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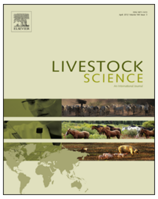

Pedigree analysis of a highly fragmented population, the Lidia cattle breed

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ABSTRACT

The aim of the study was to analyze the pedigree information of the Lidia bovine breed based on animals registered in the Herdbook and belonging to those lineages recognized as conforming to the official breed standard. Pedigree records of 272,574 animals belonging to 83 herds classified in 30 lineages were used. The average number of equivalent generations known was 4.5 (varying among lineages from 4 in Braganza to 5.2 in Baltasar Iban). The generation interval (7.5 years) was longer than that estimated in other cattle breeds. The effective size was less than 50 and consequently the estimated increase in inbreeding per generation was greater than 1% in all the lineages analyzed. The increase in inbreeding level expected for the next 50 years varied from 7.4% in Braganza to 31.3% in Diego Garrido. The ratios among the effective number of founders, the effective number of ancestors and the effective number of founder genomes was considered evidence that genetic drift explained most of the loss of genetic variability in the Lidia bovine breed due to the reduced effective population sizes of the lineages, more than bottlenecks did, as they have been less dramatic. The lineage allele loss due to the genetic drift and the effect of inbreeding are the major concerns in managing the genetic diversity of the Lidia bovine breed. The analysis of pedigree information still remains as the main useful resource to establish genetic diversity conservation guidelines in the Lidia bovine breed. Minimizing inbreeding increase within lineages in the sub-divided Lidia breed must be the major concern in managing the genetic diversity of this breed.

1. Introduction

Analysis of inbreeding rates and related parameters have traditionally been used to analyze the evolution of genetic diversity in populations (Koenig and Simianer, 2006; Cleveland et al. 2005; Sorensen et al., 2005), and the genealogical records registered in the herdbooks constitute useful data for the measurement of those population genetic parameters (Mc Parland et al., 2007; Bouquet et al., 2011; Danchin-Burge et al., 2012). Genetic drift, loss of heterozygosity and decrease in genetic variability are consequences of high rates of inbreeding over generations (Falconer and Mackay, 1996). In addition, parameters based on the probability of genetic origin from different herds (Robertson, 1953), founders (James, 1972; Lacy, 1989), and ancestors (Boichard et al., 1997) have also been used to assess changes occurring in the population over a short period of time (Boichard et al., 1997).

The Lidia breed herdbook was formally created at the beginning of the 20th century but as early as in the 17th and 18th centuries Lidia breeders registered phenotypic

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Table 1
Inbreeding coefficients (F), inbreeding rates by equivalent generation (AF), inbreeding after 50 years (F_{50}), inbreeding rate (AF(F_{50})) and affective size (N_{50}) after the next 50 years for each lineage when all the available pedigrees and only the reference population were considered. Average by lineage: average for all the lineages considered individually. Average total lineages: average when the lineages were considered as a single population (n=272,264).

Lineage[a]	**Entire pedigree**					**Reference population**		
	F	ΔF	F_{50}	$\Delta F(F_{50})$	Ne_{50}	N[b]	F	**Average relatedness**
Albaserrada (3)	11.4	1.9	14.0	2.1	23	2438	13.0	9.9
Anastasio Martín (1)	14.3	2.7	21.2	3.3	15	350	17.3	30.0
Antonio Pérez (1)	7.1	1.5	10.7	1.6	31	371	8.4	15.8
Araúz de Robles (1)	14.8	3.1	22.5	3.6	14	591	18.9	33.8
Atanasio Fernández (7)	6.3	1.3	10.3	1.5	32	4040	8.8	4.4
Baltasar Ibán (2)	8.9	2.1	14.2	2.2	23	1760	11.7	18.5
Braganza (1)	5.7	1.0	7.4	1.1	46	1110	4.7	9.1
Carlos Nuñez (6)	5.9	1.6	10.4	1.6	32	6258	8.7	5.2
Concha y Sierra (1)	8.4	2.6	16.6	2.6	19	431	16.2	15.7
Conde de la Corte (1)	7.8	2.5	14.7	2.2	22	197	12.1	20.3
Contreras (3)	7.8	1.6	11.7	1.8	28	1420	9.6	7.2
Cuadri (1)	16.8	3.1	21.0	3.3	15	504	15.9	33.9
Diego Garrido (1)	18.7	4.5	31.3	5.2	10	233	24.9	43.9
Felix Gomez (1)	5.5	1.3	8.9	1.3	38	495	8.2	14.3
Gamero Civico (5)	10.3	2.7	8.6	1.3	39	1130	15.0	7.1
Hidalgo Barquero (3)	7.5	2.1	12.5	1.9	27	1627	11.0	8.3
Jose Marzal (1)	7.4	1.4	9.8	1.5	34	1284	9.3	16.4
Juan Pedro Domecq (9)	7.1	1.5	11.1	1.7	30	8423	9.7	4.0
Manuel Arranz (1)	7.4	2.3	15.0	2.3	22	130	13.1	19.5
Maria Montalvo (1)	4.9	1.1	8.6	1.3	39	1335	7.2	7.9
Marques de Villamarta (3)	8.3	1.9	12.8	1.9	26	1351	10.4	8.5
Miura (1)	6	1.5	9.7	1.4	35	772	8.2	16.0
Murube (6)	7.3	2.4	12.1	1.8	27	3786	10.1	3.4
Pablo Romero (1)	3.8	1.1	8.3	1.2	41	367	6.3	11.0
Pedrajas (2)	18.2	4.1	28.8	4.7	11	616	21.9	24.9
Saltillo (3)	9.2	1.5	12.3	1.9	27	959	9.2	5.1
Santa Coloma (9)	10.1	2.6	18.6	2.9	17	2164	15.8	5.8
Urcola (2)	11.3	2.9	17.3	2.7	19	523	13.2	12.3
Vega Villar (4)	12.6	3.2	21.6	3.4	15	1155	16.6	7.4
Veragua (2)	11	1.6	12.4	1.9	27	1197	11.9	11.9
Average by lineage	9.4	2.2	14.5	2.2	23	1567	12.2	14.4
Average total lineages	7.8	1.9	12.2	1.8	27		10.7	0.5

