Monitoring changes in the demographic and genealogical structure of the main Spanish local beef breeds[1]

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ABSTRACT: Demographic and pedigree analyses describe the structure and dynamics of livestock populations. We studied information recorded in the herdbooks of Asturiana de los Valles (AV; N = 458,806), Avileña–Negra Ibérica (ANI; N = 204,623), Bruna dels Pirineus (BP; N = 62,138), Morucha (Mo; N = 65,350), Pirenaica (Pi; N = 217,428), Retinta (Re; N = 135,300), and Rubia Gallega (RG; N = 235,511) beef breeds from their creation until 2009. All breeds have increased in the number of registered cows in recent years. In all breeds, herds do not behave as isolated entities and a high rate of exchange of breeding males between herds exists. A percentage of herds (12–52%) make some type of selection and sell bulls to other herds. There were large differences in average number of progeny per bull, ranging from 15.6 (AV) to 373.7 animals (RG, with a high incidence of AI). Generation interval estimates ranged from 4.7 (AV) to 7.6 (RG) yr in the sire pathway and from 5.95 (AV) to 7.8 (Mo) yr in the dam pathway. Density of pedigrees varied among breeds, with Pi, ANI, and Re having the more dense pedigrees, with average completeness indexes of more than 96% in the first generation and 80% when 6 generations were considered. A general increase in average inbreeding was observed in all breeds in the years analyzed. For animals born in 2009, average inbreeding coefficients ranged from 0.6 (BP) to 7.2% (Re) when all animals were considered and from 3.6 (Pi) to 17.6% (BP) when only inbred animals were considered. Due to the lack of completeness of pedigrees in most populations, inbreeding coefficients may be considered as a lower bound of the true parameters. The proportion of inbred animals tended to increase in the periods analyzed in all breeds. Differences between inbreeding and coancestry rates (except in RG) suggest the presence of population structure. Effective population size (N_e) based on the inbreeding rate estimated by regression ranged from 43 to 378 for Re and BP, whereas N_e estimates based on coancestry were greater, with a range of 100 for RG to 9,985 for BP. These facts suggest that an adequate mating policy can help to monitor inbreeding so as not to lose genetic variability. Effective number of ancestors in 2009 for 6 of the breeds ranged from 42 (RG) to 220 (AV), with BP having much a greater value, and was lower than was the effective number of founders in all breeds, suggesting the existence of bottlenecks.

Key words: beef cattle, inbreeding, local breeds, pedigree

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INTRODUCTION

Breeds are dynamic resources, changing with each generation through interaction with the physical environment and according to the selection criteria of their keepers (FAO, 2007). Well-designed breeding programs can exploit the existing genetic variation of beef cattle breeds

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to use local available resources, produce under harsh conditions, support specific labeling of high-added-value that prevents health scandals (Tolosana et al., 2005), and contribute to maintaining rural culture diversity (Gandini and Villa, 2003). Demographic and pedigree analysis are important tools that describe the structure and dynamics of livestock populations (Vu Tien Khang, 1983). Population structure determines the development of inbreeding, whose trend is the tool most frequently used to quantify the rate of genetic drift (Wright, 1922, 1931). Pedigree analysis has been implemented for most species, such as beef and dairy cattle and sheep, among others (Boichard et al., 1997; Goyache et al., 2003; Gutiérrez et al., 2003). However, in most local breeds, the population size and selection methods are frequently subject to changes, even in short periods of time (Boichard et al., 1997). Therefore, the demographic and pedigree analysis of populations should be done periodically to assess the effect of the breeding program in the inbreeding and genetic diversity of the breed. The genetic structure of some of the Spanish breeds was studied by Gutiérrez et al. (2003), including pedigree data until the year 1995. Since then, most of the breeds have intensified performance recording and developed more or less intensive genetic selection programs based on BLUP genetic evaluation, whose impact in the breed's genetic structure is unknown. In this context, the main objective of this study is to assess the current genetic structure of 7 Spanish local beef cattle breeds by analyzing their pedigrees. This can illustrate the general behavior of local beef populations undergoing a selection process.

MATERIALS AND METHODS

Herdbook information of 7 Spanish beef breeds was analyzed from their foundation to the last year with complete records (2009). Specifically, we analyzed the following breeds and animals in the pedigree within breed: Asturiana de los Valles (**AV**; $N = 458{,}806$), Avileña–Negra Ibérica (**ANI**; $N = 204{,}623$), Bruna dels Pirineus (**BP**; $N = 62{,}138$), Morucha (**Mo**; $N = 65{,}350$), Pirenaica (**Pi**; $N = 217{,}428$), Retinta (**Re**; $N = 135{,}300$), and Rubia Gallega (**RG**; $N = 235{,}511$). These breeds represent 72% of the total census of local beef breeds in Spain. All breeds started BLUP based selection programs in the last 20 yr. The breeds differ not only in production and carcass traits (Piedrafita et al., 2003) but also in meat quality traits (Gil et al., 2001). They are reared in harsh environments, including mountains to rangelands, and the degree of crossbreeding with specialized beef meat breeds is variable as well as is the extent of AI. Further details of the breeds can be found at http://dad.fao.org. We analyzed several genetic parameters regarding demographic structure and genetic status of the populations based on pedigree information, which are briefly described in the following sections.

Demographic Structure

Breed Censuses. Breed censuses are assessed as the number of reproductive males and females giving progeny in 3 specific years: 1998 (a year close to the previous study), 2003 (the year in which common rules for direct support schemes for farmers under the Common Agricultural Policy of the European Union were established – Council Regulation EC number 1782/2003-), and 2009.

Effective Population Size. Under random mating with unequal numbers of males and females, effective population size (**N_e**) is calculated as $N_e = 4N_mN_f/(N_m + N_f)$, in which N_m and N_f are the number of males and females, respectively (Falconer and Mackay, 1996).

