Genetic relationships and admixture among sheep breeds from Northern Spain assessed using microsatellites[1]

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ABSTRACT: Although many research papers have studied diversity and differentiation within livestock species, genetic relationships among neighboring populations remain poorly understood. Here we apply recent methodologies to analyze the polymorphism of 14 microsatellites in 238 unrelated individuals belonging to six sheep breeds from Northern Spain to ascertain their historical relationships and the relative genetic contributions existing between populations. Individual genotypes were analyzed to assess the existence of an underlying genetic structure. Long-term and recent migration rates were estimated to identify patterns of relative genetic contribution among breeds. The complete data set showed a strong population structure derived from both different ancestral origins and some geographical patterns of recent gene flow. Two of the analyzed breeds (Black-faced Latxa and Churra) had a marked genetic background, supporting the hypothesis that, regardless of their phenotypical similarities, they have different ancestral origins. Some of the more presumably related breeds had negative long-term admixture coefficients, showing that they diverged only recently. In addition, we show how methodologies for estimation of long-term gene flow and recent patterns of migration are complementary, providing information about migration rates on different timescales.

Key Words: Admixture, Microsatellite, Migration Rate, Population Structure, Sheep

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Introduction

The definition of a population is typically subjective and is based on phenotypic traits and geographic location. In practice, it may be difficult to know whether the definition of a population represents a natural assignment in genetic terms. In some situations, especially in presumably genetically close breeds, we may be interested in determining whether there is agreement between subjective classifications and genetic information. In this case, we should assess the degree of subdivision that existed in our target populations and identify the relative contribution of each breed. Recently, coalescent-based methodologies have been developed to estimate admixture at population level, thereby allowing the estimation of migration rates for roughly the last $4N_e$ (N_e is the effective size of the population) generations (Bertorelle and Excoffier, 1998; Beerli and Felsenstein, 1999; Dupanloup and Bertorelle, 2001).

Genetic relationships among native sheep breeds of the Iberian Peninsula are poorly understood. Based on morphological traits (particularly the presence of long, coarse wool) and their use for dairy purposes, most of the Northern Iberian sheep breeds are included in the Churro group. These breeds were probably formed by the introgression of Central European ewes into the Iberian Peninsula (Aparicio, 1944; Sotillo and Serrano, 1985; Sánchez Belda and Sánchez Trujillano, 1986). However, there is a lack of consensus with respect to the allocation of some breeds (namely Latxa) within this group.

The number of studies using microsatellite information in sheep breeds has so far been somewhat limited (Arranz et al., 1998, 2001; Farid et al., 2000; Pariset et al., 2003). Here, we apply recent methodologies to analyze multilocus genotype information from six sheep breeds from Northern Spain. This will allow us to ascertain the recent and remote (ancestral) relative genetic contribution among the populations, thereby contribut-

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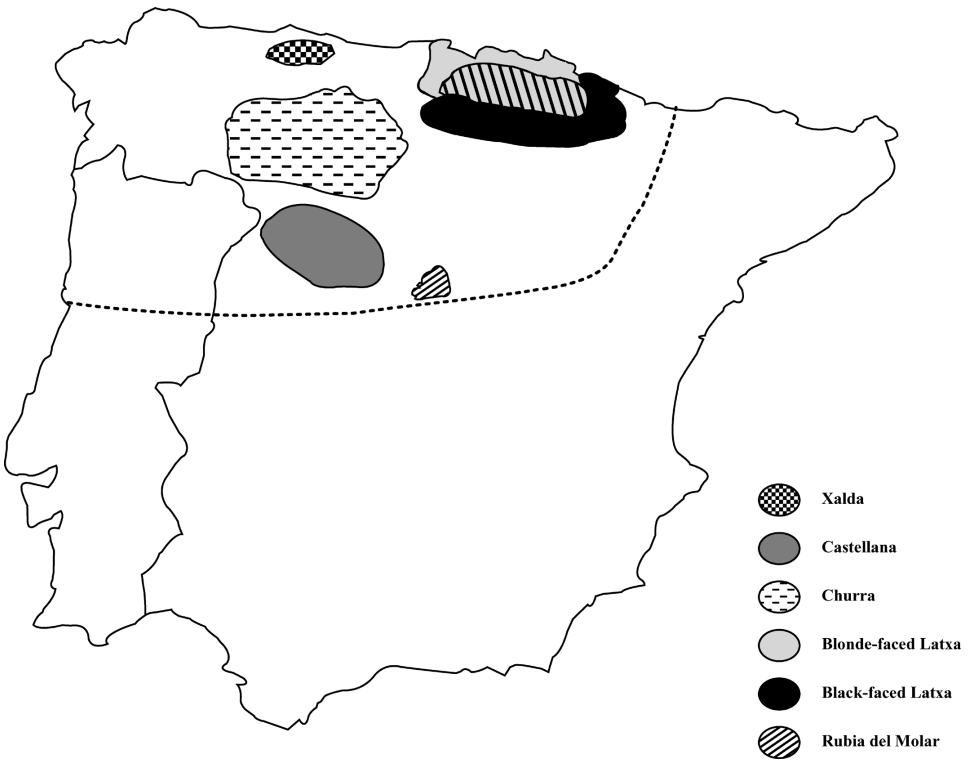

