Testing the usefulness of the molecular coancestry information to assess genetic relationships in livestock using a set of Spanish sheep breeds[1]

**I. Álvarez*, J. P. Gutiérrez†[2], L. J. Royo*, I. Fernández*, E. Gómez*,
J. J. Arranz‡, and F. Goyache*[3]**

*SERIDA-Somió, E-33203 Gijón (Asturias), Spain; †Departamento de Producción Animal,
Universidad Complutense de Madrid, E-28040-Madrid, Spain; and
‡Departamento de Producción Animal I, Universidad de León, E-24071 León, Spain

ABSTRACT: Recent studies have proposed the use of molecular coancestry coefficients as a measure of genetic variability and as a useful tool for conservation purposes. Using simulated data, molecular coancestry has been shown to become constant very quickly after separation of populations, leading to population diversity remaining constant. However, the use of molecular coancestry information to study the genetic relationships between breeds has not yet been widely explored. Here we analyze the polymorphism of 14 microsatellites in 222 unrelated individuals belonging to seven native Spanish breeds to ascertain the usefulness of molecular coancestry-based methodologies in providing information on their genetic relationships. Average kinship distance (D_k) and average molecular coancestry coefficients (f_{ij}) were compared with well-known genetic distances, such as between-breed Reynolds' distance (D_R), Nei's standard distance (D_s), and shared allele distance (D_{AS}). Kinship distance and f_{ij} have moderate to low correlations with the other genetic distances, showing that they provide different information: both D_k and f_{ij} account for the allele frequencies in the founder population, whereas D_R, D_s, and D_{AS} characterize the short-term evolution of the populations. Furthermore, D_k and f_{ij} were only moderately correlated (–0.500). The present study used field data to confirm previous research pointing out the ability of molecular coancestry coefficients to assess genetic differentiation of an ancestral origin. In this respect, molecular coancestry-based parameters may be used with classical genetic parameters to obtain information on population dynamics in livestock breeds. This study additionally presents reliable evidence on the history of these sheep breeds.

Key Words: Genetic Distance, Microsatellite, Molecular Kinship, Sheep Breeds

Introduction

Studies of genetic relationships in livestock provide useful information on the evolution of breeds, gene pool development, and the magnitude of genetic differentiation. A considerable number of methodologies have been developed to objectively quantify the genetic differences among a set of breeds from allele frequency data (Nei, 1987; Eding and Laval, 1999). However, only a combination of methods can provide sufficient information on both the genetic differences between breeds and the within-breed genetic variation (Ruane, 1999).

Recently, Caballero and Toro (2002) formalized how to obtain coancestry coefficients from molecular information by applying Malécot's (1948) definition to the marker genes, although they referred to it as identity by state instead of identity by descent. Because of its straightforward relationship with genealogical coancestry, this parameter has been shown to be useful for conservation purposes (Toro et al., 2002, 2003). Moreover, Eding and Meuwissen (2001), using simulated data, showed that molecular coancestry has some interesting properties, namely that average kinship between populations becomes constant very quickly after population fission, causing between-population diversity to remain constant. However, the possibilities of using molecular coancestry information to study the genetic relationships between breeds using actual datasets have not been widely explored (Caballero and Toro, 2002; Fabuel et al., 2004).

The aim of this study is to assess the usefulness of molecular coancestry information to ascertain the genetic relationships among livestock breeds. To do so, we use a set of seven native Spanish sheep breeds. The molecular coancestry information was compared with that provided by well-known genetic distances. Results of this analysis also will contribute to our knowledge of genetic relationships among Spanish sheep breeds.

Materials and Methods

Samples

Blood samples were obtained from 222 unrelated individuals corresponding to the following seven Spanish sheep breeds: Castellana (33), Churra (30), Black-faced Latxa (32), Blonde-faced Latxa (31), Merino (30), Rubia del Molar (32), and Xalda (34). The dataset included the three ancestral sheep groups of the Iberian Peninsula (Sánchez Belda and Sánchez Trujillano, 1986): Merino, Entrefino (represented by the Castellana breed), and Churra type (including Churra, both Latxa varieties, Rubia del Molar, and Xalda breeds). Although Latxa breeds show the phenotypic characteristics of the Churra-type group, their ancestral origin is still not well established (Sánchez Belda and Sánchez Trujillano, 1986), and are probably different from the rest of the group (Álvarez et al., 2004). All the Churra-type breeds have long coarse wool and are used for dairy, except Xalda. The Castellana breed has medium-coarse wool and is used mainly for dairy. Black-faced Latxa and Churra show particular patterns of black pigmentation in head and legs, whereas Blonde-faced Latxa and Rubia del Molar show similar reddish pigmentation patterns. The Castellana and Xalda breeds show black individuals in low and high frequencies, respectively. The Rubia del Molar and Xalda (Goyache et al., 2003) breeds are considered endangered. A more detailed description of these breeds can be found in Sánchez Belda and Sánchez Trujillano (1986), Sotillo and Serrano (1985), and Álvarez Sevilla et al. (2004). The Latxa breed has been studied at the molecular level as a single population (Arranz et al., 1998, 2001); however, phenotypic differentiation between both Latxa varieties is larger than color pattern alone (Sánchez Belda and Sánchez Trujillano, 1986), and their breeding schemes are differentiated, thereby leading to their being characterized as different populations (Álvarez et al., 2004).