[a] In brackets the number of herds included in the lineage.
[b] Total pedigree records of the reference population: 47,017.

and genealogical information in primitive herdbooks called “branding books”. The uniqueness of the selection objective of the Lidia bovine breed, based on their aggressiveness, has prompted their reproductive isolation from other cattle breeds in which this behavioral characteristic is discouraged. Nevertheless, different types of traditional popular events demand different types of behavior and this fact favoured the subdivision of the Lidia bovine breed onto lineages (called encastes) of small census (Boletín Oficial del Estado, 2001) and limited gene flow among them.

As a combined result of the genetic drift and different selection objectives, such lineages become genetically differentiated over time. The subdivided populations maximize the preservation of the genetic richness of the population. However the decrease of the population size in the subdivided groups will increase the rate of inbreeding within lineages and the inbreeding depression are expected to be higher than those in a single larger population (Falconer and Mackay 1996). A certain degree of gene flow among subpopulations has been suggested to avoid these negative effects. However, in the Lidia bovine breed the uniqueness of each lineage in terms of morphology and behavioral characteristics have been achieved through years of reproductive isolation from the rest of the lineages, severely impairing gene flow among lineages and herds.

Notwithstanding the great amount of genealogical information registered, there are no pedigree analysis references for the Lidia bovine breed. Pedigree information is not adequate for estimating kinship among isolated populations due to the absence of connections among them. In this situation, molecular markers have achieved acceptable efficiency in terms of low prediction error (Eding and Meuwissen, 2001). However, the great detail of the genealogical data makes it a useful tool to analyze within population diversity.

Previous microsatellite DNA analysis in the Lidia bovine breed showed: (i) high levels of genetic diversity as a whole, and low levels within lineages, (ii) a great level of genetic structure as a reflection of its subdivision in reproductive isolated lineages (iii) and high levels of within lineage structure in those lineages consisting of more than one herd (Cañón et al., 2008). Furthermore, significant inbreeding values have been achieved in the lineages mainly due to small population sizes. It is remarkable that the use of reproductive technology, like artificial insemination, is rare in the Lidia breed. Also, DNA mitochondrial and Y chromosome analysis have clarified the paternal and maternal influences during Lidia breed development (Cortés et al., 2008, 2011).

In the present article pedigree information on those herds previously analyzed by DNA markers of the Lidia bovine breed (Cortés et al., 2008) will be analyzed. Emphasis will be put on the analysis of genetic diversity within lineages, and the recognition of lineages in critical situations due to their inbreeding levels or effective population sizes (Ne).

2. Materials and methods

After editing the complete genealogical information available from the Unión de Criadores de Toros de Lidia (U.C.T.L.), 965,747 animals born from 1900 to 2011 were included in the pedigree file. However, many of the existing herds are the result of crosses among different lineages, so only those herds belonging to lineages recognized as conforming to the official breed standard (RD 60/2001, Boletín Oficial del Estado, 2001) were included in the analysis; these are also the lineages previously analyzed by DNA markers (Cortés et al., 2008). The pedigree information available for each lineage is shown in Table 1, including the total pedigree records (272,264), the number of lineages (30) and the number of herds (83) in each lineage. A reference population was defined as the calves born after 2004. This period was selected because the average generation interval was close to 7 years and it would comprise the time interval equivalent to the last generation of data evaluated.