Figure 1. Geographical areas in which the density of the six Spanish sheep breeds under study is higher. In practice, both Basque (Blonde- and Black-faced Latxa) and both Castilian (Churra and Castellana) breeds are highly intermingled. The dotted line shows the distribution of the Spanish Churra sheep group according to Sánchez Belda and Sánchez Trujillano (1986).

ing to the knowledge of the historical relationships among them.

Material and Methods

Samples

Blood samples were obtained from 238 unrelated individuals corresponding to six Spanish sheep breeds presumably included in the ancestral Iberian Churra sheep group. Samples were obtained from herds included in the corresponding herd books. Breeds and, in brackets, number of individuals and number of herds sampled were as follows: Blonde-faced Latxa (33; 12) Black-faced Latxa (34; 11), Rubia del Molar (34; five), Churra (36; five), Castellana (39; six), and Xalda (62; 15). At least one reproductive male was sampled in the same herd. Geographical distribution of the sampled breeds is shown in Figure 1. Our sampling scheme included all the important native breeds in both Northern Spain and the Churra group. All the sampled breeds had long, coarse wool except for the Castellana breed, and all of them were used for dairy purposes except for the Xalda breed. The Black-faced Latxa and the Churra showed particular patterns of black pigmentation on head and legs, whereas the Blonde-faced Latxa and the Rubia del Molar showed similar reddish pigmentation patterns. The Castellana and Xalda breeds had black individuals in low and high frequency, respectively. The Rubia del Molar and Xalda (Goyache et al., 2003) breeds are considered as endangered. A detailed description of these breeds can be found in Sotillo and Serrano (1985), Sánchez Belda and Sánchez Trujillano (1986), and Álvarez Sevilla et al. (2004). The Latxa breed has been studied at a molecular level as a single population (Arranz et al., 1998, 2001). However, phenotypic differentiation between the two Latxa breeds is likely to be due to more than color pattern alone (Sánchez Belda and Sánchez Trujillano, 1986). Their breeding goals were also different and breeding schemes and estimation of genetic parameters for productive traits were carried out separately (Ugarte et al., 1996; Legarra and Ugarte, 2001), leading to their being characterized as different breeds (Sánchez Belda and Sánchez Trujillano, 1986).

Total DNA was isolated from blood samples following standard procedures (Sambrook et al., 1989). Up to 14 microsatellites (BM8125, BM6526, CP34, BM757, INRA006, BM6506, BM1818, FCB128, CSSM31, CSMM66, ILSTS011, McM53, RM006, ILSTS005) were analyzed on all the individuals. The PCR products were labeled with a fluorescent method (Cy5-labeled primer) and genotyping was performed on an ALFexpressII automated sequencer (Amersham Biosciences, Barcelona).

