

Genetic Structure of the European Limousin Cattle Metapopulation Using Pedigree Analyses

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Abstract

Pedigree collected by the Interbeef service permitted to assess genetic diversity of 5 European Limousin cattle populations respectively from Denmark, France, Ireland, Sweden and United-Kingdom using pedigree analyses. Analyzed populations included 1 652 734 calves with age-adjusted weaning weights whose 91.9% were recorded in France, 4.9% in United-Kingdom, 1.8% in Denmark, 0.9% in Sweden and 0.5% in Ireland. Pedigree file included 2 409 659 animals whose 82.5% originated from FRA, 11.1% from DNK, 4.9% from UK, 0.8% from IRL, and 0.7% from SWE. Gene flows were rather limited between populations, except from France towards other countries. Pedigree knowledge was good in all 5 subpopulations and allowed tracing pedigree back to the French population. Therefore, between 71% and 96% founders of calves born between 1989 and 2008 were of French origin. In each population, it was shown that founders but also ancestors had unbalanced genetic contributions: the main 10 ancestors explained 20% of gene origin in France and about 25% in other European populations. Although main ancestors of each European subpopulation were often born in France, only a few animals were common amongst main ancestors which explained 50% of gene origin in two different countries. Moreover, main ancestors which explained 50% of gene origin respectively in Denmark, Ireland, Sweden and United-Kingdom were not found to be frequently used in France. Therefore, the subdivision of the Limousin cattle population allowed maintaining genetic diversity between populations.

I- Introduction

The Limousin breed is one of the major French beef cattle breed which has been selected since the end of the 19th century in France. Since the 1970's, some Limousin breeding stocks has been exported worldwide. The Limousin population is therefore a metapopulation subdivided in different national populations which are bred according to different selection practices or objectives.

In 2005, the Interbeef network was created to put in place international genetic evaluations of Limousin and Charolais cattle. For the European countries taking part to this project, the aim was to enlarge the choice of breeding animals to other foreign populations (Venot *et*

al., 2007). To achieve its mission, the Interbeef service collected pedigree and performance of Limousin purebred animals from 5 different countries: Denmark, France, Ireland, Sweden and United Kingdom.

Genealogical information collected in this framework gave the opportunity to assess the genetic diversity of the European Limousin metapopulation by pedigree analyses. Several studies have already been carried out at the national level in Ireland (McParland *et al.*, 2007) and in France (unpublished results). The objective of this article is to assess and compare the genetic diversity of European Limousin subpopulations taking advantage of the whole pedigree information.

II- Material and Methods

Data. Data were provided by the Interbeef network and were extracted from the European database which is used for international genetic evaluations of beef cattle. Performance and pedigree were available only from herds that were controlled by each national breed association. Controlled calves represent 20% of the whole Limousin population in IRL, 14% in FRA, 8% in DNK and 5% in UK. This proportion was not available for SWE.

Datasets gathered age-adjusted weaning weights and known pedigree of purebred Limousin animals born between 1989 and 2008 in 5 different countries. Performance dataset included 1 652 734 calves whose 91.9% were recorded in France (FRA), 4.9% in United-Kingdom (UK), 1.8% in Denmark (DNK), 0.9% in Sweden (SWE) and 0.5% in Ireland (IRL). Identification numbers (ID) were standardized according to rules described by Pabiou *et al.* (2007) so that each animal had a unique ID coded on 19 characters. Available information also included herd and date of birth of recorded calves. Pedigrees from all countries were then pooled together into a single file eliminating redundant genealogies. This resulted in a pedigree file including 2 409 659 animals whose 82.5% originated from FRA, 11.1% from DNK, 4.9% from UK, 0.8% from IRL, and 0.7% from SWE.

Demographic analysis. For each subpopulation, demographic analyses characterized 1) the evolution of the number of recorded animals over time and 2) breeding stock exchanges within and between countries.

Pedigree knowledge. Pedigree analyses were carried out with the software Pedig (Boichard, 2002) for a reference population that included animals with both parents known and born between 2004 and 2008 in each of the five countries.

Pedigree knowledge was assessed by complete generation equivalents (CGE). This number summarizes the quantity of genealogical information known in a pedigree. For a given animal, it was computed as the sum of the proportion of known ancestors over all traced generations (Boichard *et al.*, 1997). The

proportion of known ancestors at each generation was also calculated to compare depth pedigree in each subpopulation. Both analyses were performed using separately the whole pedigree file and each national pedigree file to measure the gain in genealogical information obtained by gathering all European genealogies.