Pyramid Structure. The pyramid structure is defined by the percentage of use of own reproductive males as the criterion for for classifying herds, designated as nucleus herds if they never use reproductive males born in other herds, as multipliers if they buy and sell reproductive males (Multiplier 1 or Multiplier 2 if they use or not their own bulls, respectively), and as commercial herds if they buy but do not sell bulls (Commercial 1 or Commercial 2 if they use or not their own bulls, respectively; Vassallo et al., 1986).

Generation Intervals. Generation intervals are defined as the average age of parents at the birth of their progeny kept for reproduction (James, 1977). This parameter was computed for the 4 classic pathways (sire–son, sire–daughter, dam–son, and dam–daughter) using the animals born between 2003 and 2009.

Family Size. Family size refers to the number of offspring of an individual that become breeding individuals in the next generation (Falconer and Mackay, 1996).

Pedigree Information Quality, Inbreeding Coefficient, and Effective Population Size

Pedigree Completeness Level. The pedigree completeness level is described by computing the average of the MacCluer et al. (1983) index considering 1 to 6 generations deep. The pedigree completeness index of an individual is $I_d = 4I_{d_{\text{pat}}}I_{d_{\text{mat}}} / \left(I_{d_{\text{pat}}} + I_{d_{\text{mat}}}\right)$ and $I_{d_k} = (1/d)\sum_{i=1}^{d} a_i$, k = pat, mat, in which k represents the paternal (pat) or maternal (mat) line, a_i is the proportion of known ancestors in generation i, and d is the number of generations considered in the calculation of the completeness index.

In addition, the complete generation equivalent value (Boichard et al., 1997) was estimated by averaging over the sum of $(1/2)^n$, in which n is the number of generations separating the individual from each known ancestor.

Inbreeding Coefficient. The inbreeding coefficient (F) is the probability of having 2 genes that are identical by descent (Wright, 1922).

Coancestry. The coancestry (f) is defined as the probability that a progeny of 2 parents carries 2 alleles identical by descent. Under random mating, the rate of inbreeding (ΔF) equals the rate of coancestry (Δf).

Effective Population Size. The N_e is a measure of genetic diversity within a population (Wright, 1931). The N_e was calculated using $N_e = 1/(2\Delta F)$. The rate of inbreeding per generation (ΔF) was calculated using $\Delta F = (F_n - F_{n-1})/(1 - F_{n-1})$, in which F_n and F_{n-1} are the average inbreeding of offspring and their parents, respectively (Falconer and Mackay, 1996). Animals born a number of years equal to the generation interval were considered as parents (the previous generation) of a particular cohort (animals born in the same year).

An alternative way to estimate N_e is by computing the increase of inbreeding for each individual (ΔF_i) that equals $1 - (1 - F_i)^{1/t}$, in which F_i is the inbreeding coefficient (González-Recio et al., 2007) and t can be, for each individual, the equivalent complete generations, the maximum number of generations known, or the complete generations (Gutiérrez et al., 2008). By averaging these ΔF_i, we obtain an estimate of ΔF, $\overline{\Delta F}$, in the reference population, and then a realized N_e is computed as $\overline{N_e} = 1/2\overline{\Delta F}$ (Cervantes et al., 2008).

Genetic Representation and Probabilities of Gene Origin

Effective Number of Founders. The effective number of founders (f_e) is the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study (Lacy, 1989). It is calculated as $f_e = 1/\sum_{k=1}^{f} q_k^2$, in which q_k is the probability of gene origin of the k ancestor, that is, the proportional contribution of founder k. When founders contribute unequally, the effective number of founders is smaller than is the actual number.

Effective Number of Ancestors. The previous method does not account for bottlenecks in the population, which is a major cause of gene loss in cattle populations. Effective number of ancestors (f_a) overcomes, in part, this shortcoming. It is the minimum number of ancestors, founders or not, necessary to explain the complete genetic diversity of the population under study (Boichard et al., 1997) and is computed as $f_a = 1/\sum_{j=1}^{a} q_j^2$.

In this case, q_j is the marginal contribution of the j ancestor, that is, the genetic contribution made by an ancestor that is not explained by other ancestors chosen previously.

Effective Number of Founder Herds. The initial contribution of founders can be added into each herd founder contribution, and the inverse of their added squared value gives an effective number of founder herds (Robertson, 1953).

Software

POPREP software (Groeneveld et al., 2009) was used to analyze the census trend, family sizes, average pedigree completeness traced back until the sixth generation, inbreeding, coancestry, and N_e calculated from the last 2 parameters. The software ENDOG, version 4.6 (Gutiérrez and Goyache, 2005), was used to calculate the pyramid structure, generation interval, complete generation equivalent value, individual increase of inbreeding and the corresponding realized N_e, and probabilities of gene origin: effective number of founders, effective number of ancestors, and effective number of founder herds.

RESULTS AND DISCUSSION

Censuses

The number of breeding females is one of the key parameters to assess the risk of endangerment of a local bovine population. Table 1 shows that all breeds but the Mo breed increased their censuses over time. In fact, all of the breeds have experienced an increase in the number of registered cows in relation to the period studied by Gutiérrez et al. (2003), and the support schemes for farmers established in 2003 had a variable impact on the evolution of the censuses. The group of ANI, Mo, Pi, and Re had moderate increases, ranging from 16 to 41% in the female censuses, whereas AV, BP, and RG have much larger increases (158 to 381%), probably due to a strong support of the regional governments for the selection schemes.

The number of breeding females per bull was below 10 in AV, above 30 in RG, and between 14 and 22 in the rest of the populations**.** This confirms the extended use of natural service bulls, with AI being fairly residual, with the exception of RG. In AV, the low number of cows per bull can be due to the small size and geographical isolation of herds.