Table 1. Chromosome (Chr) in which the used markers are located, number of alleles per marker, and heterozygote deficiency within population (F_{IS}) values per marker and breed

			F_{IS} values per marker and breed[a]					
Marker[b]	Chr	No.	Castellana	Churra	Black-faced Latxa	Blonde-faced Latxa	Rubia del Molar	Xalda
BM8125	17	9	0.079	–0.116	–0.156	0.255	0.006	0.157
BM6526***	26	10	0.022	0.251	0.302	0.139***	0.117*	0.006
CP34***	3	8	–0.027	–0.112	0.032	0.030	–0.003	0.108**
BM757**	9	6	–0.312*	0.017	–0.014	–0.090*	0.100	0.314**
INRA006	1	13	0.071	0.178	0.034	–0.098	–0.120	0.088
BM6506	1	8	–0.067	–0.194	–0.038	0.009	0.039	0.141
BM1818***	20	9	0.340**	0.677***	0.543***	0.371***	0.373	0.499***
FCB128	2	10	0.083	–0.110	0.012	0.012	–0.051	–0.017
CSSM31***	23	18	0.138*	0.063**	0.294*	0.098	–0.014	0.129**
CSMM66*	9	17	0.073	0.098	0.023	0.099	0.103	0.147**
ILSTS011***	9	8	–0.217	0.249*	0.241	–0.070**	0.029	0.182*
McM53	6	12	–0.179	0.011	–0.159	–0.080	0.044	0.109
RM006**	5	12	0.105	0.156	0.226***	0.157	0.059	0.179
ILSTS005***	7	13	0.100	0.241**	0.376**	–0.005	0.202	0.271**

[a]One, two, and three asterisks mean, respectively, a significant deviation from Hardy-Weinberg equilibrium for $P < 0.05$, $P < 0.01$, and $P < 0.001$.
[b]Asterisks on the label of the markers mean that the marker had a significant deviation from Hardy-Weinberg equilibrium across breeds. No within-breed linkage disequilibrium was detected for the markers located in the same chromosome, except for the pairs BM757-CSMM66 and CSMM66-ILST011 within the Xalda breed.

Statistical Analysis

The program GENEPOP v. 1.2 (Raymond and Rousset, 1995) was used to compute the deviations from the Hardy-Weinberg proportions at marker and breed levels, within-breed heterozygosity, and between-breed heterozygote deficiency due to population subdivision (paired $\boldsymbol{F_{ST}}$ distances). Additionally, linkage disequilibrium was tested for the markers on the same chromosome (see Table 1).

The program STRUCTURE (Pritchard et al., 2000) was used to analyze the genetic structure of our populations. This program infers the number of populations into which the analyzed genotypes can be divided. The program estimates the natural logarithm of the probability that a given genotype X is part of a given population K: $\ln \Pr(X \mid K)$. This ensures that the groups are, as representatively as possible, samples from a single population. The program assumes that there are K populations with unknown gene frequency distribution at each locus p_{kl} for the $k = 1 \ldots K$ populations and $l = 1 \ldots L$ loci contributing to the gene pool of the target population. Alleles at each locus are sampled independently for each individual, conditional on the proportion q_i of its genotype in a given population. The program STRUCTURE uses the Markov Chain Monte Carlo method to separately estimate the posterior probability distribution of each parameter (particularly q_i and q_{kl}) in an integrated way over all the other parameters. This means that, in contrast to previous methodologies (Rannala and Mountain, 1997), it is not necessary to specify the gene frequencies of the contributing source populations in advance. We ran the program 12 times, fitting K from 1 to 12. All runs used a burn-in period of 100,000 iterations and a period of data collection of 100,000 iterations.

Remote and recent migration rates among our populations were estimated using the programs ADMIX 2.0 and BayesAss+, respectively. The program ADMIX 2.0 (Dupanloup and Bertorelle, 2001) takes into account molecular information from any number of parental populations to compute the admixture coefficient ($\boldsymbol{m\gamma}$) described by Bertorelle and Excoffier (1998). Computation of $m\gamma$ takes into account the average squared difference in allele size and the mutation rate, assuming the strict stepwise mutation model under a coalescent approach. This is a significant extension of the methodology introduced by Bertorelle and Excoffier (1998), as it allows the estimation of the relative contribution of any parental populations to another using not only the allelic frequencies, but also the degree of molecular divergence between them. The mean coalescent time is computed as $\bar{t} = \bar{S}/2\mu$, where $\bar{S}$ is the average squared difference in allele size and μ is the global mutation rate. Parameter $m\gamma$ seems to be a good estimator of admixture proportions because of its absence of bias. All of the runs of ADMIX 2.0 were carried out fitting 1,000 random bootstrap samples.

