul (0.97 and 0.63) and Myotonic–Spanish (0.91 and 0.48), Nambi–Azul–Marota (0.09, 0.63, and 0.97), and Spanish–Nambi–Azul (0.15, 0.79, 0.18). The Spanish–Nambi–Azul–Marota admixture supports the dendrogram (Fig. 1) of grouping breeds known to have originated from Spain, Portugal, and/or Cape Verde.

To further evaluate the admixture of Spanish, STRUCTURE (Pritchard et al., 2000) was run with Nambi, Lamancha, Myotonic, Angora, and Spanish with the same number of burn-in and iterations. With this subset of breeds,  $\Delta K$  peaked at 5 clusters, indicating that all 5 breeds were unique (Fig. 2B). Despite this indication,

**Table 3.** Matrix of Nei's genetic distance (below diagonal) and pairwise effect of the subpopulation compared with total population ( $F_{st}$ ; above diagonal)

Population	Marota	Azul	Brazilian Boer	Anglo Nubian	Nambi	U.S. Boer	Lamancha	Myotonic	Spanish	Angora
Marota		0.07	0.20	0.20	0.09	0.19	0.19	0.16	0.12	0.16
Azul	0.13		0.17	0.14	0.03	0.14	0.13	0.09	0.06	0.13
Brazilian Boer	0.45	0.41		0.24	0.15	0.03	0.22	0.18	0.14	0.18
Anglo Nubian	0.41	0.28	0.58		0.09	0.22	0.18	0.17	0.10	0.18
Nambi	0.19	0.10	0.40	0.18		0.13	0.10	0.08	0.03	0.09
U.S. Boer	0.44	0.36	0.07	0.50	0.34		0.19	0.15	0.11	0.14
Lamancha	0.43	0.31	0.57	0.39	0.25	0.50		0.10	0.07	0.12
Myotonic	0.37	0.24	0.45	0.38	0.23	0.40	0.24		0.05	0.10
Spanish	0.27	0.17	0.37	0.22	0.12	0.30	0.21	0.17		0.06
Angora	0.40	0.35	0.47	0.43	0.25	0.37	0.33	0.27	0.19	

the Spanish were still more admixed than other breeds. We verified the origin of admixed animals and determined that of 7 highly admixed animals, only 2 were from the same breeder/location; the other 5 animals were from different breeders and diverse geographic locations (Virginia, west Texas, east Texas, and Oklahoma). Four of the admixed Spanish had a high proportion (ranging from 0.22 to 0.70) of Nambi. Their geographic distribution further strengthens the hypothesis that Spanish and Nambi share a common genetic basis.

Three PC explained 83.7% (47.8, 21.8, and 14.0% for PC1, PC2, and PC3, respectively) of the variation (Fig. 3). The first PC differentiated the Boer, meat and fiber goats, and, to a lesser extent, the 2 dairy goat breeds. The second PC suggested a continuum between the U.S. and Brazilian breeds with Spanish and Nambi in close proximity to one another. Ribeiro et al. (2012), using some of the same Brazilian breeds, showed a distinct separation between Portuguese and Brazilian breeds, but we found no distinct separation. This may be due to the larger number of microsatellites used in the present study.

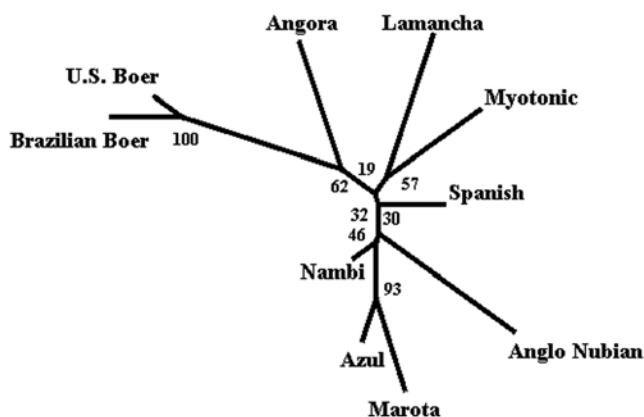
Previous research has shown that goat breeds lack the genetic structure found among other livestock species. To explore this issue, GENALEX (Peakall and Smouse, 2006) was rerun with the breeds reclassified into 3

groups: United States, Brazilian, and Boer. The effect of the subpopulation compared with total population ( $F_{st}$ ) between the Brazilian group and the U.S. group was 0.05 whereas Boer  $F_{st}$  was 0.14 (Brazilian) and 0.12 (United States). The pooled  $F_{st}$  results were lower than the breed pairwise values (Table 3), as expected. However, in a comparison of Brazilian and Portuguese goat breeds, the  $F_{st}$  was reported to be 0.15 (Ribeiro et al., 2012).