The effective number, N_e, computed by assuming a random mating population with unequal number of males and females, increased in all breeds, except Mo in 2009, in parallel to the census (Table 1). In 2009, N_e ranged from 470 in the Mo breed to 8,752 in AV breed. The differences in N_e between AV and RG (8,752 and 1,668, respectively), which had a similar number of females in 2009, are due to the extensive use of AI in the last breed. These values will be contrasted below with other estimates of the N_e that allow for more relaxed conditions.

Pyramid Structure

It is well established that genetic improvement efforts are usually made in a fraction of the population and from these animals is later on disseminated to the rest of the population. Our results show that there are not isolated herds (Table 2), and none of the herds of any breeds used only their own males for breeding, which means that no herd was classified as nucleus. In consequence,

Table 1. Number of males and females giving birth in 1998, 2003, and 2009 and the corresponding effective population sizes (N_e) under random mating and unequal number of males and females

Breed[1]	Year	Males	Females	N_e
AV	1998	1,152	8,064	4,032
	2003	1,792	15,501	6,425
	2009	2,444	20,884	8,752
ANI	1998	232	5,318	889
	2003	310	6,856	1,186
	2009	389	7,504	1,479
BP	1998	77	1,369	292
	2003	154	2,643	582
	2009	335	6,593	1,275
Mo	1998	159	1,588	578
	2003	167	3,355	636
	2009	125	1,947	470
Pi	1998	551	7,372	2,051
	2003	677	9,612	2,530
	2009	810	10,531	3,009
Re	1998	239	3,933	901
	2003	290	4,246	1,086
	2009	345	4,573	1,283
RG	1998	168	5,154	651
	2003	207	9,190	810
	2009	433	16,512	1,688

[1] AV = Asturiana de los Valles; ANI = Avileña–Negra Ibérica; BP = Bruna dels Pirineus; Mo = Morucha; Pi = Pirenaica; Re = Retinta; RG = Rubia Gallega.

all herds were assigned either to the multiplier (1 and 2) or commercial (1 and 2) categories, depending on the breed. A herd is defined as multiplier when it sells bulls to other herds, although it can use its own or purchased breeding males for mounting. In fact, in herds catalogued as Multiplier 1, the proportion of purchased bulls can be very high (close to 80% in AV and RG).

The proportion of multiplier (1 and 2) and Commercial 1 herds has increased markedly in BP at the expense of the Commercial 2 herds in the period studied, with this trend also being observed in AV, ANI, and Mo, although to a lesser extent. This evolution implies a greater involvement in the selection process of more breeders and could be related to the increment of herd sizes and the impact of genetic evaluations, which facilitate both the use of highly ranked own bulls and also the exchange of bulls with other herds. The herd structure of Pi, Re, and RG has remained more stable in the period 1998 to 2009. In the last year analyzed, the proportion of multiplier herds oscillates between 12 and 24% for ANI, Re, and RG and 43 to 52% for BP, Mo, and Pi, with an intermediate value (35%) for AV. This indicates that in the first 3 breeds, the selection efforts are concentrated in a small number of herds. In the other breeds, the proportion of herds that made some type of selection and sold bulls to other herds is greater (40–50%). A lower number of multipliers can facilitate the implementation and development of a selection program and, in the future, the genomic selection, although at the risk of increasing inbreeding if not properly monitored.

What is interesting to note is that in Vassallo et al. (1986), some herds were classified as nucleus herds, differing from the current results. This can be due to the fact that the selection program applied has changed the dynamic of the population or that the sample used for the previous study did not represent the information registered in the herdbook of the breed.

Generation Intervals and Family Size

Average generation intervals for the 4 pathways associated with the animals born in the period 2005 through 2009 are shown in Table 3. The estimates ranged from 4.7 to 7.6 yr in the sire pathway and from 5.95 to 7.8 yr in the dam pathway. In general, the average values were shorter in the sire pathway, with ANI, AV, and Mo having a more rapid replacement of sires, whereas RG sires were used almost 2 additional years on average. This fact can be due to the greater practice of AI in RG and the longer use of proven sire's semen. The average generation interval in the dam pathway was around 7 yr, due partially to a later start (30–36 mo) and longer reproductive life of the females. In addition, the greater reliability of the genetic evaluations of bulls achieved at an early age facilitates earlier selection decisions in young bulls than in cows.

The average estimates were homogeneous across breeds, with the exception again of AV, which showed a shorter interval suggesting a relative acceleration of the selection process in this breed, and the high sire–daughter interval in RG, related to the use of semen of older proven bulls as fathers of replacement cows. These estimates represent a considerable increase with respect to the generation intervals estimated by Gutiérrez et al. (2003) in AV, ANI, BP, Mo, and Pi beef breeds from the parents of the 1995 calf crop. This increase could be related to the expansion of herd censuses associated with a longer use of the cows. The current estimates, however, are in the order of the results found in other beef breeds such as Irish Charolais, Limousin, Hereford, Angus, and Simmental cattle (Mc Parland et al., 2007). Furthermore, a longer generation interval in females than in males has previously been reported in other breeds, such as Australian Shorthorn (Herron and Pattie, 1977) or British Hereford (Özkütük and Bichard, 1977), whereas in Irish Hereford only slight differences were found and in Limousin the sire–offspring pathway was 2 yr greater than the dam–offspring pathway (Mc Parland et al., 2007).