The program BayesAss+ (Wilson and Rannala, 2003) is a Bayesian method for estimating recent migration rates among populations using multilocus genotype information. This method relaxes some key assumptions of previous assignment methodologies, namely that genotypes are in Hardy-Weinberg equilibrium within populations. The program simultaneously estimates the probability distribution of allelic frequencies for each locus, migration rates among populations (m_{ij}) and a separate inbreeding coefficient for each population (F_i), assessing the relative importance of specific patterns of population dynamics. The program BayesAss+ was run using a burn-in and a data collection period of 3×10^6 iterations.

Table 2. Number of genotyped individuals per breed and expected, unbiased, and observed heterozygosity for six sheep breeds from Northern Spain

Breed	No. of individuals	Heterozygosity		
		Expected	Unbiased	Observed
Blonde-faced Latxa	33	0.689	0.700	0.661
Black-faced Latxa	34	0.654	0.664	0.594
Rubia del Molar	34	0.619	0.628	0.600
Churra	36	0.704	0.714	0.661
Castellana	39	0.708	0.718	0.712
Xalda	62	0.659	0.664	0.572

Table 4. Proportion of membership of each of the six current sheep breeds in each of the six inferred clusters using the program STRUCTURE

Source populations	Inferred populations[a]					
	1	2	3	4	5	6
Blonde-faced Latxa	0.057	0.082	0.047	0.072	0.194	**0.547**
Black-faced Latxa	0.027	0.032	0.048	0.049	**0.529**	**0.315**
Rubia del Molar	**0.847**	0.014	0.013	0.044	0.063	0.018
Churra	0.059	**0.467**	0.044	**0.331**	0.058	0.041
Castellana	0.031	0.056	0.051	**0.602**	0.176	0.085
Xalda	0.021	0.148	**0.478**	0.066	**0.208**	0.079
F_{ST} for inferred populations	0.193	0.071	0.121	0.044	0.059	0.065

[a]Estimates assumed admixture in the sampled genotypes. Contributions higher than 0.20 are in bold.

Results

A description of the used markers, including chromosome localization, number of alleles per marker, the heterozygote deficiency within population values ($\boldsymbol{F_{IS}}$), and deviation from Hardy-Weinberg equilibrium across breeds, is given in Table 1. Within breeds, the number of markers that show a significant deviation from Hardy-Weinberg equilibrium ranged from one to four. However, up to nine markers were found to be in Hardy-Weinberg disequilibrium across populations. Only the marker BM1818 was consistently in Hardy-Weinberg disequilibrium across breeds (except for the Rubia del Molar breed).

The heterozygosity values in the analyzed breeds and the paired F_{ST} distances between them are shown, respectively, in Tables 2 and 3. Overall F_{ST} value for the whole data set was 0.061. The smallest distances were between both Latxa populations (0.019), whereas the largest F_{ST} values were between Rubia del Molar and the other breeds, ranging from 0.067 to 0.095.

The analyzed data have a complex underlying genetic structure. The program STRUCTURE was first run with a number of expected populations, ranging from $K = 1$ to $K = 12$, so as to choose the appropriate value of K to better model the whole data set. The best value of ln Pr($X \mid K$) was obtained for $K = 6$(–9990.8). These six inferred populations would correspond to the "ancestral" populations from which our current breeds were derived. The program STRUCTURE computes the allelic frequencies expected in each locus for the inferred populations and, interestingly enough, the proportion of the six sampled breeds in each of the six inferred populations (Table 4). The first three inferred populations were basically formed by, respectively, Rubia del Molar, Churra, and Xalda individuals, showing that these breeds had a particular genetic background that is possible to differentiate. The fourth inferred population was formed by most of the Castellana individuals and a significant proportion of Churra samples. The fifth and sixth inferred clusters were basically formed by both Latxa varieties. Two of the inferred populations (fourth and sixth) characterize two clear geographical clusters (the Castilian cluster and the Basque cluster). Since STRUCTURE performance is based on the assumption of Hardy-Weinberg equilibrium, reliability of the reported results was checked by rerunning the program STRUCTURE twice, firstly using the five marker in Hardy-Weinberg equilibrium (BM8125, INRA006, BM6506, FCB128 and McM53; see Table 1) and then the others (not shown). The program STRUCTURE performed very robustly and the detected deviations of the Hardy-Weinberg equilibrium at a metapopulation level did not substantially affect the results. The two additional runs also gave the best value of ln Pr($X \mid K$) cases for $K = 6$ (–3955.9 and –6594.4, respectively) and the membership patterns of each of the six current sheep breeds in each of the six inferred clusters were substantially the same as that reported for the complete data set.