2.1. Pedigree analysis

In order to avoid the bias introduced by animals with limited pedigree records, the index of completeness of the pedigree for each extant parental (IC) and the equivalent complete generations (ECG) were computed taking into account all the records of each lineage. The equivalent complete generations (ECG) was computed for each animal as the sum over all known ancestors of the terms computed $(1/2)^n$ where n is the number of generations separating the individual to each known ancestor (Maignel et al., 1996). The index of completeness (IC) was estimated for each lineage (MacCluer et al., 1983).

2.2. Generation intervals

The generation intervals (GI) for the four pathways (sire-son, sire-dam, dam-son and dam-daughter) were calculated as the average age of parents at the birth of their offspring. The average generation interval for each population is defined as the average of the 4 pathways (Lacy, 1989).

2.3. Founders and ancestors

Founder animals are those with unknown parents. The total number of founders (Nf) contains limited information about the genetic diversity of the populations because some founders have been used more intensely and therefore contribute more greatly towards the reference population than other founders. The effective number of founders (f_e) is defined as the number of equally contributing founders that would be expected to produce the same genetic diversity as in the population under study and is computed:

$$f_e = \frac{1}{\sum_{k=1}^{f} q_k^2}$$

where q_k^2 is the probability origin of k ancestor.

The effective number of ancestors (f_a) is the minimum number of ancestors, not necessarily founders, explaining the complete genetic diversity of a population.

$$f_a = \frac{1}{\sum_{j=1}^{n} q_j^2}$$

where q_j^2 is the marginal contribution of j ancestor.

Within a lineage the ratio f_a/f_e indicates how equally animals have contributed to the development of a population, and thus may show the impact of the bottlenecks that have occurred from the founders to the present population (Boichard et al., 1997). The founder genome equivalents (f_g) (Ballou and Lacy, 1995) can be defined as the number of founders that would be expected to produce the same genetic diversity as in the population under study if the founders were equally represented and no loss of alleles occurred. This parameter was calculated as the inverse of twice the average coancestry of the animals of the reference population (Caballero and Toro, 2000). These parameters (f_a, f_e, f_g) were calculated for the reference population previously defined (animals born after 2004).

2.4. Inbreeding and effective population size

The rate of inbreeding by equivalent generation was computed following the methodology described in Gutiérrez and Goyache (2005).

$$\Delta F = \frac{b}{1-(F_t-b)}$$

With F_t being the average inbreeding of the t_h generation and b the regression coefficient of the individual inbreeding coefficients on the equivalent complete generations. The effective population size then was computed as:

$$\mathrm{Ne} = \frac{1}{2b}$$

Also Ne was estimated in the reference population based on the individual increase in inbreeding as suggested by Gutierrez et al. (2009) and the increase in inbreeding of the last generation.

The software packages PEDIG (Boichard, 2002) and ENDOG V4.8 (Gutiérrez and Goyache, 2005) were used to analyze the pedigree information.

The inbreeding level after 50 years (F_{50}) was computed as (Simon, 1999):

$$F_{50} = 1-(1-\Delta F)^g$$

where g is the resulting number of generations in 50 years, ΔF is computed as the ratio $(F_t - F_{t-1})/(1-F_{t-1})$, and F_t is the inbreeding average of animals belonging to the last generation and F_{t-1} is computed as $F_t - b_{f/year} \times g$

The maximum increase of inbreeding per generation (ΔF_{50}) and the effective population size after 50 years (Ne_{50}) is deduced from F_{50}:

$$\Delta F_{50} = 1-(1-F_{50})^{1/g}$$

and

$$Ne_{50} = 1(2/\Delta F_{50})$$

3. Results

The genetic population parameters of those herds previously analyzed by DNA and belonging to lineages recognized as conforming to the official breed standard are shown in Table 1. The average index of completeness of the lineages evidenced values greater than 75% for the first four generations, decreasing to 13% in the seventh generation. The equivalent complete generation values ranged from 5.2 in Baltasar Iban to 4 in Braganza. In the reference population the average index of completeness over the first ten generations and the average equivalent complete generations increased to 99% and 6.3, respectively (Table S1).