Pedigree analyses. Investigations on the genetic structure of populations were carried out using the probability of gene origin approach (James, 1972; Boichard *et al.*, 1996). In this approach, genetic contributions of founders, or ancestors, are calculated to assess how an original gene pool has been maintained across generations. Founder animals are defined as ancestors without known parents and are supposed to be unbred and unrelated.

The expected genetic contribution of a founder X is computed as the probability that a gene taken at random within the reference population comes from founder X (Boichard *et al.*, 1996). The influence of the French Limousin population on genetic diversity of other European populations was assessed by calculating genetic contributions of French founders to those populations.

The total number of founders poorly reflects the original genetic diversity of a population because founders may be related and may have unbalanced genetic contributions. Therefore, three statistics were derived from genetic contributions to better describe genetic diversity of populations: the effective numbers of founders (f_e), ancestors (f_a) and founder genomes (N_g).

Parameter f_e corresponds to the number of equally contributing founders that would be expected to produce the same genetic diversity as observed in a reference population. It is calculated from founder genetic contributions (Lacy, 1989). When founders contribute equally to the reference population, f_e equals the total number of founders. Otherwise, f_e is smaller than the number of founders. Thus, f_e measures how the balance in founder contribution is maintained across generations accounting for selection rate and variation in family size. However, it neglects the probability of gene loss from parent to progeny due to bottlenecks and genetic drift.

Parameter f_a corresponds to the number of equally contributing ancestors that would be expected to produce the same genetic diversity as observed in the reference population. Compared to f_e , f_a better accounts for bottleneck effects because it is computed from marginal genetic contributions of all ancestors, and not only founders (Boichard *et al.*, 1997).

Eventually, as the calculation of f_a does not account for random allele fluctuations induced by genetic drift, McCluer *et al.* (1986) proposed to calculate N_g by simulation. This parameter describes the number of equally contributing founders, with no random loss of founder alleles, which would be expected to produce the observed genetic diversity in the reference population.

Within a country, analyzing ratios f_a/f_e and N_g/f_a , and their relative evolution, allows to detect recent changes in breeding strategy, bottlenecks and genetic drift.

Results and Discussion

Demographic analyses. Evolutions over time of the numbers of recorded animals in total and per herd are presented in Figure 1 and 2 for each European subpopulation. Since 1989, the number of recorded calves has increased in FRA, mainly because of an increase in the number of calves recorded per herd. In SWE, the number of recorded animals has remained stable since the mid-nineties whereas the number of recorded animals per herd has clearly increased.

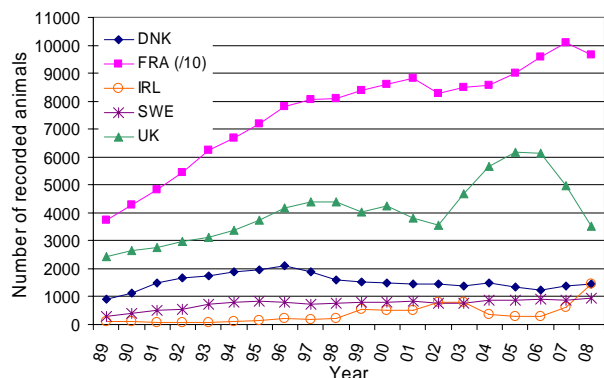


Figure 1. Evolution of the number of recorded calves in each country between 1989 and 2008. (The number of recorded calves in France was divided by 10 to fit in the graph).

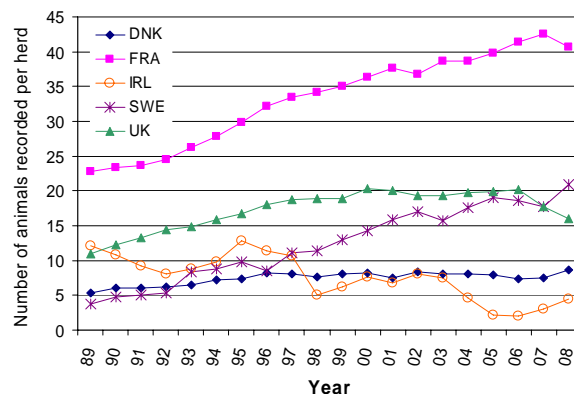


Figure 2. Evolution of the number of recorded animals per herd between 1989 and 2008.