Family size estimates from breeding animals born in 1988, 1993, and 2000 are presented in Table 4. The year 2000 was chosen back as the first one that presented

Table 2. Pyramid structure of the different breeds according to the use of own or purchased bulls. The numbers correspond to the percentage of herds belonging to the category, with the percentage of purchased bulls included between parentheses. The periods analyzed went from the starting year of recording practices to the years 1998, 2003, and 2009

		Type of herd[2]				
Breed[1]	Year	Nucleus	Multiplier 1	Multiplier 2	Commercial 1	Commercial 2
AV	1998	0	18.2 (72.02)	5.68	7.62 (81.59)	68.67
	2003	0	21.05 (75.56)	8.42	6.57 (84.84)	63.78
	2009	0	23.05 (77.70)	10.58	6.77 (84.19)	59.60
ANI	1998	0	10.14 (51.88)	3.32	7.34 (81.72)	79.20
	2003	0	10.36 (51.51)	4.33	9.12 (77.04)	76.20
	2009	0	13.64 (53.13)	5.34	9.42 (78.18)	71.59
BP	1998	0	7.89 (65.87)	0.88	4.97 (77.32)	86.26
	2003	0	11.70 (66.46)	5.34	12.48 (72.03)	70.48
	2009	0	39.85 (56.15)	3.42	20.54 (58.11)	36.19
Mo	1998	0	38.21 (45.90)	3.65	19.93 (46.99)	38.21
	2003	0	44.98 (38.21)	2.13	20.06 (42.04)	32.83
	2009	0	48.53 (35.64)	3.53	21.47 (39.2)	26.47
Pi	1998	0	21.41 (75.18)	19.19	5.66 (75.66)	53.74
	2003	0	22.62 (73.91)	18.59	5.98 (80.94)	52.81
	2009	0	23.49 (73.36)	18.68	6.19 (81.8)	51.64
Re	1998	0	18.22 (48.12)	3.78	18.44 (63.49)	59.56
	2003	0	17.82 (47.93)	3.94	17.07 (64.06)	61.16
	2009	0	18.77 (46.67)	4.61	16.72 (68.76)	59.90
RG	1998	0	5.1 (85.72)	7.22	1.19 (86.16)	86.49
	2003	0	4.66 (84.39)	5.97	1.49 (82.46)	87.88
	2009	0	5.33 (81.32)	6.42	1.98 (81.53)	86.27

[1] AV = Asturiana de los Valles; ANI = Avileña–Negra Ibérica; BP = Bruna dels Pirineus; Mo = Morucha; Pi = Pirenaica; Re = Retinta; RG = Rubia Gallega.

[2] Nucleus: herds using their own bulls and selling bulls for breeding; Multiplier 1: herds using purchased bulls and their own bulls and also selling bulls for breeding; Multiplier 2: herds using purchased bulls and selling bulls for breeding; Commercial 1: herds using purchased bulls and their own bulls; Commercial 2: herds using only purchased bulls.

estimates similar to previous years and corresponds to a reference year where the breeding animals have been able to complete their reproductive career. There were large differences in the average progeny per bull, ranging from 15.6 (AV) to 373.7 animals (RG). As before, this large progeny in RG is related to the use of AI. Most of the breeds increased the average number of progeny per sire. The average number of selected offspring per sire was in the range between 8.3 (AV) and 44 (RG), which together accounted for a percentage ranging from 15 (Pi and RG) to 26% (AV) of the total of all offspring born, this last being consistent with the lower generation interval of this breed. In addition to this between-breed variability in family size, there exists a within breed variability (not shown in tables) that can increase the rate of inbreeding and reduce N_e.

Pedigree Completeness Level

The estimates of inbreeding are dependent on pedigree completeness (Lutaaya et al., 1999; Cassell et al., 2003), and a large proportion of missing parents in the pedigree leads to an important underestimation of the inbreeding level. In this study, pedigree knowledge was assessed through the completeness index (MacCluer et al., 1983). This index is an indicator of the proportion of ancestors known in a predefined number of generations. In this study, we analyzed the results when 1, 2, 3, 4, 5, or 6 generations back were considered. The results varied among breeds. Pirenaica, ANI, and Re breeds have deeper pedigrees, with average completeness indexes of more than 96% in the first generation. Pedigree completeness decreased as more generations were considered, albeit even when 6 generations were considered, those 3 breeds had a pedigree completeness of around 80% (Table 5). In general, there has been an increase in the pedigree records across breeds from 1995 (Gutiérrez et al., 2003). This pedigree records increase might be due to the need of reliable genealogical information to implement selection programs based on BLUP predictions of breeding values. Nevertheless, the genealogy of the BP breed underwent a severe contraction in the late 1990s, from which it is slowly recovering, which led to the low proportion of known ancestors beyond grandparents.

In correspondence with the average completeness indexes estimated, 3 breeds have the highest complete generation equivalent values (3.77, 3.99, and 4.62 for Re, ANI, and Pi). To compute these values, all animals born up to

Table 3. Generation interval estimates (with SE in parentheses) for the 4 pathways corresponding to animals born in the period 2005 through 2009

Breed[1]	Sire–son	Sire–daughter	Dam–son	Dam–daughter
AV	4.70 (0.01)	4.77 (0.01)	6.24 (0.01)	5.95 (0.01)
ANI	4.79 (0.10)	5.04 (0.09)	6.87 (0.16)	6.80 (0.17)
BP	5.86 (0.16)	5.66 (0.15)	7.66 (0.24)	7.05 (0.25)
Mo	4.88 (0.21)	5.49 (0.25)	7.83 (0.43)	7.39 (0.41)
Pi	5.85 (0.15)	5.86 (0.14)	7.21 (0.13)	7.32 (0.14)
Re	5.41 (0.05)	5.27 (0.01)	7.13 (0.07)	6.86 (0.02)
RG	6.56 (0.20)	7.60 (0.22)	6.81 (0.19)	7.28 (0.20)

[1] AV = Asturiana de los Valles; ANI = Avileña–Negra Ibérica; BP = Bruna dels Pirineus; Mo = Morucha; Pi = Pirenaica; Re = Retinta; RG = Rubia Gallega.

2009 were used. These figures are in the order of those published by Boichard et al. (1997) in Abondance, Normande, and Limousine French breeds but lower than the estimates found in Danish dairy cattle (Sørensen et al., 2005).

Evolution of Inbreeding and Effective Population Sizes

A general increase in average inbreeding over time was observed in all breeds through the years analyzed. The average inbreeding coefficients of animals born in 2009 ranged from 0.6% in BP to 7.2% in Re, when all animals were considered (Table 6). In all breeds, the SE of the estimates were large. It should be highlighted that the inbreeding coefficients may be probably underestimated due to the lack of completeness of pedigrees in most populations. This can be particularly important in the breeds with the lowest quality of pedigree information.