The generation interval of the lineages based on the average age of parents at the birth of their offspring (when descendants are born) was rather high for all the lineages analyzed, from 9 years in Contreras to 6 years in Pablo Romero (Table S1). The generation interval for the reference population was 7.6.

The inbreeding coefficients (F) estimated within lineages for all registered animals are shown in Table 2. The average inbreeding coefficients of the lineages was 9.4, ranging from 18.7% to 3.8% in Diego Garrido and Pablo Romero, respectively. The inbreeding rate by equivalent generation was greater than 1.5% in 19 of the 30 lineages analyzed (Table 1).

However, in order to decrease the bias due to animals with limited pedigree records the inbreeding coefficients were also calculated in the reference population. The average inbreeding coefficient by lineage was 12.2, ranging from 4.7% in Braganza to 24.9% in Diego Garrido (Table 1). It is worth noting that the inbreeding coefficient in all the lineages considered as a single population was 7.8% and the inbreeding rate by equivalent generation was 1.9, these values being slightly smaller in the Lidia breed at 6.9% and 1,5 respectively, taking into account all the available records (965,747) (Table 1).

The lineage inbreeding after 50 years of conservation (F_{50}) ranged from 7.4 in Braganza to 31.3 in Diego Garrido.

Table 2
Probability of gene origin of the reference population. Nf (Number of founders), fe (effective number of founders), fa (effective number of ancestors), fg (effective number of founder genomes), N_{50} (number of ancestors that explain 50% of the genetic variability).

Lineage	Reference population							
	Nf	fe	fa	fg	N_{50}	fe/Nf	fa/fe	fg/fe
Albaserrada	190	23	16	10.0	6	0.1	0.70	0.43
Anastasio Martín	84	10	5	3.9	2	0.1	0.50	0.39
Antonio Pérez	137	16	9	7.1	4	0.1	0.56	0.44
Araúz de Robles	63	7	5	3.3	2	0.1	0.71	0.47
Atanasio Fernández	719	53	33	28.8	13	0.1	0.62	0.54
Baltasar Ibán	73	17	9	6.0	4	0.2	0.53	0.35
Braganza	240	25	16	10.5	6	0.1	0.64	0.42
Carlos Nuñez	887	51	22	27.1	10	0.1	0.43	0.53
Concha y Sierra	273	12	8	10.7	4	0.0	0.67	0.89
Conde de la Corte	58	15	6	6.0	3	0.3	0.40	0.40
Contreras	380	38	20	12.9	10	0.1	0.53	0.34
Cuadri	42	5	5	2.9	2	0.1	1.00	0.58
Diego Garrido	53	9	4	2.7	2	0.2	0.44	0.30
Felix Gomez	122	26	12	8.4	4	0.2	0.46	0.32
Gamero Civico	429	23	19	3.6	8	0.1	0.83	0.15
Hidalgo Barquero	208	25	20	14.1	7	0.1	0.80	0.56
Jose Marzal	125	18	10	6.8	4	0.1	0.56	0.38
Juan Pedro Domecq	838	53	37	29.2	16	0.1	0.70	0.55
Manuel Arranz	67	13	7	7.0	3	0.2	0.54	0.54
Maria Montalvo	311	44	21	16.4	8	0.1	0.48	0.37
Marques de Villamaría	230	35	17	14.2	7	0.2	0.49	0.41
Miura	72	15	12	7.5	4	0.2	0.80	0.50
Murube	565	80	43	35.1	15	0.1	0.54	0.44
Pablo Romero	90	27	14	11.6	6	0.3	0.52	0.43
Pedradas	127	10	8	4.4	4	0.1	0.80	0.44
Saltillo	446	46	23	22.1	9	0.1	0.50	0.48
Santa Coloma	705	41	24	23.4	11	0.1	0.59	0.57
Urcola	128	24	11	8.8	4	0.2	0.46	0.37
Vega Villar	226	40	24	14.6	9	0.2	0.60	0.37
Veragua	138	28	13	9.5	5	0.2	0.46	0.34
Average by lineage	268	27.6	15.8	12.3	6.4	0.1	0.59	0.4

Furthermore, in the Lidia breed and in the lineages considered as a single population the F_{50} were 10 and 12.2, respectively (Table 1). In all the lineages analyzed, in the lineages as a single population and in the Lidia breed the minimum effective population size deduced from the F_{50} parameter was less than 50.

The individual average relatedness coefficient in the reference population was also high, ranging from 37.4% in Diego Garrido to 3.7% in Carlos Nuñez (Table 1). Finally, the average relatedness evidenced greater differences among the lineage values (average 14.4%) and the lineages as a single population (0.5%) (Table 1).