Total DNA was isolated from blood samples following standard procedures (Sambrook et al., 1989). A set of 14 microsatellites (BM8125, BM6526, CP34, BM757, INRA006, BM6506, BM1818, FCB128, CSSM31, CSMM66, ILSTS011, McM53, RM006, ILSTS005) previously used in Álvarez et al. (2004) was analyzed in all individuals. The PCR products were labeled using a fluorescent method (Cy5 labeled primer) and genotyping was performed on an ALFexpressII automated sequencer (Amersham Biosciences, Barcelona, Spain).

Statistical Analyses

Genetic diversity of the analyzed dataset was assessed computing the expected heterozygosity (H_e), the heterozygote deficiency within population (F_{IS}), and the polymorphic informative content (**PIC**; Botstein et al., 1980), computed as $PIC = 1 - \sum_{i} p_i^2 - \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} 2p_i^2 p_j^2$, where p_i and p_j are the frequencies of alleles i and j at a given locus. The gene flow among breeds and genetic differentiation was assessed by computing the following between-breed genetic parameters: molecular coancestry (f_{ij}, Caballero and Toro, 2002); kinship distance (D_k, Caballero and Toro, 2002); Reynolds' distance ($D_R = -\ln[1 - F_{ST}]$; Reynolds et al., 1983), where F_{ST} is the heterozygote deficiency due to population subdivision (Wright, 1969); Nei's standard distance (D_s; Nei, 1987); and shared allele distance (D_{AS}; Chakraborty and Jin, 1993), which is computed as $D_{AS} = 1 - \dfrac{2\overline{P}_{SAkm}}{\overline{P}_{SAk} + \overline{P}_{SAm}}$, where $\overline{P}_{SAk}$ and $\overline{P}_{SAm}$ are the average proportion of shared alleles between individuals belonging to populations k and m, respectively, and $\overline{P}_{SAkm}$ is the average proportion of shared alleles between individuals belonging to populations k and m.

Following Caballero and Toro (2002), most of these parameters were computed in terms of molecular coancestry. The molecular coancestry between two individuals i and j is the probability that two randomly sampled alleles from the same locus in two individuals are identical by state (Caballero and Toro, 2002). Molecular coancestry between two individuals i and j at a given locus can be computed using the following scoring rules (Eding and Meuwissen, 2001; Caballero and Toro, 2002): $f_{ij,l} = \frac{1}{4}[I_{11} + I_{12} + I_{21} + I_{22}]$, where I_{xy} is 1 when allele x on locus l in individual i and allele y in the same locus in individual j are identical and zero otherwise. Notice that this value can only have four values: 0, ¼, ½, and 1. The molecular coancestry between two individuals i and j (f_{ij}) can be obtained by simply averaging over L analyzed loci $f_{ij} = \dfrac{\sum_{i=1}^{L} f_{ij,l}}{L}$. The molecular coancestry of an individual i with itself is self-coancestry (called s_i), which is related to the coefficient of inbreeding of an individual i (F_i) by the formula: $F_i = 2s_i - 1$. In turn, the (kinship) distance (here called D_k) between two individuals i and j is $D_k = ([s_i + s_j]/2) - f_{ij}$ (Caballero and Toro, 2002). Within- and between-breeds molecular coancestry and D_k were simply computed by averaging the corresponding values for all the within- or between-population pairs of individuals. Molecular coancestry is related to most of the genetic distances used for between-population studies (Eding and Meuwissen, 2001): a) Nei's standard distance (Nei, 1987) between populations k and m can be written as $D_s = -\ln[f_{km}/(f_{kk} \times f_{mm})^{1/2}]$, where f_{kk} and f_{mm} are the average coancestry between individuals belonging to populations k and m,

Table 1. Number of alleles, expected heterozygosity (He), and polymorphic informative content (PIC) value for each of the 14 microsatellites used in the present analysis