The proportion of inbred animals tended to increase in all breeds. In the year 2009 it had a range from 38 (AV) to 95% (Pi), with the exception of BP (3.5%). The greater percentages belong to the breeds with better pedigree knowledge (Pi, ANI, and Re).

The average inbreeding coefficient of inbred animals was below 11%, with the exception of BP and Mo. The SE of the estimates were also large. In all breeds, individuals exceeding an inbreeding coefficient of 40% could be found. In general, no correlation existed between the percentage of inbred animals and the average inbreeding of inbred animals. Whereas Pi is the breed with the most inbred animals, the F average stayed at around 3.5%, suggesting that breeders avoid matings between close relatives. Another cause of this low F average can be a larger number of Multiplier 1 herds than in ANI and Re, populations that have similar pedigree completeness. On the contrary, the particularly high average inbreeding of inbred animals born in 2009 in BP (17.6%) suggests that a relevant number of matings between close relatives occurs, which should be subjected to careful monitoring to avoid the loss of genetic variability in this population.

Table 4. Average family sizes of breeding animals born in 1988, 1993, and 2000

		All offspring[2]		Selected offspring[3]	
Breed[1]	Year	Sires	Dams	Sires	Dams
AV	1988	15.6	3.1	8.3	1.9
	1993	24.3	3.4	11.9	1.8
	2000	35.9	3.6	9.3	1.5
ANI	1988	92.9	4.3	29.6	2.1
	1993	83.1	4.5	24.9	1.9
	2000	89.8	3.2	18.9	1.5
BP	1988	36.5	3.1	11.0	1.6
	1993	40.5	3.0	10.5	1.5
	2000	52.0	2.8	9.3	1.2
Mo	1988	25.6	2.6	19.4	1.6
	1993	70.5	3.3	32.4	1.7
	2000	55.1	2.1	13.8	1.3
Pi	1988	40.6	5.2	15.0	2.2
	1993	43.7	5.4	13.7	2.0
	2000	65.1	4.2	10.0	1.3
Re	1988	63.0	3.5	21.3	1.9
	1993	68.9	3.9	22.9	1.9
	2000	67.6	3.3	13.8	1.3
RG	1988	79.1	3.2	39.8	1.8
	1993	373.7	3.6	87.7	1.7
	2000	299.5	3.7	44.0	1.4

[1] AV = Asturiana de los Valles; ANI = Avileña–Negra Ibérica; BP = Bruna dels Pirineus; Mo = Morucha; Pi = Pirenaica; Re = Retinta; RG = Rubia Gallega.

[2] All offspring born in the population.

[3] Offspring that have at least a service record.

In general, all breeds have experienced an increase of inbreeding in relation to the 1995 estimates (Gutiérrez et al., 2003), both for the whole populations and for inbred animals. This is probably a consequence of the increase of depth in pedigree information. Our estimates are much greater than are the ones found in Irish cattle, where the estimates of mean inbreeding of animals born in 2004 were in the range of 0.54 to 2.19% for Charolais and Hereford breeds, respectively, with complete generation equivalents around 5 (Mc Parland et al., 2007).

Other interesting parameters to monitor the evolution of populations are the rate of inbreeding and the potential inbreeding that could be obtained if all matings were made at random from all members of the population. This last parameter is the average coancestry of all possible pairs of individuals in the population, and its evolution is the rate of coancestry. Estimates of both rates are presented in Table 7. The estimates of the rate of inbreeding and the N_e from animals born in the years 1998, 2003, and 2009 were highly heterogenous, and no clear trend can be inferred (Table 7A). The estimates of the rate of coancestry and the corresponding effective numbers were also diverse, but with the exception of RG and some particular years in different breeds, the increase of coancestry was much lower than was that of inbreed-

Table 5. Average pedigree completeness index (%) considering 1 to 6 generations deep for animals born in 2009 and average complete generation equivalent values for animals born up to 2009

Breed[1]	Number of animals	Number of generations known 1	2	3	4	5	6	Average complete generation equivalents
AV	21,418	91.7	83.4	75.8	67.6	58.6	50.2	2.18
ANI	8,052	96.7	91.9	88.5	85.8	82.9	79.3	3.99
BP	6,902	83.2	59.1	42.1	32.0	25.7	21.5	1.01
Mo	2,223	86.8	77.9	70.8	64.8	59.4	53.6	2.17
Pi	10,845	99.0	97.9	96.8	95.2	92.0	86.7	4.62
Re	4,928	96.3	91.7	88.6	86.5	84.6	80.9	3.77
RG	17,124	94.4	83.2	75.1	69.0	63.5	57.9	3.08

[1] AV = Asturiana de los Valles; ANI = Avileña–Negra Ibérica; BP = Bruna dels Pirineus; Mo = Morucha; Pi = Pirenaica; Re = Retinta; RG = Rubia Gallega.

ing. This fact was confirmed when a longer period was analyzed, and both rates were estimated as the regression on the year of birth (Table 7B). The N_e based on the increment of inbreeding ranged from 43 to 378 for Re and BP, whereas N_e based on coancestry were greater, with a range of 100 for RG to 9,985 for BP. Note that the coancestry rate of Pi was even negative and the corresponding effective size could not be calculated and also that the very high value of the N_e of BP may be overestimated due to the low completeness of its pedigree.

The estimates for N_e in Table 7B are much lower than are those presented in Table 1. This indicates that the breeds studied are far from the conditions of an idealized population where bulls and cows can mate at random. In fact, the differences between inbreeding and coancestry rates suggest the presence of population structure (Fernández et al., 2008), either by geographical reasons or selection policies within farms or groups of farms. These differences indicate, however, the potential feedback for the implementation of a mating system to control possible losses of variability in the populations studied. Two examples illustrating what has been just discussed are presented in Fig. 1. In the RG breed, the evolution of inbreeding and coancestry was very close, probably due to the greater deployment of AI that exists in this breed, whereas Re, similarly to the other breeds studied, presents a steeper increase of the average inbreeding coefficient, suggesting the existence of some kind of mating structure.