The high levels of reproductive isolation among herds within lineages (Cañón et al., 2008) may explain that the lineages with lower average relatedness values are generally composed of more than one herd. The average relatedness value among lineages is 0.144, a very high score compared with other cattle breeds (Bouquet et al., 2011).

The effective number of founders (fe), effective number of ancestors (fa), and effective number of founder genomes (fg) of animals in the reference population showed a high variability among lineages (Table 2). Also, when all the available pedigrees of the Lidia breed were considered as a single population ($n=965{,}747$) the fe and fa were 468 and 275, respectively.

The number of ancestors explaining 50% of the gene origin was less than 10 in 24 of the 30 lineages analyzed (Table 2).

The average fa/fe ratio was 0.571 and showed great heterogeneity among lineages, and ranged from 1 in Cuadri to 0.4 in Conde de la Corte (Table 2). The average fg/fe ratio was 0.444. The fe and fa values in the Lidia breed were, as expected, higher than that in lineages at 414 and 275, respectively.

The lineage effective population sizes based on the increase in inbreeding by equivalent generation were lower than 50 with the exception of Braganza (50.5) (Table 3). When the reference population was considered, the Ne based on the individual increase in inbreeding ranged from 45.8 in Bragranza to 9.5 in Diego Garrido, and when the last generation inbreeding increase was the criterion used, the same lineages showed the higher (42.9) and lower (9) Ne values. The Ne based on the individual increase in inbreeding when all the lineages were considered as a single population was 26.7 ($n=272{,}264$). When all the pedigree records available in the Lidia breed were considered as a whole ($n=965{,}747$), the calculated Ne based on the regression of inbreeding coefficient in the number of equivalent generations was 35.7.

Table 3
Values of Ne estimated. (1) Effective size based on increase in inbreeding by equivalent generation in the entire pedigree. (2) Effective size based on individual increase in inbreeding in the reference population and (3) effective size based on increase in inbreeding in the last generation in the reference population. Average by lineage: average of all the lineages considered individually. Average total lineages: average when all the lineages were considered as a single population ($n=272{,}264$). Average Lidia breed: average when all the available pedigrees of the Lidia breed were considered as a single population ($n=965{,}747$).

Lineage	Entire pedigree	Reference population	
	Ne^1	Ne^2	Ne^3
Albaserrada	26.4	17.8	21.5
Anastasio Martín	18.6	13.9	14.1
Antonio Pérez	34.5	30.8	29.2
Araúz de Robles	16.0	13.2	13.2
Atanasio Fernández	38.3	27.1	30.5
Baltasar Ibán	24.2	23.0	21.8
Braganza	50.5	45.8	42.9
Carlos Nuñez	31.8	28.8	30.3
Concha y Sierra	19.5	16.3	18.3
Conde de la Corte	19.9	19.1	21.0
Contreras	31.0	23.9	26.6
Cuadri	14.7	11.2	14.2
Diego Garrido	11.0	9.5	9.0
Felix Gomez	38.7	33.2	35.6
Gamero Civico	18.6	16.9	16.8
Hidalgo Barquero	24.1	20.8	25.0
Jose Marzal	35.2	26.2	32.2
Juan Pedro Domecq	32.8	25.8	28.2
Manuel Arranz	22.1	18.9	20.5
Maria Montalvo	46.4	40.4	36.9
Marques de Villamarta	26.0	22.2	24.3
Miura	33.2	30.1	32.6
Murube	20.7	22.5	25.8
Pablo Romero	44.2	40.4	38.4
Pedrajas	12.2	11.7	9.9
Saltillo	34.2	27.8	25.3
Santa Coloma	19.2	17.6	16.3
Urcola	17.2	16.7	17.6
Vega Villar	15.6	13.9	13.8
Veragua	30.7	20.3	25.1
Average by lineage	26.9	22.9	24.6
Average total lineages	26.7		
Average Lidia Breed	35.7		