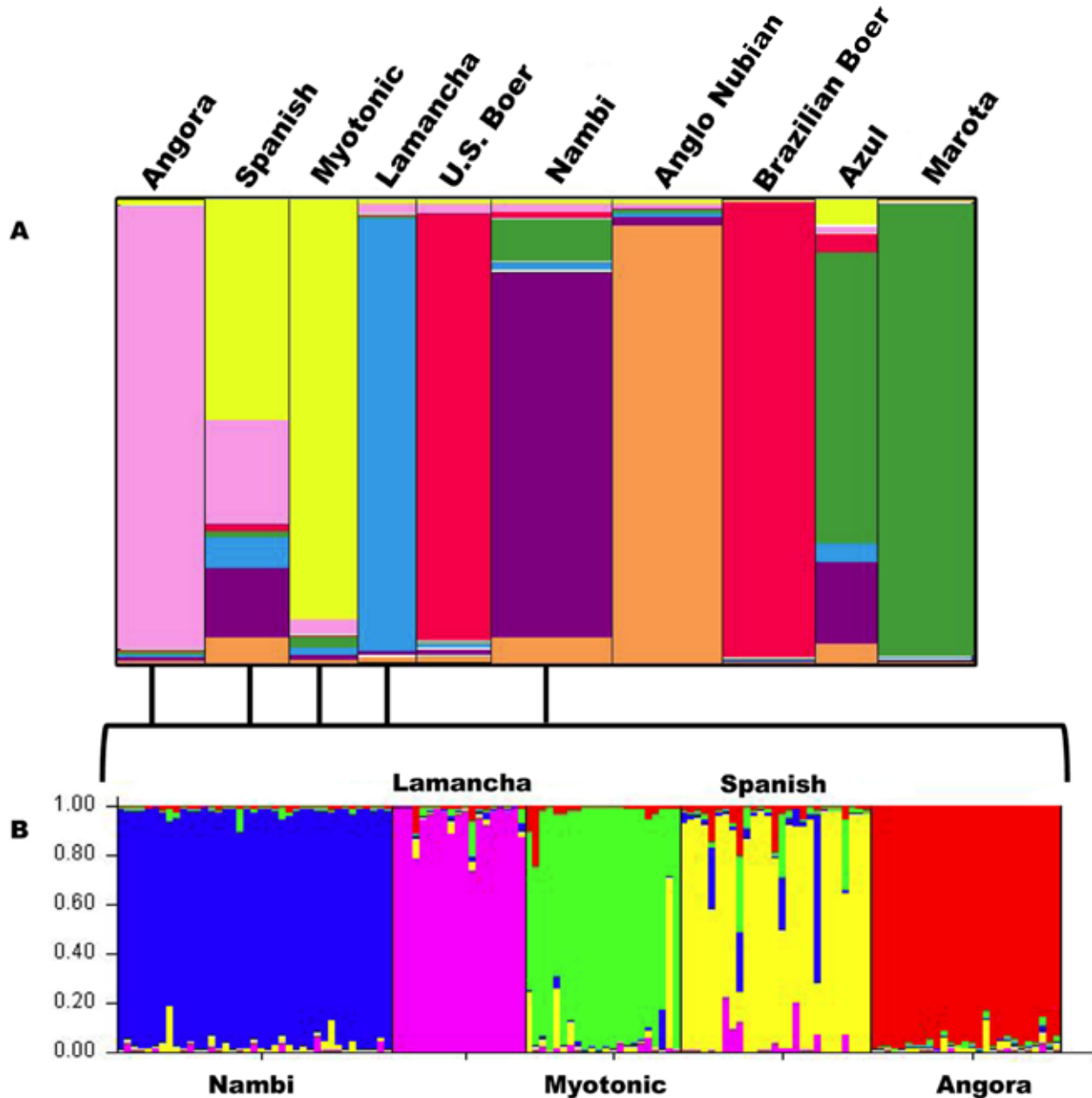
## DISCUSSION

Goat breeds with origins from a wide variety of geographic locations are represented in this study. Genetic differentiation was found to be substantial, suggesting a range of opportunities exists to use these resources within the context of the Western Hemisphere. The Boer, as a relatively new breed, provides an interesting cross-country comparison. The presence of private alleles among each country's population suggests sampling differences among the imported animals. But the small  $F_{st}$  (0.03) between the 2 populations suggests sampling differences and genetic drift have impacted the Boers less than U.S. and Brazilian Dorper sheep ( $F_{st}$  of 0.09), which were shown to be more distinct and distant from each other (Paiva et al., 2011). All methods of assessing genetic differences between the Boers and other breeds suggests heterosis can be obtained by using this breed in crossbreeding programs, which is what has largely occurred in the meat goat industry of both countries.

The STRUCTURE (Pritchard et al., 2000) results (Fig. 2) generally support the breeds' dendrograph in Fig. 1. The close placement of the Spanish with Brazilian breeds supports the findings of Amills et al. (2009), who used mitochondrial DNA and found Spanish closely positioned to Brazilian breeds. That report also suggested Brazilian and Spanish breeds originated from Cape Verde and may have been a combination of Spanish/Portuguese and African goats. Although the distinct placement of Boer, Angora, and Anglo Nubian should be expected



**Figure 1.** Neighbor joining tree for Brazilian and United States goat breeds.

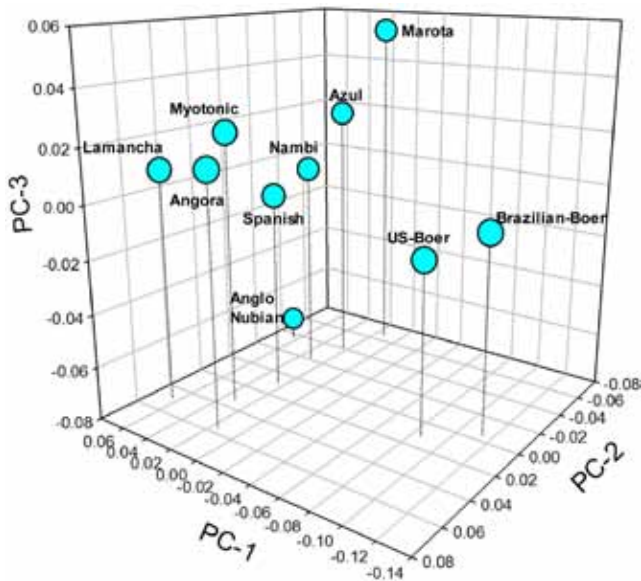


