



Mitochondrial and Y chromosome genetic diversity in the Portuguese Lidia bovine breed

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ABSTRACT - A total of 80 samples were collected to analyze the mitochondrial DNA (mtDNA) and Y chromosome genetic diversity of two main Portuguese Lidia bovine populations and clarify their genetic relationships with Spanish Lidia lineages. A 521-bp D-loop fragment was sequenced in 40 animals belonging to four herds (three Brava dos Açores and one Casta Portuguesa) and the same number of samples were collected with equal distribution from males in order to genotype six microsatellites, one single nucleotide polymorphism, and one indel. The mtDNA diversity recorded was similar to that observed in Lidia cattle. Haplotype T3 was the most common (62.5%), followed by the African T1 haplotype (25%); very low frequencies were recorded for haplotypes T2 (2.5%) and the Lidia haplogroup L4 (10%). The results support the existence of two major ancestral lines for the Lidia breed: European and African, similar to other Mediterranean breeds. However, the genetic diversity in the Y chromosome was lower in Portuguese Lidia lineages than in Lidia cattle and other bovine breeds (haplotype diversity = 0.09). The two major paternal haplogroups, Y1 and Y2, were present with 2.5% and 97.5%, respectively. Our results evidenced a similar paternal and maternal genetic pattern to those found in Spanish Lidia lineages and a high reproductive isolation.

Key Words: Lidia cattle, mitochondrial DNA, Portuguese lineages, Y chromosome

Introduction

The Lidia bovine breed is mainly distributed in the west and southwest of Spain, Portugal, south of France, and in South America. The Lidia bovine breeding and selection objective, which is based on aggressiveness, is unique and has led to its reproductive isolation from other cattle breeds, in which this behavioral characteristic is discouraged (Silva et al., 2006; UCTL, 2011). Nevertheless, traditional events have created a demand for different types of behavior and this need has favored the subdivision of the Lidia bovine breed into lineages (called “encastes”) (BOE, 2001), with limited gene flow among them. Portugal has a unique Lidia cattle lineage, called Casta Portuguesa, which is considered one of the most important Portuguese Lidia

breed resources (Lucas, 2006; Correia et al., 2014; Mateus and Russo-Almeida, 2014).

The arrival of bovines in the Azores began in the 15th century with the colonization of the islands, primarily by the Portuguese. Also, at the beginning of the 20th century, different Lidia lineages, that also included Casta Portuguesa, began to be selected on Terceira Island (Azores) for a cultural event called “Tourada à Corda” (Bruges, 1915; Silva, 2011; Correia et al., 2015). This cattle population located on Terceira Island is recognized as Toiro da Terra or Brava dos Açores (Department of Azorean Agriculture and Forestry, 2010).

Previous analysis with autosomal microsatellites showed a Lidia lineage crossbreeding origin from Brava dos Açores breed and higher genetic diversity than the Casta Portuguesa lineage (Correia et al., 2014). Presently, the “Tourada à Corda” event is important for the local economy, as well as for the Azorean social and cultural heritage, and also ensures the viability of Brava dos Açores breed. However, in spite of the genetic, economic, and social importance of Casta Portuguesa and Brava dos Açores breeds, their maternal and paternal genetic influences have not yet been analyzed. The objective of this study is to analyze the mitochondrial DNA (mtDNA) and Y chromosome genetic diversity of Brava dos Açores and

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Casta Portuguesa and evaluate the paternal and maternal relationships between Portuguese and Spanish Lidia lineages.

Material and Methods

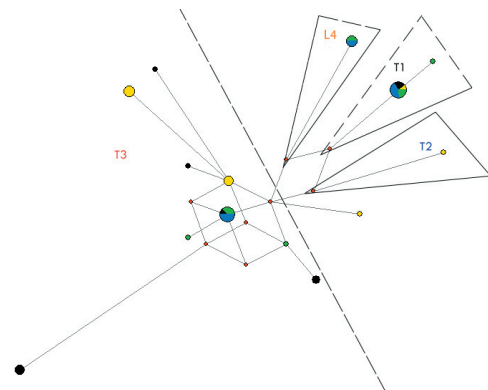
A total of 80 peripheral blood samples were collected: Irmãos Dias (ID; n = 20), belonging to Casta Portuguesa; and three herds belonging to Brava dos Açores - José Albino Fernandes (JAF; n = 20), Rego Botelho (RB; n = 20), and Eliseu Gomes (EG; n = 20). Samples were collected from unrelated individuals registered in herdbooks (whenever available). Biological samples were collected by qualified veterinarians during their routine practice, according to the framework of official programs. We extracted DNA by standard methods (Sambrook et al., 1989). A 521-bp fragment of the mtDNA D-loop was sequenced following the procedure described in Cortés et al. (2008). The primer sequences and annealing temperature of the six Y chromosome microsatellites (DYZ1, BYM1, BM861, UMN0307, INRA189, and UMN0103), the single nucleotide polymorphism (UTY19), and the indel (ZFY10) were described in Cortés et al. (2011) (Table 1). To study the genetic relationships among Portuguese bovine populations and Spanish Lidia breed lineages, mtDNA sequences and Y chromosome genotypes belonging to 30 previously analyzed Spanish Lidia lineages were added to the analysis (Cortés et al., 2008; 2011).