4. Discussion

At present the Lidia bovine breed is mainly found in the West and Southwest of the Iberian Peninsula, without any particular distribution pattern across the geographical areas, as well as in France and in numerous Central and South American countries. The Lidia breed is divided into lineages (called encastes) with high levels of reproductive isolation among them, partially as a result of different public events that demand bulls with different behavioral characteristics, which severely impaired gene flow among lineages and herds. The Lidia bovine breed showed higher genetic variability in previous DNA autosomal microsatellite analysis than other Spanish and European cattle breeds (European Cattle Genetic Diversity Consortium, 2006; Cortés et al., 2008). However, the average genetic diversity values within lineages were lower than those for other cattle breeds (Cortés et al., 2008). The pedigree analysis showed similar results than molecular ones, higher inbreeding coefficients in the Lidia breed lineages, considered individually or as a single population, than those found in other cattle breeds (Danchin-Burge et al., 2012; Bouquet et al., 2011; Mc Parland et al., 2007; Gutiérrez et al., 2003). Therefore, taken into account the reluctance of the breeders to introduce animals of other lineages, the apparently good “genetic health” status of the breed is at the expense of genetic risk for the lineages, many of them being genetically compromised by demographic stochasticity. It is well known that in populations with a high level of subdivision and limited gene flow, the subpopulations act as genetic reservoirs with a total genetic variability of $(1+F)V_G$, being V_G the original genetic variability (Falconer, 1986). It is important to emphasize two facts affecting the Lidia breed: (1) contrary to most domestic bovine breeds, around 20% of its genetic diversity is allocated within the lineages; and (2) the genetic variation present as differences among lineages cannot be readily regenerated (Cañón et al., 2007). The genetic variation within and between the Lidia lineages is used to meet the present demand of the different "popular fairs". As consequence of a systematic mating of animals within a subgroup of the population and the lack of connections among Lidia breed lineages, the within lineage average relatedness (12.5%) was greater when was estimated individually than in the lineages considered as a single population (0.4%). The results shown in this paper for a bovine domestic breed are the opposite of those shown by Robertson and Rendel (1954) for 3 bovine dairy breeds in which, as consequence of the pyramidal reproductive structure, all the genetic variance was within herd, being null the genetic variance among herds. So, the use of traditional pedigree tools for the analysis of population structure that consider the Lidia bovine breed as whole and ignore the division in lineages could misinterpret the current genetic health of this breed.

Breeders are becoming aware of the risks of inbreeding increase and parameters derived from probability of genes origin are been widely used to precisely monitor the genetic diversity within subpopulations after a small number of generations. Also, parameters derived from probabilities of gene origin may provide a better understanding of the changes taking place in the genetic pool of a breed, especially when those are considered over a small number of generations (Boichard et al., 1997). The significant differences between the number of founders (Nf) and the effective number of founders (fe) in all the lineages is a symptom of the genetic diversity loss from the founders to the extant population. Also the number of founders that explain 50% of the genetic variability (average by lineage, $N_{50}=6.4$) suggest an excess of some animals as parents over generations and could explain the loss of genetic diversity in the lineages. Lineages have often been generated from a small number of animals that share a particular phenotype and, traditionally, few bulls are used for breeding practice within herds/lineages, justifying the reduced fe and fa values. Therefore, selection of parents with minimum coancestry should be a valid strategy for all lineages in order to maintain their genetic diversity. As expected, lineages with greater census showed lower fg/fe ratios, since that ratio is consequence of the genetic drift related to random allele sampling in a finite population. In all the lineages, except Carlos Nuñez and Concha y Sierra, the ratio fg/fe was low than fa/fe showing a higher effect of the genetic drift than the bottleneck in the loss of the genetic variability. The small size of the lineages supported the higher effect of the genetic drift than bottlenecks. However the low number of males for breeding practice could simultaneously increase the genetic drift and the bottleneck effects. For example the fa/fe ratio of Cuadri (1) not evidenced recent bottlenecks; however, the fg/fe ratio (0.58) showed significant loss of genetic diversity by genetic drift due to their small size.

The fe and fa values estimated when all the available pedigree records of the Lidia breed was considered as a single population were clearly greater than those estimated in dairy and beef cattle breeds (Bouquet et al., 2011; Danchin-Burgue et al. 2012; Melka et al., 2013) and than those calculated in each lineage individually. These result evidenced different genetics origins of the Lidia lineages and as a consequence a great genetic variability in origin of the Lidia bovine breed considered as a whole. The high isolation among lineages which are genetically different in origin has consequently preserved the high genetic richness observed in this breed. So, each lineage is the reservoir of a part of the original genetic variability and it loss would reduced the total genetic variability that could not be regenerated. However, the reproductive isolation among lineages have been a consequence of random decisions by breeders which left many lineages in a compromised situation in terms of survival. In this scenario, demographic stochasticity (infections, human or economic factors,…) could be a relevant factor in decreasing the genetic variability of this breed because of the extinction of units where reside a large proportion of that variability, so action should be taken in order to preserve lineages and, as a consequence, the genetic health of the Lidia breed.