Marker	No.	He	PIC
BM8125	9	0.743	0.606
BM6526	10	0.646	0.397
CP34	10	0.790	0.660
BM757	7	0.727	0.562
INRA006	13	0.673	0.598
BM6506	9	0.689	0.522
BM1818	9	0.444	0.206
FCB128	10	0.782	0.645
CSSM31	18	0.886	0.812
CSMM66	17	0.899	0.820
ILSTS011	8	0.749	0.519
McM53	12	0.706	0.560
RM006	11	0.639	0.443
ILSTS005	13	0.746	0.600

respectively, and f_{km} is the average coancestry between individuals belonging to populations k and m; and b) Wright's (1969) F-statistics, F_{IS}, F_{ST}, and F_{IT} (defined as heterozygote deficiency within population, heterozygote deficiency due to population subdivision, and heterozygote deficiency in the total population, respectively) are obtained as $F_{IS} = \dfrac{\tilde{F} - \tilde{f}}{1 - \tilde{f}}$, $F_{ST} = \dfrac{\tilde{f} - \bar{f}}{1 - \bar{f}}$, and $F_{IT} = \dfrac{\tilde{F} - \bar{f}}{1 - \bar{f}}$, where $\tilde{f}$, $\tilde{F}$ are the mean coancestry and the inbreeding coefficient for the entire population, respectively, and $\bar{f}$ is the average coancestry for the subpopulation (see Eq. [3] and [6] in Caballero and Toro, 2002). Notice that $\tilde{F}$ is not genealogical inbreeding, defined as the probability that an individual has two identical alleles by descent (Malécot, 1948), but homozygosity, referred to as identity by state, which is defined as the probability that two alleles chosen at random from the population are the same (Nei, 1987).

The above computations (H_e, PIC, f, D_k, D_R, D_s, D_{AS}, F_{IS}, F_{ST}, and F_{IT}) were performed using the program MolKin 1.0 (Gutiérrez and Goyache, 2004), which is available upon request. The correlation between different sets of distance matrices was carried out using Mantel's test, as implemented in the program Arlequin 2.0 (Schneider et al., 2000). Mantel's test consists of testing the significance of the correlation between two or more matrices by a permutation procedure allowing one to obtain empirical null distribution of the correlation coefficient, taking into account the autocorrelations of the elements of the matrix. The statistical significance of the correlation coefficients was estimated by permutation analysis using 1,000 replications.

Multidimensional scaling analysis was carried out on the genetic distance matrices using the MDS procedure of SAS/STAT (SAS Inst., Inc., Cary, NC). Multidimensional scaling analysis is an exploratory technique that allows for the visualization of proximities in a low dimensional space. The interpretation of the dimensions obtained from the analysis can lead to an understanding of the processes underlying the perceived nearness of entities.

Results

Parameters describing the variability of the markers used are given in Table 1. The 14 microsatellites had a total of 156 alleles, ranging from 7 to 18 alleles per marker. The average PIC for the whole dataset was high (0.723), and most of the markers used had PIC values higher than 0.50. The lower PIC markers were BM1818, BM6526, and RM006 (0.21, 0.40, and 0.44, respectively), whereas CSSM31 and CSMM66 had PIC values above 0.80. The F_{IS}, F_{ST}, and F_{IT} statistics (Wright, 1969) computed for the complete dataset had the following values, respectively: 0.066, 0.070, and 0.131. Table 2 describes the genetic variability of the analyzed populations. The lowest average number of alleles per breed was found in the Rubia del Molar (5.4) and Black-faced Latxa (6.6) breeds, whereas the same parameter in the other breeds varied from 7.1 to 7.7. No breed had an excess of heterozygotes; F_{IS} values ranged from close to 0 for the Castellana breed, to 0.11 and 0.15 for the Merino and Xalda breeds, respectively. The lowest within-breed D_k was in the Rubia del Molar breed (0.31), whereas the highest values were found in the Merino (0.40) and Xalda breeds (0.37). The average

Table 2. Number of available samples, expected heterozygosity (He), heterozygote deficiency within a population (F_{IS}), average polymorphic informative content (PIC), average number of alleles per loci (k), within-breed kinship distance (D_k), and within-breed molecular coancestry (f_{ii}) for each analyzed sheep breed

Breed	No.	He	F_{IS}	PIC	k	D_k	f_{ii}
Castellana	33	0.701	−0.008	0.531	7.1	0.348	0.299
Churra	30	0.744	0.055	0.572	7.6	0.365	0.307
Black-faced Latxa	32	0.706	0.086	0.519	6.6	0.354	0.348
Blonde-faced Latxa	31	0.738	0.027	0.562	7.3	0.353	0.312
Merino	30	0.782	0.113	0.608	7.6	0.405	0.272
Rubia del Molar	32	0.667	0.033	0.483	5.4	0.314	0.391
Xalda	34	0.692	0.154	0.510	7.7	0.374	0.353
Total	222	0.568	0.066	0.723	11.2		0.276

Table 3. Correlation between matrices of the corresponding between-population genetic distance matrices: Reynolds' distance (D_R), Nei's standard distance (D_s), shared allele distance (D_{AS}), kinship distance (D_k), and molecular coancestry (f_{ij})

Distance	D_R	D_s	D_{AS}	D_k
D_s	0.956***			
D_{AS}	0.961***	0.986***		
D_k	0.461	0.587*	0.553*	
f_{ij}	0.080	−0.197	−0.165	−0.497*

*$P < 0.05$.
***$P < 0.001$.

molecular coancestry and $\tilde{F}$ estimated from the set of microsatellites for the whole dataset were 0.276 and 0.380, respectively. Merino had the largest D_{AS}, showing that the individuals belonging to this breed shared the lowest number of alleles of any sheep population in the dataset. The other within-breed D_{AS} values ranged between 0.507 for Rubia del Molar and 0.591 for the Churra breed.