The mtDNA sequence alignment was performed using free software available at <http://bioinfo.hku.hk/EMBOSS/> (the European Molecular Biology Open Software Suite). The mean number of pairwise differences (MNPD) and nucleotide diversity were obtained using MEGA software version 2.1 (Kumar et al., 2001). The F_{ST} genetic distances was carried out using ARLEQUIN package version 3.11 (Excoffier et al., 2005). Reduced median networks were generated using software NETWORK version 4.6.1.3 (Bandelt et al., 1999).

Results

The Portuguese Lidia populations showed MNPD values ranging from 3.7 in Rego Botelho to 6.5 in Eliseu Gomes (Table 1). The nucleotide diversity ranged from 0.5% to 0.8% (Table 1).

The 40 DNA mitochondrial sequences revealed 20 haplotypes defined by 48 polymorphisms, 45 transitions, and three transversions (Table 2). The most common haplogroup was T3 in Casta Portuguesa (80%) and Brava dos Açores (57%) (Table 1). However, there were notable differences in frequency of haplogroup T3 among Brava dos Açores herds (José Albino Fernandes, 50%; Rego Botelho, 40%; and Eliseu Gomes and Irmãos Dias, 80%). The haplogroup T1 was identified in both Portuguese bovine populations (Brava dos Açores, 30%; Casta Portuguesa, 10%), ranging from 10% to 30% in Brava dos Açores herds. Finally, haplogroup T2 was only found in Casta Portuguesa (10%) and L4 in Brava dos Açores (José Albino Fernandes, 20%; Rego Botelho, 20%) (Figure 1).



Dashed line identifies T3 from other haplogroups marked with triangles. Circle size is proportional to sequence frequency. Line colors: green = José Albino Fernandes; blue = Rego Botelho; black = Eliseu Gomes; yellow = Irmãos Dias.

Figure 1 - Reduced median-joining network constructed from 20 maternal haplotypes from Portuguese lineages (Brava dos Açores and Casta Portuguesa), belonging to main maternal haplogroups previously published (T1, T2, and T3) and L4.

Table 1 - Mean number of pairwise differences (MNPD), nucleotide diversity, and frequencies of the main maternal haplotypes for each herd

	Herd	MNPD	Nucleotide diversity	Haplotypes (%)			
				T1	T2	T3	L4
Brava dos Açores	José Albino Fernandes	4.2±2.3	0.005±0.003	30		50	20
	Rego Botelho	3.7±2.1	0.005±0.003	40		40	20
	Eliseu Gomes	6.5±3.3	0.008±0.005	20		80	
	Total	4.8	0.006	30		56.7	13.3
Casta Portuguesa	Irmãos Dias	3.9±2.2	0.005±0.003	10	10	80	
Portuguese Lidia Populations		4.6	0.006	25	2.5	62.5	10

Among Portuguese Lidia populations, Casta Portuguesa showed the highest F_{ST} genetic distances, ranging from 18% to 27% (Table 3). The average F_{ST} genetic distances among Brava dos Açores, Casta Portuguesa, and the Iberian Peninsula Lidia lineages ranged from 3.2% for Braganza to 20.3% for Pedrajas (Table 2). In addition, Portuguese bovine populations showed average F_{ST} genetic distances higher than 10% (José Albino Fernandes, 10.1%;

Table 2 - Average F_{ST} value from maternal DNA for each lineage with respect to the others

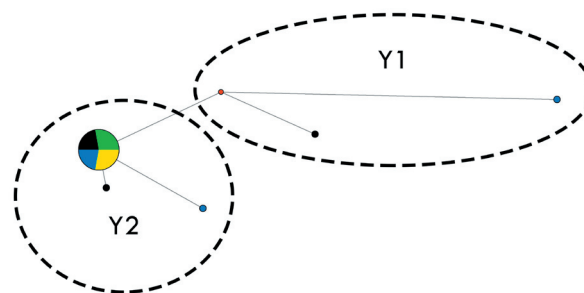
Herd	F_{ST} distance %
Pedrajas	20.3
Maria Montalvo	15.6
Rego Botelho	14.7
Miura	14.5
Eliseu Gomes	14.2
Atanásio Fernández	13.5
Irmãos Dias	13.1
Antonio Pérez	12.5
Concha y Sierra	10.5
Baltasar Ibán	10.3
Vega Villar	10.1
José Albino Fernandes	10.1
Félix Gómez	9.7
Marqués de Albaserrada	9.1
Urcola	8.7
Pablo Romero	8.3
Manuel Arranz	8.1
Anastasio Martín	7.8
Conde de la Corte	7.6
Hidalgo Barquero	7.6
Murube	7.3
Cuadri	7.3
Arauz de Roblez	7.2
Santa Coloma	6.9
Juan Pedro Domecq	6.4
Veragua	6.1
Contreras	6.1
Gamero Cívico	6.1
Marqués de Villamarta	6
Carlos Núñez	5.9
Saltillo	4.4
Diego Garrido	4.1
Jose Marzal	4
Braganza	3.2