Inbreeding rates less than 1% per generation and a Ne of 50 have been recommended to avoid inbreeding depression and to maintain genetic diversity at sustainable levels for populations in the mid-term (FAO, 1988). Thus taken into account the high level of reproductive isolation among lineages in the Lidia bovine breed, this benchmark could be considered a valid value to asses the lineages viability. In this scenario a total of 18 lineages evidenced average inbreeding coefficients greater than 10 (Table 1). Also, the maximum increase in inbreeding per generation after 50 years (ΔF_{50}), computed under the assumption that reproduction occurred as in an ideal population, is greater than 1% in all the lineages analyzed and consequently the effective population sizes after 50 years (Ne_{50}) obtained from ΔF_{50} were lower than 50. Furthermore, using the reference population, a total of 19 and 15 lineages showed values of effective population sizes lower than 25 when inbreeding coefficients were based on individual increase in inbreeding or on increase in inbreeding of the last generation, respectively. Following classification of breed endangerment based on effective population size proposed by Simon (1999), a total of 12 and 10 lineages were classified as endangered (fourth of fifth levels) when the individual increase in inbreeding or increase in inbreeding of the last generation were used to estimate the effective population size, respectively. Even if we consider the different lineages effective population sizes computed or the inbreeding rates per generation within lineages, it remains below the FAO recommendations for maintaining the long-term genetic diversity (Ne=50).

In highly subdivided populations different alternatives have been postulated to maximize effective population size in order to reduce the loss of genetic diversity and the increase of inbreeding and its deleterious effects (Toro and Caballero, 2005; Fernandez et al., 2011). Those alternatives which involve exchange animals between lineages and herds are severely limited due to the reluctance of the breeders and their interest in maintaining their differentiation from the rest of lineages. On the other hand, this situation is similar to that in other cattle breeds with high inbreeding coefficients where the exchange of animals of other breeds is not considered. So, efforts should be directed towards balancing the contribution of ancestors or avoiding mating of high-related animals. The first alternative is against the traditionally selection procedure in the Lidia bovine breed, where few reproductive males are used. The second alternative has been carried out in lineages/herds for years. The simplest way to implement unrelated mating is to ban crosses beyond a specific degree of relatedness. However, these strategies are effective in the first few generations but not in the long run (Fernandez et al., 2011). The availability of dense marker maps allows new strategies of minimizing mendelian sampling for increasing effective population size, even over 2N (Wang and Hill, 2000). Also, dense marker maps would allow a differential management of specific genome areas with higher homozygosity rates. In this production system, the limiting factor of genotyping cost could be outweighing by the reduction of the high costs of maintaining fewer animals.

5. Conclusions

The subdivision of the Lidia breed in highly isolated lineages has favoured the maintenance of the original genetic richness. However, the low effective size of the lineages jeopardize its genetic sustainability and, as consequence, the genetic health of the breed. Traditional alternatives to preserve the loss of genetic diversity in subdivided populations are not enough in Lidia bovine breed in the long term due its peculiarities. Thus, novel tools based on the information given by dense markers maps would allow to implement better conservation strategies for the extant genetic diversity in the Lidia bovine breed.

Conflict of Interest statement

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.livsci.2014.05.011.

References

Ballou, J.D., Lacy, R.C., 1995. Identifying genetically important individuals for management of genetic variation in pedigreed populations. In: Ballou, J.D., Gilpin, M., Foose, T.J. (Eds.), Population Management for Survival and Recovery: Analytical Methods and Strategies in Small Population Management, Columbia University Press, New York, pp. 76–111.

Boichard, D., Maignel, L., Verrier, E., 1997. The value of using probabilities of gene origin to measure genetic variability in a population. Genet. Sel. Evol. 29, 5–23.

Boichard D., 2002. PEDIG: a fortran package for pedigree analysis suited for large populations. In: Proceedings of the 7th World Congress of Genetics Applied to Livestock Production, Montpellier (France), pp. 19–23 August.

Bouquet, A., Venot, E., Laloë, D., Forabosco, F., Fogh, A., Pabiou, T., Moore, K., Eriksson, J.A., Renand, G., Phocas, F., 2011. Genetic structure of the European Charolais and Limousin cattle metapopulations using pedigree analyses. J. Anim. Sci. 89, 1719–1730.

Boletín Oficial del Estado, 2001. Real Decreto 60/2001,de 26 de enero, sobre prototipo racial de la raza bovina de Lidia. Bol. Of. del Estado 38, 5255–5261.

Caballero, A., Toro, M.A., 2000. Interrelations between effective population size and other pedigree tools for the management of conserved populations. Genet. Res. Camb. 75, 331–343.

Cañón, J., Fernandez, J., Garcia-Atance, M.A., Tupac-yupanqui, I., Dunner, S., 2007. Genetic relationship among fighting-bull breeders by their historic origin. Arch. Zootecnia 56, 383–390.