González-Recio et al. (2007) and Gutiérrez et al. (2008) presented an alternative method for the estimation of realized effective size from pedigrees based on the definition of the individual increase in inbreeding coef-

Table 6. Average inbreeding coefficients of all animals and inbred animals born in 1998, 2003, and 2009

Breed[1]	Year	All animals Number	All animals Maximum *F*	All animals Average *F* (SD)	Inbred animals Number (%)	Inbred animals Average *F* (SD)
AV	1998	11,454	0.4248	0.0102 (0.0428)	1,270 (11.1)	0.0921 (0.0947)
	2003	18,361	0.4219	0.0112 (0.0429)	3,586 (19.5)	0.0573 (0.0823)
	2009	21,418	0.5361	0.0142 (0.0474)	8,175 (38.2)	0.0371 (0.0710)
ANI	1998	6,145	0.4629	0.0472 (0.0746)	3,980 (64.8)	0.0728 (0.0820)
	2003	7,924	0.4681	0.0518 (0.0751)	5,910 (74.6)	0.0711 (0.0794)
	2009	8,052	0.4911	0.0611 (0.0805)	6,522 (81.0)	0.0754 (0.0832)
BP	1998	3,142	0.2500	0.0030 (0.0224)	80 (2.5)	0.1162 (0.0811)
	2003	3,592	0.3125	0.0035 (0.0228)	132 (3.7)	0.0951 (0.0740)
	2009	6,902	0.4375	0.0062 (0.0372)	243 (3.5)	0.1758 (0.0972)
Mo	1998	2,170	0.5098	0.0485 (0.0883)	799 (36.8)	0.1316 (0.1013)
	2003	3,811	0.4805	0.0645 (0.0909)	2,015 (53.0)	0.1221 (0.0927)
	2009	2,223	0.4893	0.0593 (0.0919)	1,233 (55.5)	0.1116 (0.1009)
Pi	1998	7,825	0.3821	0.0261 (0.0532)	6,508 (83.2)	0.0313 (0.0509)
	2003	10,174	0.5000	0.0330 (0.0601)	9,112 (89.6)	0.0368 (0.0643)
	2009	10,845	0.4975	0.0345 (0.0581)	10,303 (95.0)	0.0363 (0.0590)
Re	1998	4,942	0.5434	0.0628 (0.0891)	2,781 (55.7)	0.1127 (0.0930)
	2003	5,278	0.5449	0.0620 (0.0874)	3,161 (59.8)	0.1036 (0.0920)
	2009	4,928	0.4591	0.0722 (0.0870)	3,599 (73.0)	0.0988 (0.0879)
RG	1998	7,303	0.3984	0.0140 (0.0427)	2,612 (35.8)	0.0390 (0.0641)
	2003	11,166	0.4688	0.0211 (0.0502)	5,952 (53.3)	0.0396 (0.0632)
	2009	17,124	0.5039	0.0269 (0.0529)	10,130 (59.2)	0.0455 (0.0623)

[1] AV = Asturiana de los Valles; ANI = Avileña–Negra Ibérica; BP = Bruna dels Pirineus; Mo = Morucha; Pi = Pirenaica; Re = Retinta; RG = Rubia Gallega.

Table 7. Inbreeding (ΔF) and coancestry (Δf) rates and effective population size (N_e) by generation

A. Estimated in 3 different periods (1998, 2003, and 2009)

Breed[1]	Year	ΔF	N_e (ΔF)	Δf	N_e (Δf)
AV	1998	0.00682	73	0.00148	338
	2003	0.00242	207	0.00046	1,087
	2009	0.00253	198	0.00025	2,000
ANI	1998	0.00199	251	0.00050	1,000
	2003	0.00095	526	0.00088	568
	2009	0.00981	51	0.00427	117
BP	1998	0.00120	417	0.00022	2,273
	2003	0.00080	625	–0.00084	–
	2009	0.00291	172	0.00008	6,250
Mo	1998	0.00823	61	0.00141	355
	2003	0.02359	21	0.00090	556
	2009	–0.00309	–	0.00097	515
Pi	1998	0.00815	61	0.00269	186
	2003	0.01105	45	0.00265	189
	2009	0.00155	323	0.00272	184
Re	1998	0.01295	39	0.00233	215
	2003	0.00372	134	0.00379	132
	2009	0.01087	46	0.00550	91
RG	1998	0.00855	58	0.00620	81
	2003	0.01031	48	0.01067	47
	2009	0.00937	53	0.00786	64

B. Estimated by regression of the average inbreeding and coancestry coefficients on year of birth

Breed	Period	ΔF	N_e (ΔF)	Δf	N_e (Δf)
AV	1975–2011	0.00266	188	0.00045	1,123
ANI	1970–2011	0.01085	46	0.00220	228
BP	1979–2011	0.00132	378	0.00005	9,985
Mo	1976–2011	0.01141	44	0.00201	249
Pi	1934–2010	0.00227	221	–0.00180	–
Re	1960–2011	0.01157	43	0.00161	310
RG	1973–2011	0.00437	114	0.00499	100

[1] AV = Asturiana de los Valles; ANI = Avileña–Negra Ibérica; BP = Bruna dels Pirineus; Mo = Morucha; Pi = Pirenaica; Re = Retinta; RG = Rubia Gallega.

