



HAL
open science

Genetic structure of the European Charolais and Limousin cattle metapopulations using pedigree analyses

Alban A. Bouquet, Eric Venot, Denis Laloë, F. F. Forabosco, A. A. Fogh, T. T. Pabiou, K. K. Moore, Gilles G. Renand, Florence Phocas

► **To cite this version:**

Alban A. Bouquet, Eric Venot, Denis Laloë, F. F. Forabosco, A. A. Fogh, et al.. Genetic structure of the European Charolais and Limousin cattle metapopulations using pedigree analyses. *Journal of Animal Science*, 2011, 89 (6), pp.1719-1730. <10.2527/jas.2010-3469>. <hal-01000450>

HAL Id: hal-01000450

<https://hal.science/hal-01000450v1>

Submitted on 29 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

JOURNAL OF ANIMAL SCIENCE

The Premier Journal and Leading Source of New Knowledge and Perspective in Animal Science

Genetic structure of the European Charolais and Limousin cattle metapopulations using pedigree analyses

A. Bouquet, E. Venot, D. Laloë, F. Forabosco, A. Fogh, T. Pabiou, K. Moore, J.-Å. Eriksson, G. Renand and F. Phocas

J ANIM SCI 2011, 89:1719-1730.
doi: 10.2527/jas.2010-3469

The online version of this article, along with updated information and services, is located on the World Wide Web at:

<http://www.journalofanimalscience.org/content/89/6/1719>



American Society of Animal Science

www.asas.org

References

This article cites 31 articles, 6 of which you can access for free at:
<http://www.journalofanimalscience.org/content/89/6/1719#BIBL>

Citations

This article has been cited by 1 HighWire-hosted articles:
<http://www.journalofanimalscience.org/content/89/6/1719#otherarticles>

Genetic structure of the European Charolais and Limousin cattle metapopulations using pedigree analyses

A. Bouquet,*†¹ E. Venot,* D. Laloë,* F. Forabosco,‡ A. Fogh,§ T. Pabiou,# K. Moore,||
J.-Å. Eriksson,¶ G. Renand,* and F. Phocas*

*INRA, Animal Genetics and Integrative Biology, UMR 1313, Domaine de Vilvert, F-78352 Jouy-en-Josas, France; †AgroParisTech, 16, rue Claude Bernard, F-75231 Paris Cedex 5, France; ‡Interbull Centre, Department of Animal Breeding and Genetics, SLU, Box 7023, 750007 Uppsala, Sweden; §Danish Agricultural Advisory Service, National Centre, Aarhus, Denmark; #Irish Cattle Breeding Federation, Highfield House, Bandon, Co. Cork, Ireland; ||Scottish Agricultural College, Pentland Building, Bush Estate, Penicuik EH26 0PH, Edinburgh, United Kingdom; and ¶Swedish Dairy Association, Box 10, 101 24 Stockholm, Sweden

ABSTRACT: Pedigree collected by the Interbeef service allowed genetic diversity to be assessed by using pedigree analyses for the European Charolais (CHA) and Limousin (LIM) cattle populations registered in national herdbooks in Denmark (DNK), France (FRA), Ireland (IRL), Sweden (SWE), and, solely for the LIM breed, the United Kingdom (UK). The CHA data set included 2,563,189 calves with weaning performance, of which 96.1% were recorded in FRA, 3.0% in SWE, 0.5% in IRL, and 0.4% in DNK. The LIM data set included 1,652,734 calves with weaning performance, of which 91.9% were recorded in FRA, 4.9% in UK, 1.8% in DNK, 0.9% SWE, and 0.5% in IRL. Pedigree files included 3,191,132 CHA and 2,409,659 LIM animals. Gene flows were rather limited between populations, except from FRA toward other countries. Pedigree completeness was good in all subpopulations for both breeds and allowed the pedigree to be traced back to the French population. A relatively high level of genetic diversity was assessed in each CHA and LIM subpopulation by estimating either effective population sizes ($N_e > 244$ and $N_e > 345$ in the CHA and LIM subpopulations, respectively), relationship coefficients within

subpopulations (<1.3% in both breeds), or probability of gene origins. However, in each subpopulation, it was shown that founders and also ancestors had unbalanced genetic contributions, leading to a moderate but continuous reduction in genetic diversity. Analyses between populations suggested that all European CHA and LIM populations were differentiated very little. The Swedish CHA population was assessed as genetically more distant from the other CHA populations because of fewer gene flows from other countries and because of the use of North American sires to introgress the polled phenotype. In each European subpopulation, most of the main ancestors, which explained 50% of gene origin, were born in FRA. However, those main ancestors were different between countries. Moreover, in both breeds, the main ancestors, which explained 50% of the gene origin in DNK, IRL, SWE, and UK for the LIM breed, were found to be infrequently used in FRA. Those results were consistent with the low relationship coefficients estimated between subpopulations (<0.6% in both the CHA and LIM breeds). Therefore, in both breeds, each subpopulation may constitute a reservoir of genetic diversity for the other ones.