Five between-breed genetic distances were computed for the complete dataset: D_R, D_s, D_{AS}, D_k, and f_{ij}, which is actually a similarity measure. Correlations between the corresponding matrices are given in Table 3. Correlations between genetic D_R, D_s, and D_{AS} matrices were positive and highly significant. Correlations between these three distances and D_k were moderate. Understandably, correlations involving f_{ij} were negative, except for D_R, which was virtually zero, and low and non-significant except for the correlation between the between-breed molecular coancestry and D_k, which was moderate (−0.497; $P < 0.05$).

Table 4 shows the between-breed D_R and D_{AS} distances. Regarding pairwise D_R, the highest differentiation (above 0.06) was found in the Rubia del Molar breed (especially with both Latxa varieties and the Xalda breed). The lowest differentiation was found between both Latxa varieties, and between Castellana and both Merino and Blonde-faced Latxa breeds (D_R values below 0.03). The highest D_{AS} values (around 0.24) were found to be related to the Rubia del Molar breed and to the Churra breed (around 0.20), whereas the lowest were found between both Latxa varieties (0.098).

The f_{ij} and D_k are shown in detail in Table 5. Most paired molecular coancestry values that were higher than those for the complete population were found to be related to the Rubia del Molar and Xalda breeds. The lowest values of between-breed D_k (below 0.40) were found between both Latxa populations and between Castellanas and Latxas, whereas the highest values (above 0.43) are basically related to the Merino, Rubia del Molar, and Xalda breeds.

Figure 1 shows the multidimensional scaling plots constructed using D_R, D_s, and D_{AS} paired values. The three plots essentially give the same information. On Dimension 1, the Churra breed, and especially the Rubia del Molar breed, are highly differentiated from the other breeds. The Latxa breeds were closely related among themselves. In the plot constructed using D_{AS}, no breed can be easily differentiated from the others except for the Churra and Rubia del Molar breeds.

Figure 2 shows the multidimensional scaling plots constructed using the between-breed D_k matrix and the f_{ij} values. Notice that molecular coancestry is the second term in the formula used to compute the kinship distance: $D_k = ([s_i + s_j]/2) − f_{ij}$. The plots give different images, which are in turn clearly different to those shown in Figure 1. Using D_k, the Rubia del Molar and Churra breeds are still separated on Dimension 1 of the plot, whereas the Merino and Xalda breeds are differentiated with respect to the rest of the breeds on the second dimension. The plot constructed using between-breed molecular coancestry was somewhat similar to that constructed with D_k, although Xalda and the two Latxa breeds formed a cluster that is clearly separated from the Castellana breed.

Discussion

The main goal of this research was to assess the usefulness of molecular coancestry information to characterize genetic relationships between livestock breeds. To do so, we used a set of microsatellite markers that had been shown previously to be useful in obtaining sound assessments of genetic relationships among breeds (Álvarez et al., 2004). The microsatellite set used here is, as a whole, highly informative as characterized by the PIC value. The parameter PIC was originally introduced by Botstein et al. (1980). It refers to the

Table 4. Pairwise Reynolds' distance values (above diagonal) and pairwise allele shared distance (D_{AS}) values (below diagonal) for all analyzed populations

Population	1	2	3	4	5	6	7
Castellana (1)		0.041	0.035	0.027	0.025	0.061	0.038
Churra (2)	0.196		0.050	0.048	0.037	0.051	0.052
Black-faced Latxa (3)	0.155	0.200		0.020	0.040	0.069	0.041
Blonde-faced Latxa (4)	0.130	0.217	0.098		0.025	0.064	0.039
Merino (5)	0.131	0.192	0.186	0.130		0.056	0.038
Rubia del Molar (6)	0.245	0.211	0.247	0.249	0.238		0.070
Xalda (7)	0.169	0.206	0.156	0.165	0.174	0.252	

Table 5. Between-breed paired molecular coancestry (f_{ij}; below diagonal) and pairwise kinship distance (D_k; above diagonal) for all analyzed populations

Population	1	2	3	4	5	6	7
Castellana (1)		0.414	0.398	0.388	0.412	0.411	0.411
Churra (2)	0.246		0.427	0.425	0.438	0.407	0.439
Black-faced Latxa (3)	0.276	0.260		0.381	0.435	0.421	0.418
Blonde-faced Latxa (4)	0.268	0.244	0.302		0.415	0.417	0.416
Merino (5)	0.250	0.237	0.255	0.256		0.435	0.442
Rubia del Molar (6)	0.265	0.282	0.283	0.268	0.257		0.432
Xalda (7)	0.275	0.261	0.297	0.280	0.260	0.284	

value of a marker for detecting polymorphism within a population, depending on the number of detectable alleles and the distribution of their frequency and has been proved to be a general measure of how informative a marker is (Guo and Elston, 1999); the higher the PIC value, the more informative a marker.