Rego Botelho, 14.7%; Eliseu Gomes, 14.2%, and Irmãos Dias, 13.1%).

The six Y chromosome microsatellites revealed a total of three haplotypes. The haplotype H1 was the most frequently detected in both Portuguese bovine populations analyzed (95%) (Table 3). The haplotypes H3 and H5 were identified in Brava dos Açores Eliseu Gomes and Rego Botelho herds, respectively (EG - H3, 10%; RB - H5, 10%). According to the two major paternal haplogroups identified in European bovine populations, H1 and H5 haplotypes belong to haplogroup Y2 (total frequency of 97.5%) and H3 to haplogroup Y1 (2.5%) (Table 3).

The Portuguese bovine populations evidenced low average F_{ST} genetic distances as a consequence of their high H1 haplotype frequency, which is the most frequent in Spanish Lidia lineages (Table 4).

The relationships among Y chromosome haplotypes were shown in the Median-Joining network (Figure 2). The haplotypes belonging to haplogroups Y1 and Y2 were clearly separated into two clusters.



The sizes of the circles are proportional to their frequencies and their classification into the two main European haplogroups (Y1 and Y2). Colors: green = José Albino Fernandes; blue = Rego Botelho; black = Eliseu Gomes; yellow = Irmãos Dias.

Figure 2 - Network representation of the three haplotypes identified in the Portuguese Lidia lineages (Brava dos Açores and Casta Portuguesa).

Table 3 - Number of samples analyzed (N), percentage of haplotype and haplogroup frequencies, and haplotype diversity (H_e) for each lineage and for the entire population

Herd	N	Haplotype (%)			Haplogroup (%)		H_e
		H1	H3	H5	Y1	Y2	
Brava dos Açores	José Albino Fernandes	10	100			100	0
	Rego Botelho	10	90		10	100	0.2
	Eliseu Gomes	10	90	10		90	0.17
	Total	30	93.3	3.3	3.3	96.7	0.12
Casta Portuguesa	Irmãos Dias	10	100			100	0
Portuguese Lidia populations		40	95	2.5	2.5	97.5	0.09

Table 4 - Average F_{ST} value from Y chromosome genetic diversity for each lineage with respect to the others

Herd	F_{ST} distance %
Miura	96.3
Pablo Romero	89.4
Marqués de Albaserrada	82.7
Manuel Arranz	81.6
Cuadri	79.8
Vega Villar	77.5
Saltillo	72.2
Contreras	66.5
Atanásio Fernández	34.6
Gamero Cívico	25.1
Carlos Núñez	25.1
Veragua	24.9
Concha y Sierra	24.3
Braganza	24.1
Anastasio Martin	24.1
Urcola	24.1
Pedrajas	24.1
Baltasar Ibán	24.1
Antonio Pérez	24.1
Marqués de Villamarta	24.1
Jose Marzal	24.1
Hidalgo Barquero	24.1
Arauz de Roblez	24.1
Félix Gómez	24.1
Diego Garrido	24.0
Conde de la Corte	23.9
Rego Botelho	23.7
Eliseu Gomes	23.5
José Albino Fernandes	23.4
Irmãos Dias	23.4
Santa Coloma	23.0
Murube	22.4
Maria Montalvo	21.6
Juan Pedro Domecq	20.8

Discussion

The MNPD in Portuguese Lidia populations were equal to or higher than those observed in Spanish Lidia breed (3.7) (Cortés et al. 2008), European, African, Middle Eastern (4.0), or Anatolian bovine breeds (3.7) (Bradley et al., 1996; Troy et al., 2001; Carvajal-Carmona et al., 2003; Ginja et al., 2010). In addition, the nucleotide diversity was higher in Portuguese Lidia populations than in other European bovine breeds, which ranged from 0.11% to 0.57% (Loftus et al., 1994), and was lower than in the Lidia cattle breed (0.4% to 1.1%) (Cortés et al., 2008).