Estimates of the admixture coefficient $m\gamma$ (Bertorelle and Excoffier, 1998) are shown in Table 5. This parame-

Table 3. Heterozygote deficiency due to population subdivision (F_{ST}) values for each pair of the six analyzed populations

	Black-faced Latxa	Rubia del Molar	Churra	Castellana	Xalda
Blonde-faced Latxa	0.019	0.090	0.058	0.030	0.044
Black-faced Latxa		0.095	0.066	0.042	0.038
Rubia del Molar			0.067	0.082	0.086
Churra				0.044	0.062
Castellana					0.042

Table 5. Admixture coefficients ($m\gamma$) for the complete data set using the program ADMIX 2.0

	Derived population[a]					
Parental population	1	2	3	4	5	6
1. Blonde-faced Latxa	—	0.54	–0.12	0.09	0.13	–0.71
2. Black-faced Latxa	1.00	—	0.83	–0.13	0.35	0.73
3. Rubia del Molar	–0.08	0.22	—	0.25	–0.21	–0.16
4. Churra	0.33	–0.15	0.73	—	0.53	0.66
5. Castellana	0.19	0.12	–0.17	0.33	—	0.47
6. Xalda	–0.45	0.27	–0.26	0.46	0.21	—
Average SD[b]	0.85	0.52	0.91	0.62	1.47	0.73

[a]Each breed was considered as derived from the other five breeds. Rows show the genetic contribution of each breed as a parental population to the derived breed, which is in the columns. Contributions higher than 0.50 are in bold.

[b]The last row shows the average standard deviation of the estimates of $m\gamma$ for each breed as derived population.

ter was computed assuming that each breed was derived (admixed) from the rest of the populations. Estimates had large standard deviations, thus allowing limited confidence on $m\gamma$ values. The robustness of the results was tested by computing the admixture coefficients simply using the allelic frequencies as proposed by Bertorelle and Excoffier (1998). New admixture coefficients (not shown) consistently showed the same pattern and sign as those computed taking into account the average square difference in allele size shown in Table 5. High $m\gamma$ values may be considered an indicator of a remote gene flow between populations. In this sense, the Black-faced Latxa and Churra breeds would act as major genetic sources for the analyzed populations. The Castellana breed would have been affected by an important genetic introgression from the Churra breed (0.53), whereas both the Rubia del Molar and Xalda breeds would have been ancestrally derived from both the Black-faced Latxa and Churra source populations. Some of the $m\gamma$ estimates between breeds that were assumed to be strongly admixed were negative (no admixture). This draws attention especially to the admixture coefficient between Blonde-faced Latxa and both the Rubia del Molar (–0.08) and Xalda (–0.45) breeds.

Estimates of recent migration rates between populations (up to the second generation of migrants) are shown in Table 6. Means and standard deviations of the posterior distribution of inbreeding coefficient for each population are also shown. Half of the breeds (Black-faced Latxa, Rubia del Molar, and Xalda) have not received a significant proportion of migrants. Significant recent introgression rates (approximately 30%) were found between neighboring breeds (both Basque and both Castilian breeds) and from Blonde-faced Latxa to Castellana. Estimates of F point to possible local inbreeding effects in Xalda (0.1620) and Black-faced Latxa (0.1073). The estimate of F for the Churra breed was the highest (0.4978). However, the estimate of the associated standard deviation was also large (0.2956).