The f_{ij} matrix was not significantly correlated with those computed for the major (D_R, D_s, and D_{AS}) genetic distances (Table 3), illustrating that the information provided by this parameter accounts for the allele-frequencies in the founder population (Eding and Meuwissen, 2001; Eding et al., 2002), whereas D_R, D_s, and D_{AS} characterize the short-term evolution of the populations. The genetic distances used here (including D_k) are highly dependent on the observed allele frequencies, which are in turn highly dependent on recent evolutionary processes such as genetic drift. However, the information provided by D_k is not the same as that provided by the classical genetic distances because in D_k recent between-breeds differentiation is corrected for allele frequencies before separation of populations (f_{ij}; Eding et al., 2002). This situation is the basis of the moderate
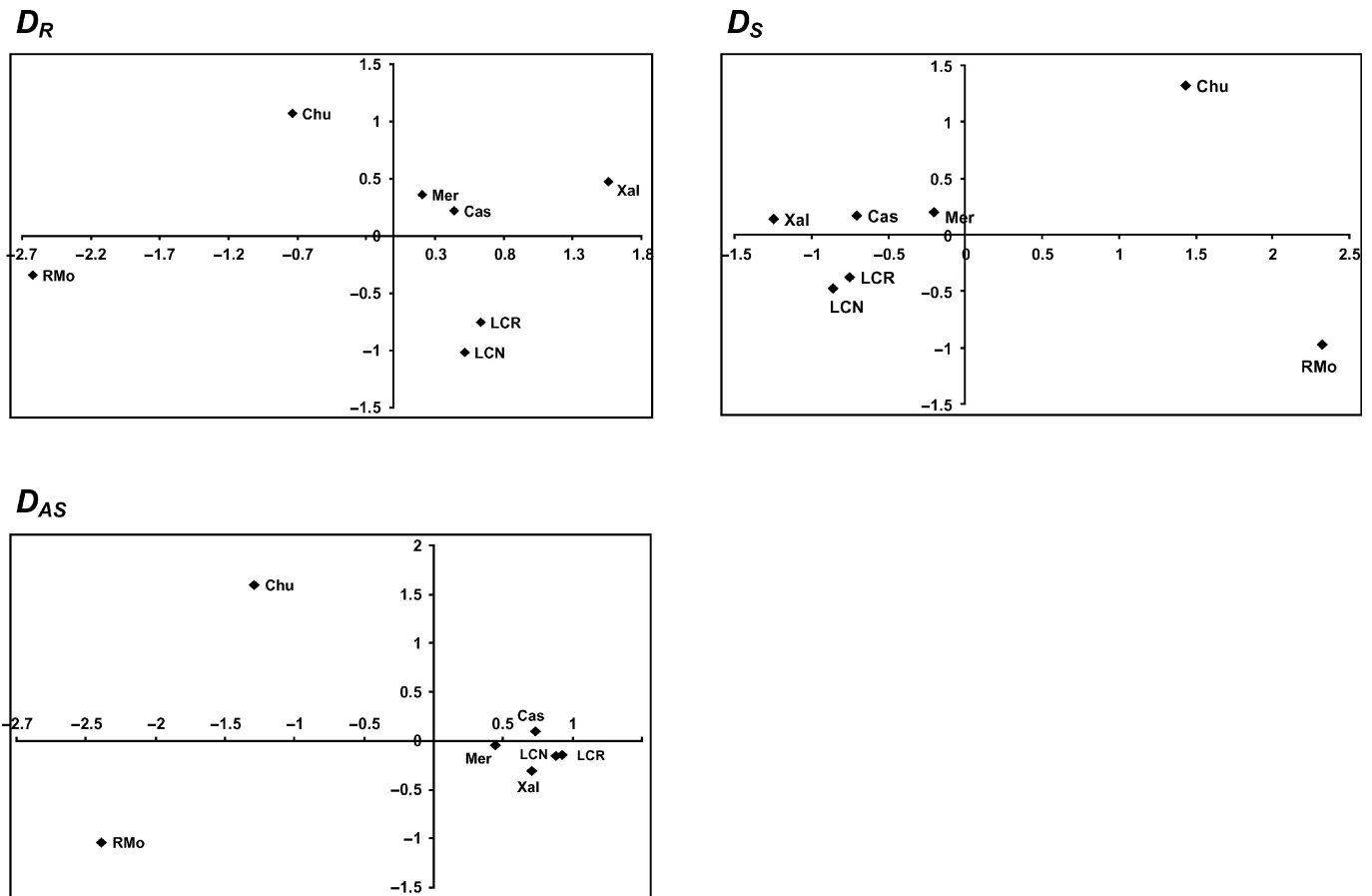