Table 8. Averages of individual increase of inbreeding of animals born in 3 yr (1998, 2003, and 2009) and realized effective population sizes (N_e) computed from them

		By maximum generations		By complete generations		By equivalent generations	
Breed[1]	Year	ΔF	N_e	ΔF	N_e	ΔF	N_e
AV	1998	0.0026	194	0.0106	47	0.0068	73
	2003	0.0020	254	0.0097	52	0.0059	85
	2009	0.0018	281	0.0093	54	0.0056	90
ANI	1998	0.0080	63	0.0209	24	0.0141	35
	2003	0.0071	70	0.0200	25	0.0131	39
	2009	0.0067	74	0.0199	25	0.0126	40
BP	1998	0.0025	199	0.0086	58	0.0062	80
	2003	0.0026	189	0.0102	49	0.0074	68
	2009	0.0028	181	0.0099	50	0.0078	64
Mo	1998	0.0126	40	0.0379	13	0.0265	19
	2003	0.0115	43	0.0407	12	0.0278	18
	2009	0.0101	49	0.0398	13	0.0263	19
Pi	1998	0.0012	408	0.0107	47	0.0071	71
	2003	0.0014	348	0.0106	47	0.0073	69
	2009	0.0017	300	0.0103	48	0.0073	68
Re	1998	0.0074	67	0.0258	19	0.0191	26
	2003	0.0069	72	0.0244	20	0.0175	29
	2009	0.0065	77	0.0229	22	0.0162	31
RG	1998	0.0026	192	0.0100	50	0.0059	85
	2003	0.0028	177	0.0116	43	0.0066	76
	2009	0.0030	167	0.0143	35	0.0080	62

[1] AV = Asturiana de los Valles; ANI = Avileña–Negra Ibérica; BP = Bruna dels Pirineus; Mo = Morucha; Pi = Pirenaica; Re = Retinta; RG = Rubia Gallega.

ficient (ΔF_i). Although still dependent on the completeness of the pedigree, the realized N_e appears more stable than does that estimated based on regressions and is less affected by changes in the mating policy or the accumulation of pedigree. Depending on the value of t used for computing ΔF_i, maximum number of generations known, complete generations, or complete equivalent generations, we can obtain an upper estimate, a lower estimate, or the actual estimate of the realized N_e. Table 8 presents the estimates in the 7 breeds in the 3 reference years. In general, the changes of estimates from different years were small, although 3 breeds showed an increase of realized N_e and 2 showed a decrease. For the year 2009, the estimates ranged from 19 for Mo breed to 90 for AV breed. The values estimated by computing F_i using complete generations were lower in general than were those computed by regression. It is difficult to assess what estimate better reflects the true evolution of inbreeding according to the particular characteristics of pedigree regarding the degree of completeness, mating strategies, and presence or not of bottlenecks. Cervantes et al. (2008) have tested the properties of the method and they conclude that the procedure provides stable estimates when considering pedigrees with 4 or more equivalent generations known, which would make the method desirable only for ANI, Pi, and Mo. Estimates based on linkage disequilibrium of SNP markers might contribute new insights to the estimation of N_e, as in de Roos et al. (2008).

For genetic improvement, an inbreeding rate of 1% per generation (N_e = 50) is accepted because such slow inbreeding allows selection to remove deleterious alleles without endangering the population (Franklin, 1980). Disregarding the method of estimation, 3 of the breeds (ANI, Mo, and Re) presented an inbreeding rate exceeding 1%, which led to N_e lower than 50. Fortunately, the N_e estimated from the increment of coancestry (Δf) were bigger, which suggest that the populations may well maintain genetic variability if appropriate mating policies were implemented.

Low effective numbers are common in livestock. In beef cattle, Mc Parland et al. (2007) have found effective sizes of 64 and 127 in Irish Hereford and Simmental, respectively, whereas Cleveland et al. (2005) found that the

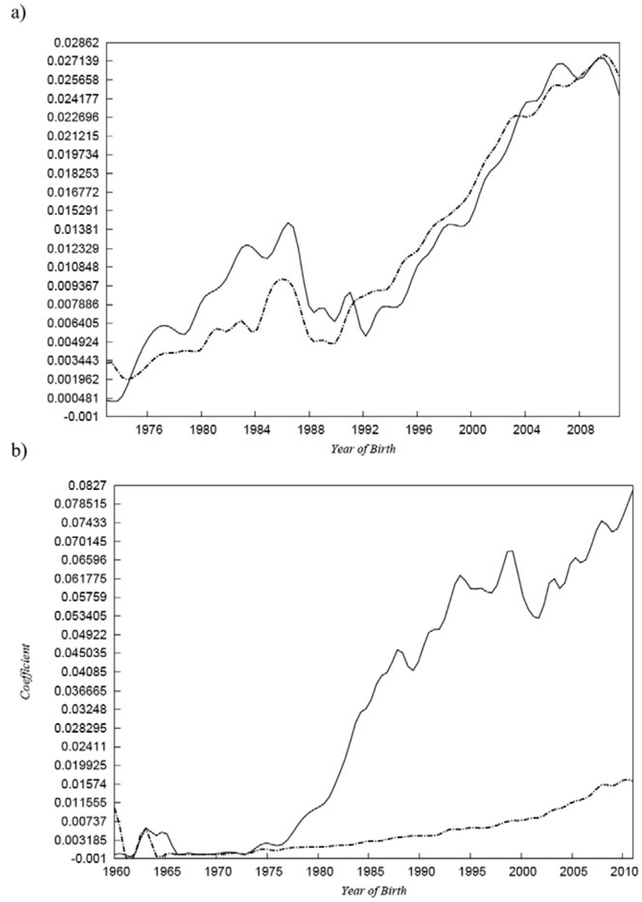

Figure 1. Inbreeding (–) and coancestry (- · -) coefficients evolution by year of birth in Rubia Gallega (a) and Retinta (b) breeds.