**Figure 2.** Inferred proportional population assignments via STRUCTURE (Pritchard et al., 2000) when the assigned number of clusters was 7 (A) and the subset of 5 breeds (B).

given their origins, the Marota and Lamancha showed distinct branching for different reasons. The Lamancha appear to be distinct (Fig. 1) but showed admixture with Spanish and, to a lesser extent, with Azul and Nambi, which supports the concept that the breed did have some origins from Spain (Fig. 2A and 2B). Since breed formation in the United States, they have been developed into a dairy breed. Although the breed had approximately 4,600 registrations in 2012, genetic drift plus selection for milk have contributed to its differentiation from other breeds. The Marota are known to be derived from creole goats broadly classified as “without defined race”; Mason (1996) reported that Anglo Nubian and/or Bhuj were used in the formation of the Marota. However,

these results suggest no genetic association between the Marota and Anglo Nubian. As with Ribeiro et al. (2012), the Maroata and Azul were admixed.

Lamancha and Nambi breed descriptions indicate both are earless (missing pinnae). But in Brazil, Nambi breeders have asserted that the earless condition makes it genetically unique compared with other goat breeds. These results suggest Lamancha and Nambi are genetically distant with a Nei's distance of 0.25 (Table 3); however, Fig. 2 does indicate some admixture between these 2 breeds. Review of the literature shows that among small ruminants, the occurrence of the earless condition has a broad occurrence geographically and across breeds (Lush, 1930; Epstein, 1946). Therefore,



**Figure 3.** Principal coordinate (PC) analysis accounting for 83.7% of the variation (47.8, 21.8, and 14.0% for PC1, PC2, and PC3, respectively).

due to the potential association (Fig. 2) between Lamancha and Nambi, an assertion of uniqueness by Nambi breeders appears unfounded.