Figure 1. Multidimensional scaling plots constructed using between-breed Reynolds' distance (D_R), Nei's standard distance (D_s), and shared allele distance (D_{AS}). Dimension 1 is on the x-axis, whereas Dimension 2 is on the y-axis. Abbreviations correspond to Castellana (Cas), Churra (Chu), Black-faced Latxa (LCR), Blonde-faced Latxa (LCN), Merino (Mer), Rubia del Molar (RMo), and Xalda (Xal) sheep breeds.
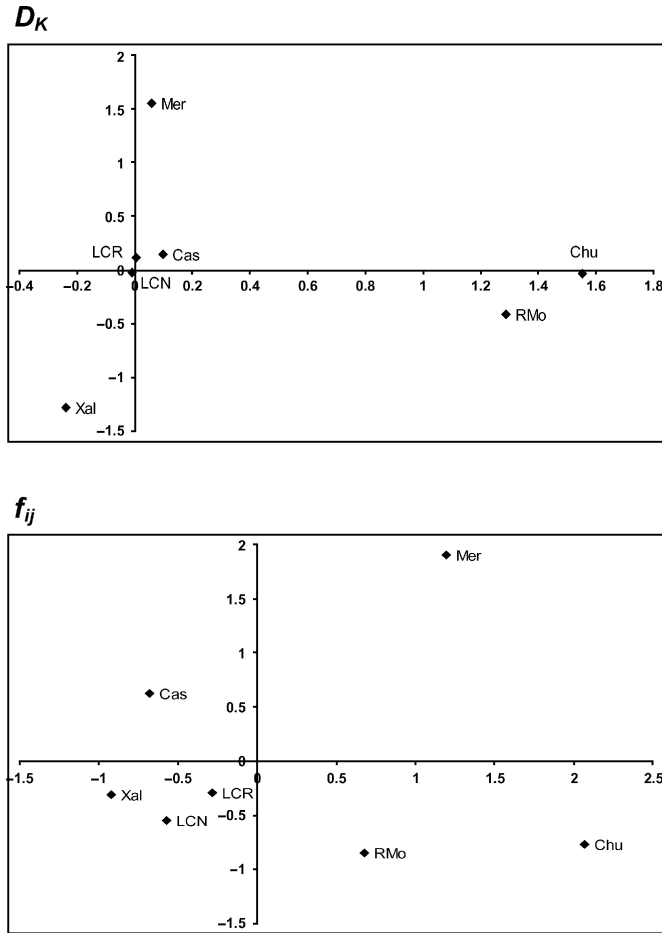
D_K

f_{ij}

Figure 2. Multidimensional scaling plots constructed using the between-breed kinship distance (D_k) matrix and between-breed molecular coancestry values (f_{ij}). Dimension 1 is on the x-axis, whereas Dimension 2 is on the y-axis. Abbreviations correspond to Castellana (Cas), Churra (Chu), Black-faced Latxa (LCR), Blonde-faced Latxa (LCN), Merino (Mer), Rubia del Molar (RMo), and Xalda (Xal) sheep breeds.

to low correlation found between D_k and D_R, D_s, and D_{AS} (Table 3).

The high correlation generally found between distance matrices is not surprising, as genetic distances tend to be highly related (Takezaki and Nei, 1996); however, neither the D_k nor the f_{ij} matrix provided the same information as the other parameters, and their combined use with classical parameters is recommended. At the same time, the correlation between the D_k and f_{ij} matrices (roughly –0.50) showed that they do not offer the same information, and their comparison may be useful to ascertain evolutionary processes.

The information provided by the classical genetic distances used here (D_R, D_s, and D_{AS}) on the genetic relationships among breeds was basically the same (Figure 1). The Latxa breeds had the lowest differentiation, whereas the Rubia del Molar breed (and to a lesser extent the Churra) had the highest. Only the plot con-

structed using the D_R matrix allows differentiation of the Xalda breed and both Latxa varieties to the other breeds. The D_R has been shown to be an appropriate measure for livestock populations with short-term divergence (Reynolds et al., 1983; Laval et al., 2002). It has been pointed out that the typically high within-population variability of microsatellites may result in a low magnitude of differentiation measures (Hedrick, 1999; Balloux and Lougon-Moulin, 2002). In addition, some degree of genetic admixture among breeds due to geographical proximity should be assumed, leading to a lack of differentiation between breeds. Most sampled breeds did not implement Herd Book organizations before the late 1980s or early 1990s, making the existence of introgression processes possible.