The haplogroup distribution in Casta Portuguesa and Brava dos Açores has a pattern similar to that in Spanish Lidia lineages or Iberian bovine breeds (Cortés et al., 2008; Ginja et al., 2010). Our results showed clear similarities between Portuguese Lidia populations and Spanish Lidia lineages, in which two major haplogroups were identified (T3 and T1), and supported historical documents that describe the Azorean Lidia cattle as coming from the

Iberian Peninsula (Lucas, 2006; Cortés et al., 2008; UCTL, 2011). However, the African influence in Casta Portuguesa, revealed by T1 haplotype frequency, is lower than that previously estimated in Spanish Lidia lineages by Cortés et al. (2008).

The remarkably high frequency of the haplogroup L4, previously described by Cortés et al. (2008), in several Spanish Lidia lineages (Pablo Romero, Contreras, Baltasar Iban, and Carlos Núñez lineages), suggests crossbreeding among Lidia lineages and Brava dos Açores populations during their development (Correia et al., 2014).

The presence of the T2 haplogroup identified in Casta Portuguesa has two possible explanations: the well-known genetic relationship between the Concha y Sierra Lidia lineage (in which the T2 haplogroup has been previously observed) and Portuguese Lidia populations (Correia et al., 2014); and the role of populations from the North of Portugal in the development of Casta Portuguesa (Neves, 1992), such as the Marinhoa breed, in which T2 haplogroup has been previously identified (Ginja et al., 2010).

The reproductive isolation of Portuguese and Spanish Lidia lineages could likely explain the higher levels of genetic differentiation among them, evidenced by the high F_{ST} values. Furthermore, the low number of animals in both Portuguese bovine populations could have increased the genetic drift effect and, as a consequence, the genetic differentiation from Spanish Lidia lineages.

The higher number of haplotypes in Portuguese bovine populations were grouped in three well-differentiated clusters in a phylogeny network, according the three major haplogroups: T3, T2, and T1. Moreover, the new haplotypes identified in Portuguese bovine populations (L4) were detected in a new cluster, but closer to the T1 than to the T3 cluster. This result could support an African origin of the L4 haplogroup.

The three paternal haplotypes evidenced in Portuguese bovine population (H1, H3, and H5) can be attributed to different origins. In Lidia lineages, those haplotypes have been identified in Saltillo and other Lidia lineages that share similar origins (Cortés et al., 2011; UCTL, 2011). The relationship between Saltillo lineage and Portuguese Lidia bovine populations has been previously established (López del Ramo, 2002). Otherwise, H3 was identified in a native bovine breed from Terceira Island, Ramo Grande, which originated from ancient Iberian cattle (Ginja et al., 2010), and the presence of this haplotype in Eliseu Gomes could be evidence of ancestral crossbreeding between both populations (Correia et al., 2014).

The H5 haplogroup, detected in the Domecq Spanish Lidia lineage and Rego Botelho herd, supported the

introgression previously described in the Rego Botelho herd Domecq lineage during the 1990s (Lucas, 2006). In addition, the H3 haplogroup identified in the Eliseu Gomes herd could be considered an influence of the Domecq lineage according to a recent study by Pelayo et al. (2015), despite the absence of historical documents to support it (ARCTTC, 2006). While the frequency of H3 and H5 were low, this finding may suggest a recent introgression of the Spanish Lidia lineages in the Brava dos Açores breed.

The low haplotype diversity found in the analyzed Portuguese bovine populations supports previous analyses conducted on the Lidia bovine breed (Cortés et al., 2011) and other Iberian Peninsula bovine breeds (Ginja et al., 2010). There are several, nonexclusive explanations for the low levels of haplotype diversity in Spanish and Portuguese Lidia bovine populations: low Y chromosome genetic diversity in the ancestral populations of the present bovine breeds; reproductive isolation between lineages and low effective population size (approximately 30 on average); and the traditional practice of using a small number of bulls when trying to fix desirable behavioral traits through inbreeding (Cortés et al., 2011; 2014).

The high frequency of the Y2 haplogroup shown in Portuguese Lidia bovine populations is higher than that previously found in Spanish Lidia lineages (Cortés et al., 2011; Pelayo et al., 2015). Recent studies have suggested that the Y1 haplogroup is more widely distributed than previously assumed as supported by the identification of Y1 exclusively in haplotypes in Spanish cattle breeds (Pelayo et al., 2015). Therefore, the low frequency of the Y1 haplogroup detected in the analyzed Portuguese Lidia bovine populations could be the consequence of the small number of bulls used for reproduction.

Conclusions

The analyzed Portuguese Lidia populations revealed paternal and maternal genetic patterns similar to those previously described in Spanish Lidia lineages. Two major maternal lineages have been identified (T3 and T1). The Brava dos Açores population evidenced more genetic relationships with Lidia lineages than Casta Portuguesa; however, a high reproductive isolation was observed among Portuguese and Spanish Lidia cattle, which suggests the hypothesis to determine the “lineage” (encaste) as a conservation unity as a consequence of their high reproductive isolation and their genetic differences.

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