Angora originated from Turkey and, therefore, was developed close to a center of domestication, implying the breed should have a high level of genetic variation (Loftus et al., 1999; Peter et al., 2007; Tapio et al., 2010; Blackburn et al., 2011). Since importation in the 1800s, the breed has undergone substantial selection for various mohair characteristics (e.g., fiber diameter, fiber length, fleece weight). Measures of heterozygosity, average number of alleles, and number of private alleles suggest this breed does have a wide range of genetic variability. Angora is commercially viable but there has been a significant reduction in population size during the past 15 yr. In addition, development of breeding animals (particularly bucks) resides in the hands of a limited number of breeders. Even though demographic changes are indicative of contracting genetic diversity, our results suggest no contraction is occurring at this point in time, especially when our levels of heterozygosity are compared with Angoras in Turkey (Ağaoğlu and Ertuğrul, 2012).

The foundation breed or breeds and the origin of the genetic mutation causing the myotonic condition in the Myotonic is unclear (Mason, 1996), other than being commonly found in Tennessee. Our results place this breed in close proximity to Spanish (Fig. 2 and 3). However, we do not believe the proximity to Spanish suggests the latter was a progenitor breed but rather admixture that has been relatively recent as the Myotonic has gained popularity. Myotonic and Lamancha were placed on the same branch of the neighbor joining tree but with a weak bootstrap value.

Neighbor joining tree (Fig. 1) and PC analysis (Fig. 3) placed Spanish more closely to the Brazilian breeds. The STRUCTURE (Pritchard et al., 2000) results (Fig. 2) also support these findings. We know of no exchange of these breeds and, therefore, the genetic similarity identified with STRUCTURE predates importation (approximately 400 yr) and suggests Amills et al. (2009) finding that these breeds came to the Western Hemisphere via the Canary Islands and Cape Verde. Among the Brazilian, Azul, Nambi, and Marota appear to have been derived from colonial importations. Their relatively low genetic distances (0.10 to 0.19) and close positioning when evaluated with the neighbor joining tree (Fig. 1) and PC analysis (Fig. 3) indicate either common origins, recent admixture, and/or both.

The smaller *Fst* values computed in this study would be in agreement with previous work (Naderi et al., 2008) using mitochondrial mtDNA. But as Groeneveld et al. (2010) states, much of the genetic distinction of goats is closely tied to geographic differences, suggesting goats in previous analyses were derived from small isolated populations in which genetic drift and selection occurred at faster rates when compared with our study. Additionally, breeding of meat goats in the United States and Brazil tends to be panmictic, which serves to reduce population structures. The linkage found in this study between Spanish and Nambi also support this contention given that there has been no known admixture between these breeds.

The genetic structure of meat goats from colonial periods of time leads us to explore the question of how meat goat production across a broad geographic expanse might be advanced. Formalized structure within the meat goat sector is lacking, particularly in terms of breed identity and long-term selection strategies and tools (EBV) that are used by breeders. Given these circumstances, previous reports in the literature, and our results, we propose that formalized breed structure may not be critical for this sector. Rather, it is more important to achieve a balanced genotype for multiple characteristics.

For example, the need to match (or balance) genotypic potentials for mature size, milk production, and ovulation rate in resource-limiting environments for small ruminants has been demonstrated (Blackburn and Cartwright, 1987; Figueiredo et al., 1989; Blackburn, 1995). In addition, in challenging environments, herd productivity may be an important indicator of how well balanced a genotype is for a specific environment. Browning et al. (2011) demonstrated the important role of balanced genotypes and herd productivity (kg kid weaned/doe) in subhumid environments. Their work also underscored the important role of resilience to endoparasites.

Another important issue to consider is the type of genetic resources that are exchanged between countries.