The situation described for the Rubia del Molar and Xalda breeds using classical genetic distances may be partially explained by the recent genetic bottleneck experienced by both breeds (Álvarez et al., 2004). Though the Xalda breed has suffered an intense genetic bottleneck (Goyache et al., 2003; Álvarez et al., 2004), its differentiation is not as clear as that of Rubia del Molar. The available Xalda individuals are a sample of the founders used for the recovery of the breed; they show a clear heterozygote deficiency (F_{IS} = 0.154) but also the highest average number of alleles per locus (see Table 2). The Xalda founders analyzed were recovered in different genetically isolated locations, probably leading to the fixation of different alleles that, as a whole, capture the genetic variability existing in the Xalda breed before the population bottleneck.

In general, the information offered by D_k in the present study allowed a better differentiation among breeds. This was especially true for the Merino breed, which showed a high within-breed genetic variability characterized by the lowest within-breed f_{ij} (Table 2). High within-breed genetic variability of the Iberian Merino populations has been previously reported (Díez-Tascón et al., 2000; Arranz et al., 2001). This makes it difficult (contrary to other Iberian sheep breeds) to differentiate the Merino individuals in a single cluster (Arranz et al., 2001). Because the analyzed breeds have markedly different origins (Sotillo and Serrano, 1985; Sánchez Belda and Sánchez Trujillano, 1986), the aforementioned facts (genetic bottlenecks and introgression processes) cannot be the sole explanation of the genetic situation found here. Because coancestry between populations remains constant over time after meta-population fission, a genetic distance between populations is determined in terms of coefficient of kinship by the increase in within-population coancestry after separation (Eding and Meuwissen, 2001). The formula used to compute the kinship distance, $D_k = ([s_i + s_j]/2) - f_{ij}$ (Caballero and Toro, 2002), has two terms that may be useful in assessing whether differentiation among breeds may be recent or remote in origin. In the plot summarizing the D_k matrix (Figure 2), both the Merino and the Xalda breeds are well differentiated with respect to the others, whereas both the Latxa and

Castellana breeds form a clear cluster. The plot showing the between-population coancestry (f_{ij}) in Figure 2 would represent the between-breed genetic relationships at the moment of separation (ancestral differentiation). The plotted situation would be consistent with the markedly different ancestral genetic origins hypothesized for the Iberian sheep (Sotillo and Serrano, 1985; Sánchez Belda and Sánchez Trujillano, 1986): the Merino, Churra-type, and Entrefino (represented by the Castellana breed) groups would be placed in different quadrants of the plot. Within the Churra-type group, the first dimension would differentiate the Churra and Latxa-related breeds, supporting the hypothesis that they could have different ancestral origins (Sánchez Belda and Sánchez Trujillano, 1986; Arranz et al., 1998; Álvarez et al., 2004). The Xalda would ancestrally be derived from a "Latxa" metapopulation, whereas the origin of the Rubia del Molar breed would be close to the Churra breed. Consequently, the differentiation arising between the Xalda and both Latxa breeds when D_k is used would have occurred only recently in genetic terms (Álvarez et al., 2004), which is in turn reflected by the largest F_{IS} values found in the present work. Moreover, the lack of differentiation found between the Castellana and the Latxa breeds when D_k is used has recent causes. Álvarez et al. (2004) estimated high recent migration rates between the Castellana and the Blonde-faced Latxa breeds using Bayesian methodologies (Wilson and Rannala, 2003). The present results confirm the hypothesis of Álvarez et al. (2004) that the genetic similarities found between the Castellana and Latxa breeds using F_{ST}-based estimators come from recent admixture rather than from a common ancestral origin.

Implications

The present study provides evidence that the genetic differentiation of livestock breeds may be approached using methodologies based on molecular coancestry information. The most striking characteristic of the new methodologies is the ability to assess whether genetic differentiation is recent or ancestral in origin. Thus, molecular coancestry-based parameters may be superior to some classical genetic distances when obtaining information on population dynamics in livestock breeds. To illustrate the possibilities of using the new methodologies, we analyzed a set of native sheep breeds from Spain. This research presents reliable evidence of the history of these sheep breeds.

Literature Cited

Álvarez, I., L. J. Royo, I. Fernández, J. P. Gutiérrez, E. Gómez, F. Goyache. 2004. Genetic relationships and admixture among Northern Spain sheep breeds assessed using microsatellites. J. Anim. Sci. 82:2246–2252.

Álvarez Sevilla, A., J. P. Gutiérrez, I. Fernández, L. J. Royo, I. Álvarez, E. Gómez, and F. Goyache. 2004. Conservación de la oveja Xalda de Asturias. AGRI 34:41–49.

Arranz, J. J., Y. Bayón, and F. SanPrimitivo. 1998. Genetic relationships among Spanish sheep using microsatellites. Anim. Genet. 29:435–440.

Arranz, J. J., Y. Bayón, and F. SanPrimitivo. 2001. Differentiation among Spanish sheep breeds using microsatellites. Genet. Sel. Evol. 33:529–542.