The number of recorded animals progressively rose in UK till the late 1990's and then reached a peak in 2005-2006. This peak is mainly due to an increase of the number of recorded herds because the number of calves recorded per head remained constant. In DNK, the number of recorded animals has slightly declined since 1996 mainly due to a decrease in the number of recorded herds. Eventually, the number of recorded animals fluctuated in IRL till 2005 and went up on the last 2 years. In DNK and IRL, the number of calves controlled per herd remained very low (<10).

Gene flows within and between populations.

For each European subpopulation, Table 1 presents the proportion of calves born in each country according to its sire nationality. The French population is a closed population: all sires used in FRA were born in FRA. Then, numerous gene flows were observed within this population. A selection nucleus comprising about 10% of herds provided about 70% of natural service (NS) bulls used in the FRA population (unpublished results).

Table 1. Proportion (in %) of calves born in 2008 in each European country according to its sire nationality.

		Sire birth country					
		DNK	FRA	IRL	SWE	UK	Others
Calf Birth country	DNK	77	22	0	0	0	1
	FRA	0	100	0	0	0	0
	IRL	0	50	49	0	1	0
	SWE	1	4	0	94	0	1
	UK	0	23	0	0	77	0

In the nineteen-seventies and eighties, gene flows across countries were only observed from France towards other European countries to constitute Limousin purebred populations (results not shown). In 2008, FRA still provided a notable proportion of NS bulls or semen straws to other countries, except to SWE (Table 1). Apart from genetics originating from France, bull and semen exchanges between European subpopulations were rather limited, especially during the last decade. Cow and embryo flows between countries were much more limited than bull and semen flows (results not shown). Bull flows were observed within population in DNK, SWE and UK. Such domestic gene flows were not detected in IRL.

Pedigree knowledge. Complete generation equivalents (CGE) are presented in table 2 for calves born between 2004 and 2008 for each European subpopulation. CGE were computed considering either the whole European pedigree file or only pedigrees available in each country. Pedigree knowledge was good in all five countries, even if assessed only with the national pedigree file (CGE>5). Pedigree knowledge was actually almost exhaustive on the first 3 generations for animals recorded in DNK, SWE and UK.

Table 2. Number of generation equivalents known in the pedigree of calves born between 2004 and 2008.

Country	National pedigree file	Whole pedigree file
DNK	5.6	7.3
FRA	6.9	6.9
IRL	5.2	6.5
SWE	6.3	7.5
UK	6.8	7.5

The highest national pedigree CGE was found in FRA. Including all European genealogies did not change the French CGE since there were no gene importations in the French population. In other countries, it markedly improved pedigree knowledge from 0.7 to 1.7 generation equivalents respectively for UK and DNK. Improvement in pedigree knowledge was detected from the 4th generation in IRL and the 5th generation in SWE, DNK and UK, indicating that the French pedigree file

mainly provided relatively old genealogical information. Therefore, pedigree knowledge became better for animals born in DNK, SWE and UK than those born in the French population. However it should be mentioned that pedigree knowledge is heterogeneous in the French population: CGE of calves born in nucleus breeder herds was as high as 7.9, while it was only 6.8 for calves born in beef producer herds. Knowledge of pedigree in DNK, SWE and UK populations is therefore very similar to the one in the French nucleus breeder herds.

Genetic composition of European Limousin subpopulations. The proportion of French founders in each European calf population born between 1989 and 2008 is presented in Figure 3.

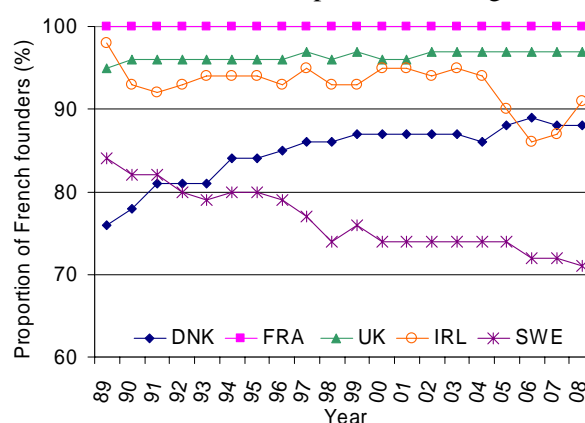


Figure 3. Proportion of French founders in the pedigree of each European calf population born between 1989 and 2008.

In subpopulations other than FRA, the proportion of French founders remained quite stable and high in IRL and UK (about 90-95%), increased in DNK (from 76% to 89%) and decreased in SWE (from 85% to 71%). Therefore, even in countries in which importations of breeding stock and semen from FRA were limited during the last decade (SWE, DNK), a substantial part of founder genes stemmed from the French population. This highlights the good pedigree knowledge which allows tracing back genealogies to the French population.