Table 9. Estimates of parameters of probability of gene origin

Breed[1]	Year	Reference population size	Effective number of founder herds	Effective number of founders	Effective number of ancestors	Ancestors explaining 50%
AV	1998	48,188	64	1,301	211	422
	2003	119,015	119	871	215	382
	2009	237,320	196	694	220	304
ANI	1998	76,879	7.3	88	84	52
	2003	111,597	6.8	81	77	46
	2009	151,380	6.3	76	72	40
BP	1998	9,467	4.3	185	170	111
	2003	16,206	5.6	273	250	175
	2009	46,580	17.1	838	739	417
Mo	1998	11,185	36.0	177	166	85
	2003	26,883	39.7	185	158	87
	2009	39,287	43.6	199	159	89
Pi	1998	84,711	66.6	182	87	60
	2003	128,946	60.2	176	83	49
	2009	197,027	56.2	162	74	40
Re	1998	59,346	22.0	334	196	126
	2003	81,092	20.3	280	154	102
	2009	108,637	18.2	228	117	81
RG	1998	49,832	52.9	102	62	30
	2003	87,127	44.8	102	50	20
	2009	166,255	33.0	104	42	17

[1] AV = Asturiana de los Valles; ANI = Avileña–Negra Ibérica; BP = Bruna dels Pirineus; Mo = Morucha; Pi = Pirenaica; Re = Retinta; RG = Rubia Gallega.

effective size of the U.S. Hereford was 85 and Boichard et al. (1997) estimated the effective sizes of Abondance and Normande breeds at 106 and 47, respectively. In 3 Danish dairy cattle breeds, Sørensen et al. (2005) estimated much lower effective sizes ranging from 47 to 53, whereas in U.S. Holsteins the effective size was 39 (Caraviello, 2004). There is no agreement about the effective size of the populations to avoid genetic diversity loss. Meuwissen and Woolliams (1994) reported critical N_e for maintaining fitness ranging from 25 to 255, Meuwissen (1999) suggested that a N_e below 100 animals implies a reduction of population fitness, and the Food and Agriculture Organization of the United Nations (1998) and FAO (2007) recommended that an effective size of at least 50 animals be maintained. As was said before, some of the studied breeds have effective numbers lower than these limits, which would suggest that these populations would require the implementation of strategies to control the rate of inbreeding.

Probability of Gene Origin

The parameters of probability of gene origin are less sensitive to the pedigree completeness level than are the parameters related to inbreeding (Boichard et al., 1997). These parameters indicate how the overrepresentation of certain males (unbalanced contribution of genes) can reduce the gene pool of the population, leading to effective number of herds, ancestors, and founders lower than the actual values.

The unbalanced contribution of genes from herds, founders, and ancestors is common among the different breeds studied, as the effective numbers of these parameters are lower than the observed values (not shown in tables). The effective number of founder herds has diminished in 4 of the breeds in the period studied, probably related to the selection practiced and the extinction by the concentration of some herds. In the other 3 breeds, however, there has been an increase in the effective number of founder herds, probably due to the fact that they maintained the herdbooks open. In 2009, the number of founder herds ranged from 6 to 196 for ANI and AV but, in general, a limited number of herds, below 56, have provided the gene pool of the different breeds (Table 9). The good reputation of some breeders considered as leaders could have been responsible for this fact.

The effective number of founders presents an irregular evolution across years, ranging from 76 (ANI) to 228 (Re) in 2009, with the exception of BP (838) and AV (694), both breeds having the lowest complete generation equivalent values.

The effective number of ancestors is a measure of genetic diversity that accounts for recent bottlenecks and, as a consequence, accounts, in part, for the loss of allelic diversity from the foundation population. In the years analyzed, the effective number of ancestors generally has been slightly reduced, with the exception of Re, where the reduction was more pronounced, whereas BP experienced a large increase due to having maintained the herdbook open. The effective number of ancestors in 2009 for 6 of the breeds ranged from 42 (RG) to 220 (AV), with BP having much greater value. In general, the effective number of ancestors was lower than was the effective number of founders in all breeds, suggesting the existence of more or less strong bottlenecks. In particular, Pi, RG, and AV could have undergone the stronger bottlenecks, whereas the ANI breed presents no evidence of this phenomenon. The number of ancestors explaining 50% of the variability ranged from 17 (RG) to 89 (Mo), again excluding AV and BP, which showed much greater values. In all breeds, both the effective number of founders and the effective number of ancestors increased in comparison to the 1995 study (Gutiérrez et al., 2003). This can be due to the increase of herds involved in the herdbook.

Reduced values for the number of ancestors similar to the ones found in this study have been frequently found in beef and dairy cattle populations. Values of 25, 40, and 360 were estimated for Abondance, Normande, and Limousine (Boichard et al., 1997); a range between 35 and 82 were estimated for Irish Charolais, Limousine, Simmental, Hereford, and Aberdeen Angus (Mc Parland et al., 2007); and even lower values were reported in Danish dairy cattle (20.6, 23.8, and 34.6 for Holstein, Jersey, and Danish Red, respectively).

Conclusions

We have studied the population dynamics of 7 Spanish beef breeds under BLUP-based selection programs. Notwithstanding the differences in herd sizes, rearing environments, and degree of crossbreeding with other breeds, the pedigree analysis of the breeds shows that 1) data recording is in expansion in most of the breeds; 2) family sizes suggest a low use of AI, except in the case of the RG breed; 3) there is an extensive exchange of males among farms of the same breed and none of the farms behaves as though belonging to a closed selection nucleus; 4) the pedigree completeness level varies among breeds but shows that in all breeds, the records are very complete in recent generations; 5) the evolution of inbreeding has led to effective population size estimates, in some breeds, that are lower than are the minimum recommended for the maintenance of genetic variability; 6) there is evidence of population structure that restricts matings within herds or groups of herds, as suggested by the fact that the increase of inbreeding is greater than is that of coancestry; and 7) most of the breeds have experienced some bottlenecks as the effective number of founders exceeds the number of ancestors. All of these findings strongly suggest the necessity of monitoring inbreeding in the populations studied to maintain future improvements by genetic selection.

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