Rather than exchanging highly specialized breeds, it could be more beneficial to exchange breeds that have been bred in resource-challenged environments found in Brazil and the United States. Taken a step further, breeds per se may not be critical compared with useful combinations of alleles. By taking such an approach, it may be possible to better maintain or achieve optimal production levels without the need for external production inputs. Such concepts are consistent with response surface and adaptive peak analysis discussed by Wright (1969) and phenotypic plasticity (de Jong and Bijma, 2002). These areas have not been explored with meat goats and it would seem their use could contribute to increasing meat goat production in challenging environments.

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### Appendix I. Measures of genetic diversity<sup>1</sup> within 23 microsatellite loci

Locus	$F_{is}$	$F_{it}$	$F_{st}$	$N_a$	$H_o$	$H_e$
BM1258	-0.047	0.064	0.106	7.2	0.793	0.757
CSRD247 <sup>2</sup>	-0.033	0.101	0.129	5.8	0.741	0.717
ETH152	-0.033	0.021	0.052	2.4	0.125	0.121
ETH10 <sup>2</sup>	-0.088	0.049	0.126	3.1	0.616	0.566
HSC	-0.035	0.099	0.130	9.5	0.818	0.790
ILSTS005	-0.049	0.154	0.193	3.9	0.532	0.507
ILSTS008	0.006	0.116	0.110	3.9	0.442	0.444
ILSTS19	0.029	0.139	0.113	5	0.602	0.620
ILSTS87 <sup>2</sup>	-0.117	0.078	0.174	5.4	0.675	0.605
INRA005 <sup>2</sup>	0.062	0.152	0.096	3.4	0.537	0.573
INRA006	-0.055	0.087	0.134	7.6	0.791	0.750
INRA063 <sup>2</sup>	-0.072	0.070	0.133	4	0.587	0.548
INRA172 <sup>2</sup>	-0.118	-0.005	0.101	5.5	0.797	0.713
F209	-0.030	0.209	0.232	2.4	0.379	0.368
F65	0.057	0.196	0.147	7.2	0.668	0.708
McM527 <sup>2</sup>	0.016	0.152	0.138	5.9	0.696	0.707
OarAE129	-0.078	0.077	0.144	5.7	0.706	0.655
OarFCB20 <sup>2</sup>	0.015	0.159	0.146	5.1	0.597	0.606
SPS113 <sup>2</sup>	-0.040	0.087	0.122	6.4	0.757	0.728
SRCRSP5 <sup>2</sup>	-0.003	0.113	0.116	6.8	0.727	0.725
SRCRSP8 <sup>2</sup>	-0.022	0.132	0.150	5.6	0.705	0.690
TCRCG4	0.038	0.134	0.100	5.4	0.645	0.671
TGLA53 <sup>2</sup>	0.033	0.210	0.183	5.1	0.555	0.574

<sup>1</sup> $N_a$  = number of alleles;  $H_o$  = observed heterozygosity;  $H_e$  = expected heterozygosity;  $F_{is}$  = inbreeding of the individual relative to the subpopulation;  $F_{it}$  = inbreeding of the individual relative to the total population;  $F_{st}$  = effect of the subpopulation compared with total population.

<sup>2</sup>Food and Agriculture Organization of the United Nations 2011 markers list (FAO, 2011).

### Appendix II. Summary of private alleles by population

Population	Locus	Allele	Frequency
Marota	ILSTS005	191	0.0484
Brazilian Boer	SRCRSP5	165	0.0500
Nambi	CSRD247	237	0.0641
Nambi	F65	145	0.0128
Nambi	OarAE129	154	0.0128
U.S. Boer	ETH10	213	0.0625
U.S. Boer	SPS113	138	0.0417
Myotonic	ILSTS008	181	0.0455
Myotonic	F65	155	0.0455
Myotonic	SRCRSP8	242	0.0227
Spanish	CSRD247	245	0.0185
Spanish	ILSTS005	185	0.0185
Spanish	ILSTS87	137	0.0185
Spanish	F65	111	0.0556
Spanish	F65	131	0.0185
Spanish	OarAE129	150	0.0185
Spanish	SPS113	158	0.0185
Spanish	SRCRSP8	210	0.0185
Spanish	SRCRSP8	234	0.0185
Angora	BM1258	119	0.0357
Angora	HSC	299	0.0179
Angora	ILSTS19	148	0.0179
Angora	INRA006	125	0.0179
Angora	SPS113	130	0.0893
Angora	SPS113	136	0.0357
Angora	SRCRSP8	236	0.0357