In DNK, IRL and UK, most of non French founders generally stemmed from the considered country. This was different in the SWE population in which the proportion of founders from North-America has been increasing since 1999 to reach about 15% in

2008. This increase is due to the use of a few Canadian and American bulls which gendered Swedish bulls which more largely diffused in the SWE population.

Results of this study are of great importance for the definition of unknown parent groups for the international genetic evaluation of the Limousin metapopulation. Indeed, different founder origins could suggest genetic heterogeneity amongst the founder population.

Genetic contributions of founders and ancestors. Table 3 presents statistics concerning probability of gene origin in each European subpopulation of calves born between 2004 and 2008. In each population, the number of efficient founders (f_e) is much lower than the total number of founders indicating that the genetic contributions of founders are very unbalanced.

The ratio f_a/f_e is relatively low, comprised between 0.28 and 0.37. This result indicates that marked bottlenecks exist in each European subpopulation. Consequently, marginal contributions of ancestors are very unbalanced. It was found that the main 10 ancestors explained about 20% of the genes in the French population and about 25% in DNK, IRL, SWE and UK subpopulations (Table 3).

Table 3. Effective numbers of founders (f_e), of ancestors (f_a) and of founder genomes (N_g) and genetic contributions of the main 10 ancestors (C_{10}) for each European calf population born between 2004 and 2008.

Country	Number of male calves	Number of founders	f_e	f_a	N_g	C_{10}
DNK	3360	2495	310	92	48	25
FRA	217606	43064	468	156	89	20
IRL	1745	3261	395	110	60	23
SWE	2213	1520	274	77	39	27
UK	13 237	4098	232	86	48	26

The N_g/f_a ratio is related to genetic drift: lower value indicates more genetic drift. The evolution of N_g/f_a ratio showed that genetic drift differently affected genetic diversity of each Limousin subpopulation. For all five populations of calves born between 1999 and 2003, this ratio was around 58% (result not shown). Five years later, i.e. approximately one generation later, this ratio was equal to 57% in

FRA, 56% in UK, 55% in IRL, 52% in DNK and 51% in SWE. Genetic drift effects appeared stronger in DNK and SWE because both countries use mostly bulls bred in their own respective country, importing few genetics from foreign Limousin populations. Although the IRL population was also a small population with large bottlenecks, greater importations of bulls and semen from France allowed maintaining a certain level of genetic diversity. Results were in agreement with those reported by McParland *et al.* (2007) on Irish Limousin cattle.

Table 4 presents the number of common ancestors between main ancestors explaining 50% of gene origins in two different countries. Very few animals diffused in several different countries. It generally concerned popular French AI bulls or very old French base founders which diffused a lot via their offspring and grand-offspring.

Table 4. Number of main ancestors explaining 50% of gene origins in each country (on the diagonal) and number of common animals between those main ancestors pools in 2 different countries (above diagonal).

	DNK	FRA	IRL	SWE	UK
DNK	36	9	5	3	4
FRA		80	17	3	13
IRL			40	3	11
SWE				27	1
UK					44

Main ancestors are different in DNK, IRL and UK populations even if lots of them were born in France. They are generally French bulls exported to be used by AI or in breeder herds. For example, amongst the 44 main ancestors which explained 50% of gene origins in UK, 38 were born in FRA (data not shown).

The SWE population presents a greater diversity of ancestor geographic origins. Among the main 27 ancestors which explained 50% of gene origins, 3 were born in Canada, 6 in DNK, 2 in Finland, 9 in FRA, 1 in Luxemburg and 6 in SWE.

Among main ancestors which explained 50% of gene origins respectively in DNK, IRL, SWE and UK but were not represented among main ancestors in FRA, only 0 to 3 ancestors were

found to have genetic contributions above 1/10 000 in the current French population. It means that ancestors which were frequently used in DNK, IRL, SWE and UK populations were rarely used in France. Then, the subdivision of the Limousin cattle population allowed maintaining genetic diversity between populations.

Conclusion

This study gives an overview of the genetic diversity of each European purebred Limousin cattle subpopulation using pedigree analyses. If most of founder genes come from the French subpopulation, it appeared that the evolution of the genetic structure of subpopulations mainly depended on the offer of AI bulls in each country and importations of semen or breeding stock from France. Parameters derived from probability of gene origin were useful to detect bottlenecks and genetic drift affecting each European population. The largest genetic drift effects were observed in DNK and SWE populations. Further investigations are still required to evaluate inbreeding and coancestry trends in the European Limousin metapopulation.

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