Discussion

The average observed heterozygosity found here was lower than that of 0.77 previously reported for several Spanish sheep breeds (Arranz et al., 2001). The overall F_{ST} value for the whole data set is also slightly lower than that of around 0.07 previously reported by Arranz et al. (1998, 2001). However, the present and previous studies on Spanish sheep breeds cannot be directly compared owing to the different marker sets used. Paired F_{ST} distances suggest that the Churra and Rubia del Molar breeds are the most differentiated populations, whereas both Latxa varieties could be roughly considered to be a single population. The marked deviation of the Hardy-Weinberg proportions observed for the marker BM1818 (Table 1) may be explained by unobserved null alleles leading to high within-breed F_{IS} values, ranging from 0.340 to 0.677.

Estimation of genetic differentiation using F-statistics can be criticized. These parameters do not allow gene flow patterns among breeds to be ascertained. It has been suggested that the typical high within-population variability of microsatellites may result in a low magnitude of differentiation measures (Hedrick, 1999;

Table 6. Means of the posterior distribution of the migration rates (m), and means and standard deviations of the posterior distribution of the inbreeding coefficient (F) of each population estimated using the program BayesAss+

	Derived population[a]						F	
Parental population	1	2	3	4	5	6	Mean	SD
1. Blonde-faced Latxa	**0.6892**	0.0025	0.0033	0.0086	**0.2923**	0.0208	0.0444	0.0286
2. Black-faced Latxa	**0.2857**	**0.9876**	0.0027	0.0047	0.0185	0.0381	0.1073	0.0242
3. Rubia del Molar	0.0077	0.0026	**0.9864**	0.0045	0.0043	0.0026	0.0636	0.0296
4. Churra	0.0046	0.0022	0.0024	**0.6756**	0.0041	0.0022	0.4978	0.2956
5. Castellana	0.0062	0.0025	0.0029	**0.3022**	**0.6763**	0.0034	0.0900	0.0247
6. Xalda	0.0066	0.0027	0.0024	0.0043	0.0044	**0.9330**	0.1620	0.0275

[a]The populations into which individuals are migrating (derived populations) are in the columns, whereas the origins of the migrants are listed in the rows. Values on the diagonal are the proportions of individuals derived from the source populations each generation. Contributions higher than 0.10 are in bold. Average standard deviations of all distributions of m for each source population ranged from 0.006 to 0.013.

Balloux et al., 2002). Thus, the order of magnitude of the genetic differentiation between breeds assessed using F_{ST} estimators seems to be always low and rather constant regardless of the species (MacHugh et al. 1998; Laval et al., 2000; Arranz et al., 2001). In addition, commonly used estimators of gene flow, such as $4N_em = 1/F_{ST} - 1$, are derived on the basis of simplified models of population structure that assume constant population sizes, symmetrical migration at constant rates, and population persistence for periods long enough to achieve genetic equilibrium (Wright, 1969). These shortcomings highlight the need to apply new, more informative methodologies to ascertain the evolutionary history of present-day populations in both the long term of gene flow and the recent patterns of migration (Wilson and Rannala, 2003).

Results obtained using the program STRUCTURE suggested that the studied populations had large cryptic structures. Theoretically, this structure would be a consequence of the genetic background of the original populations from which present-day breeds were derived. However, the inferred populations do not necessarily correspond to "real" ancestral populations, and they can be determined simply by the sampling scheme (Pritchard et al., 2000). It seems to be quite difficult to estimate the allelic frequencies of the "original" populations when populations are not well differentiated, and a large proportion of individuals have some degree of admixture. The genetic structure observed here could be a consequence of both the absorption of individuals from other populations and reproductive isolation producing bottlenecks at a population level. Both aspects could affect the present results. Firstly, Churra and Latxa individuals have been involved in genetic exchanges because of their successful use for dairy purposes (Sánchez Belda and Sánchez Trujillano, 1986). Secondly, the possible presence of genetic bottlenecks in our data was tested using the program BOTTLENECK (Luikart et al., 1998; Piry et al., 1999). Under the conservative two-phase model (Di Rienzo et al., 1994), the Wilcoxon sign-rank test gave significant support to the presence of a genetic bottleneck in Rubia del Molar ($P = 0.025$ for heterozygosity excess) and Xalda ($P = 0.012$ for heterozygosity deficiency), which thus probably affected our results.