Balloux, F., and N. Lugon-Moulin. 2002. The estimation of population differentiation with microsatellite markers. Mol. Ecol. 11:155–165.

Botstein, D., R. L. White, M. Skolnick, and R. W. Davis. 1980. Construction of a genetic linkage map in man using restriction fragment polymorphisms. Am. J. Hum. Genet. 32:314–331.

Caballero, A., and M. A. Toro. 2002. Analysis of genetic diversity for the management of conserved subdivided populations. Conservation Genetics 3:289–299.

Chakraborty, R., and L. Jin. 1993. Determination of relatedness between individuals using DNA fingerprinting. Hum. Biol. 65:875–895.

Díez-Tascón, C., R. P. Littlejohn, P. A. R. Almeida, and A. M. Crawford. 2000. Genetic variation within the Merino sheep breed: Analysis of closely related populations using microsatellites. Anim. Genet. 31:243–251.

Eding, H., R. P. M. A. Crooijmans, M. A. M. Groenen, and T. H. E. Meuwissen. 2002. Assessing the contribution of breeds to genetic diversity in conservation schemes. Genet. Sel. Evol. 34:613–633.

Eding, J. H., and G. Laval. 1999. Measuring genetic uniqueness in livestock. Pages 33–58 in Genebanks and the Conservation of Farm Animal Genetic Resources. J. K. Oldenbroek, ed., DLO Inst. Anim. Sci. and Health. Lelystad, The Netherlands.

Eding, H., and T. H. E. Meuwissen. 2001. Marker-based estimates of between and within population kinships for the conservation of genetic diversity. J. Anim. Breed. Genet. 118:141–159.

Fabuel, E., C. Barragan, L. Silio, M. C. Rodríguez, and M. A. Toro. 2004. Analysis of genetic diversity and conservation priorities in Iberian pigs based on microsatellite markers. Heredity 93:104–113.

Goyache, F., J. P. Gutiérrez, I. Fernández, E. Gómez, I. Álvarez, J. Díez, and L. J. Royo. 2003. Monitoring pedigree information to conserve the genetic variability in endangered populations: the Xalda sheep breed of Asturias as an example. J. Anim. Breed. Genet. 120:95–103.

Guo, X., and R. C. Elston. 1999. Linkage informative content of polymorphic genetic markers. Hum. Hered. 49:112–118.

Gutiérrez, J. P., and F. Goyache. 2004. MolKin (version 1.0): A computer program for genetic analysis of populations using molecular coancestry information. Universidad Complutense de Madrid, Spain.

Hedrick, P. W. 1999. Highly variable loci and their interpretation in evolution and conservation. Evolution 53:313–318.

Laval, G., M. Sancristobal, and C. Chevalet. 2002. Measuring genetic distances between breeds: use of some distances in various short term evolution models. Genet. Sel. Evol. 34:481–507.

Malécot, G. 1948. Les Mathématiques de l'Hérédité. Masson et Cie, Paris, France.

Nei, M. 1987. Molecular Evolutionary Genetics. Columbia Univ. Press, New York.

Reynolds, J., B. S. Weir, and C. C. Cockerham. 1983. Estimation of the coancestry coefficient: Basis for a short-term genetic distance. Genetics 105:767–769.

Ruane, J. 1999. A critical review of the value of genetic distance studies in breed conservation. J. Anim. Breed. Genet. 116:317–323.

Sambrook, J., E. F. Fritsch, and T. Maniatis. 1989. Molecular Cloning: A Laboratory Manual. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.

Sánchez Belda, A., and M. C. Sánchez Trujillano. 1986. Razas ovinas españolas. Segunda Edición. Publicaciones de Extensión Agraria, M.A.P.A., Madrid, Spain.

Schneider, S., D. Roessli, and L. Excoffier. 2000. Arlequin v.2.0: A software for population genetics data analysis. Genetics and Biometry Laboratory, Univ. of Geneva, Geneva, Switzerland.

Sotillo, J. L., and V. Serrano. 1985. Producción Animal I. Etnología Zootécnica. Ediciones Tebar-Flores, Madrid, Spain.

Takezaki, N., and M. Nei. 1996. Genetic distances and reconstruction of phylogenetic trees from microsatellite DNA. Genetics 144:389–399.

Toro, M. A., C. Barragan, and C. Ovilo. 2003. Estimation of genetic variability of the founder population in a conservation scheme using microsatellites. Anim. Genet. 34:226–228.

Toro, M., C. Barragan, C. Ovilo, J. Rodrigañez, C. Rodríguez, and L. Silió. 2002. Estimation of coancestry in Iberian pigs using molecular markers. Conservation Genetics 3:309–320.

Wilson, G. A., and B. Rannala. 2003. Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177–1191.

Wright, S. 1969. Evolution and the Genetics of Populations: The Theory of Gene Frequencies, Vol. 2. Univ. of Chicago Press, Chicago, IL.