Cañón, J., Tupac-Yupanqui, I., Garcia-Atance, M.A., Cortes, O., Garcia, D., Fernandez, J., Dunner, S., 2008. Genetic variation within the Lidia bovine breed. Anim. Genet. 39, 439–445.

Cleveland, M.A., Blackburn, H.D., Enns, R.M., Garrick, D.J., 2005. Changes in inbreeding of US Herefords during the twentieth century. J. Anim. Sci. 83, 992–1001.

Cortés, O., Tupac-Yupanqui, I., Dunner, S., García-Atance, M.A., García, D., Fernández, J., Cañón, J., 2008. Ancestral matrilineages and mitochondrial DNA diversity of the Lidia cattle breed. Anim. Genet. 39, 649–954.

Cortés, O., Tupac-Yupanqui, I., Dunner, S., Fernández, J., Cañón, J., 2011. Y chromosome genetic diversity in the Lidia bovine breed: a highly fragmented population. J. Anim. Breed. Genet. 128, 491–498.

Danchin-Burge, C., Leroy, G., Brochard, M., Moureaux, S., Terrier, E., 2012. Evolution of the genetic variability of eight French dairy cattle breeds assessed by pedigree analysis. J. Anim. Breed. Genet. 129, 206–217.

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

European Cattle Genetic Diversity Consortium, 2006. Marker assisted conservation of European cattle breeds: an evaluation. Anim. Genet. 37, 475–481.

Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics, fourth ed. Longman Editors, Essex, UK.

Fernandez, J., Meuwissen, T.H.E., Toro, M.A., Maki-Tanila, A., 2011. Management of genetic diversity in small farm animal populations. Animal 5, 1684–1698.

FAO, 1998. Secondary guidelines for development of national farm animal genetic resources management plans: management of small populations at risk. FAO, Rome, Italy.

Gutiérrez, J.P., Altarriba, J., Díaz, C., Quintanilla, A.R., Cañón, J., Piedrahita, J., 2003. Genetic analysis of eight Spanish beef cattle breeds. Genet. Sel. Evol. 35, 43–64.

Gutiérrez, J.P., Goyache, F., 2005. A note on ENDOG: a computer program for analysing pedigree information. J. Anim. Breed. Genet. 122, 172–176.

Gutierrez, J.P., Cervantes, I., Goyache, F., 2009. Improving the estimation of realized effective population sizes in farm animals. J. Anim. Breed. Genet. 126, 327–332.

James, J., 1972. Computation of genetic contributions from pedigrees. Theor. Appl. Genet. 42, 272–273.

Koenig, S., Simianer, H., 2006. Approaches to the management of inbreeding and relationship in the German Holstein dairy cattle population. Livest. Sci. 103, 40–53.

Lacy, R.C., 1989. Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. Zoo Biol. 8, 111–123.

MacCluer, J., Boyce, B., Dyke, L., Weitzkamp, D., Pfenning, A., Parsons, C., 1983. Inbreeding and pedigree structure in Standardbred horses. J. Hered. 74, 394–399.

Maignel, L., Boichard, D., Verrier, E., 1996. Genetic variability of French dairy breeds estimated from pedigree information. Interbull 14, 49–54.

Mc Parland, S., Kearney, J.F., Rath, M., Berry, D.P., 2007. Inbreeding trends and pedigree analysis of Irish dairy and beef cattle populations. J. Anim. Sci. 85, 322–331.

Melka, M.G., Stachowicz, K., Miglior, F., Schenkel, F.S., 2013. Analyses of genetic diversity in five Canadian dairy breeds using pedigree data. J. Anim. Breed. Genet. 130, 476–486.

Robertson, A., 1953. A numerical description of breed structure. J. Agric. Sci. 43, 334–336.

Robertson, A., Rendel, J.M., 1954. The performance of heifers got by artificial insemination. J. Agric. Sci. 44, 184–192.

Simon, D.L., 1999. European approaches to conservation of farm animal genetic resources. Anim. Genet. Resour. 25, 77–97.

Sorensen, A.C., Sorensen, M.K., Berg, P., 2005. Inbreeding in Danish dairy cattle breed. J. Dairy Sci. 88, 1865–1872.

Toro, M.A., Caballero, A., 2005. Characterization and conservation of genetic diversity in subdivided populations. Philos. Trans. R. Soc. B 360, 1367–1378.

Wang, J., Hill, W.G., 2000. Marker-assisted selection to increase effective population size by reducing mendelian segregation variance. Genetics 154, 475–489.