Long-term migration rates estimated using the admixture coefficient $m\gamma$ mainly reflect the existence of two contact zones between major source populations that have produced two particular breeds (Rubia del Molar and Xalda). The negative $m\gamma$ coefficients estimated for some breeds (Table 5) should be appropriately interpreted. Negative contributions may result from the large variance associated with the estimator, based on the average squared difference in allele size. Bertorelle and Excoffier (1998) suggest that negative admixture coefficients should not be observed in a pure admixture model, but they could become quite common in breeds that diverged only recently. Negative admixture coefficients are very unlikely to result if two populations are genetically admixed and the divergence time between them is longer than $0.2N_e$ generations (Bertorelle and Excoffier, 1998). Negative estimates of $m\gamma$ obtained from several independent loci, such as in our data set, are indicative of an admixture event that is currently occurring.

Estimates of admixture proportions under the coalescent theory are useful to reflect the genetic history of the populations under study. However, because these methodologies assume that all possible parental populations are sampled, their results depend on the specific population model fitted. Moreover, they cannot reflect the moment at which one population has contributed to another. Parental populations contributing more recently to a derived population tend to show higher similarity values than those with more ancient contributions (Dupanloup and Bertorelle, 2001). Furthermore, these methodologies give reliable estimates when parental populations are well differentiated (Bertorelle and Excoffier, 1998). This assumption does not coincide exactly with the situation of livestock breeds.

Most sampled breeds did not implement herd book organizations until the late 1980s or early 1990s. Thus, some degree of genetic admixture among breeds should be assumed owing to geographical proximity and traditional commercial flows. In consequence, estimates of remote admixture proportions must be checked by applying methodologies able to extract information about recent migration patterns from transient disequilibrium observed in individual genotypes of migrants or individuals recently descended from migrants (Wilson and Rannala, 2003). These methods require fewer assumptions than estimators of long-term gene flow, and constitute a complementary methodology that provides information in different timescales. An interesting feature arising from the present analysis is the large estimates of both mean and standard deviation of F for the Churra breed. Large standard deviations of F are related to the presence of a high proportion of first and second generation of migrants (Wilson and Rannala, 2003). This would result in a lack of information for the method for estimating F. However, other breeds, such as Black-faced Latxa and Castellana, have received proportions of migrants similar to those estimated for Churra, although both the estimated mean and standard deviation for F are low. The large estimates for mean and standard deviation of the posterior distribution of F for the Churra breed may be the result of a process of admixture (happening at present) between two breeds, Churra and Castellana, which have very different genetic backgrounds. Additionally, estimates of recent migration rates suggest that the genetic similarities found between the Castellana and Churra breeds do not come from a common ancestral origin. These figures point to an absorption process led by the Churra breed. Moreover, the Castellana breed is known to have experienced recent introgression of white-coated breeds to change its color pattern (Sotillo and Serrano, 1985). During the first half of the 20th century,

most Castellana individuals were black (Aparicio, 1994). Selection for white wool was mediated by the use of white-coated breeds (Sotillo and Serrano, 1985).

Summarizing the results reported in the present study, the methodologies used here were superior to classical *F*-statistics in obtaining information on population dynamics in livestock breeds. The main shortcoming of the methodologies used here was the assumption that all possible genetically related populations were sampled. The sampling scheme included all the important sheep breeds in the geographical area under study. Thus, this research presents reliable evidence of the history of these sheep breeds.

Implications

The identification of genetic relationships and gene flow patterns among livestock populations is important for breeders and conservationists. The use of classical parameters, such as *F*-statistics, to assess genetic differentiation and gene flow assumes models of population structure that do not coincide well with present-day livestock breeds. We point out the need to apply more informative methodologies to ascertain the evolutionary history of current populations. As an example, we applied recent methodologies to study the genetic background of sheep breeds from Northern Spain. Two breeds, Black-faced Latxa and Churra, were identified as present-day representatives of two different genetic stocks, supporting the hypothesis that they could have different ancestral origins. Also, we show how methodologies for estimating recent patterns of migration furnish complementary information, allowing recent introgression processes to be ascertained.

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