Key words: beef cattle, founder, genetic distance, genetic diversity, pedigree analysis, subdivided population

©2011 American Society of Animal Science. All rights reserved.

J. Anim. Sci. 2011. 89:1719–1730
doi:10.2527/jas.2010-3469

INTRODUCTION

The Charolais (CHA) and Limousin (LIM) populations are the 2 main beef cattle breeds in France (FRA). Owing to their high growth and muscularity performance, those breeds have been used worldwide for beef production in pure or cross-breeding systems. Since the

1960s, French breeding animals have been steadily exported abroad to establish local purebred populations able to provide bulls to commercial herds (Bouglér et al., 1973; Blackburn and Gollin, 2009). The different national CHA and LIM subpopulations are bred according to different selection practices or objectives and are connected by limited gene flows. They therefore constitute metapopulations. As a result of genetic drift or different selection, such subpopulations become genetically differentiated over time. This differentiation is nevertheless counterbalanced by gene flows between

¹Corresponding author: alban.bouquet@gmail.com
Received August 29, 2010.
Accepted January 6, 2011.

populations (Wang and Caballero, 1999). To date, 2 pedigree analyses of CHA and LIM populations have been carried out at the national level to assess within-population diversity in Ireland (**IRL**; Mc Parland et al., 2007) and FRA (Bouquet et al., 2009). Both studies revealed a moderate decline in genetic diversity within national populations. However, it is possible that the subdivision could help to maintain genetic diversity in the global population.

In 2007, the Interbeef project was launched to develop international genetic evaluations of CHA and LIM cattle. For the European countries taking part in this project, the aim was to enlarge the choice of breeding animals to other foreign populations based on a common genetic evaluation (Venot et al., 2007). Pedigree and performance were therefore collected for CHA and LIM purebred animals from 4 different countries—Denmark (**DNK**), FRA, IRL, and Sweden (**SWE**)—and from the United Kingdom (**UK**) for the LIM breed. The aim of this article was to assess, for both breeds, the within- and between-population genetic diversity by taking advantage of the whole pedigree information collected among countries.

MATERIALS AND METHODS

Animal Care

Animal care and use committee approval was not necessary for this study because data were obtained from preexisting databases.

Data

Data were provided by 5 national organizations via the Interbeef service. Pedigree and performance data were extracted from the international database, which is used for beef cattle international genetic evaluations. They were available only from herds for which performance recording was carried out by each national breed association. In each country, recorded calves represent a small part of the entire national purebred population: 7% (A. Fogh, personal communication), 13% (Bouquet et al., 2009), and 33% (R. Evans, Irish Cattle Breeding

Federation, personal communication) in DNK, FRA, and IRL, respectively, for the CHA population and 8% (A. Fogh, personal communication), 14% (Bouquet et al., 2009), 20% (R. Evans, Irish Cattle Breeding Federation, personal communication), and 5% (K. Moore, personal communication) in DNK, FRA, IRL, and UK, respectively, for the LIM population. This information was not available in SWE (J.-Å. Eriksson, personal communication). Performance data sets included 2,563,189 CHA and 1,652,734 LIM age-adjusted weaning weights of purebred calves born between 1989 and 2008. The numbers of weaning weights recorded per birth country are presented in Table 1 for both breeds. Available information in the performance file also included herd and birth year of calves. Animal identification numbers were standardized according to rules described by Pabiou et al. (2007) so that each animal had a unique identification number. Pedigrees from all countries were then pooled together into a single file, eliminating redundant genealogies. After editing, the pedigree file included 3,191,132 CHA and 2,409,659 LIM animals, whose distribution per birth country is presented in Table 1 for both breeds. A detailed description of the data structure was given by Venot et al. (2009). Only important facts are mentioned here to facilitate the understanding of subsequent analyses. At first, the numbers of recorded animals in total and per herd differed markedly between countries, although their evolution was similar for both breeds within a country. In IRL, the CHA and LIM populations had a particular data structure, with a large increase in the number of animals recorded per year since 2006 because of an increase in the number of recorded herds. Furthermore, the number of calves recorded per herd was very low in this country because crossbred animals were discarded for international genetic evaluations and because recording of herds was not exhaustive. Nonexhaustive recording in IRL was also supported by a larger proportion of males among the recorded calves than in other countries (Table 1).

Both breeds were analyzed separately. A demographic analysis was first carried out to reveal differences in the genetic management of each breed between countries. Pedigree analyses were then used to study the current

Table 1. Number of genealogies and performances recorded in each European Charolais and Limousin population

Country	Charolais			Limousin		
	Genealogies, n	Performance		Genealogies, n	Performance	
		n	Proportion of males, %		n	Proportion of males, %
Denmark	15,956	10,897	52.7	270,153	30,559	51.0
France	3,060,296	2,462,902	49.9	1,985,829	1,519,011	49.1
Ireland	25,529	11,547	59.9	23,878	7,463	55.1
Sweden	89,351	77,843	50.0	19,126	14,897	49.1
United Kingdom	—	—	—	129,067	80,770	50.5
Total	3,191,132	2,563,189	50.0	2,409,659	1,652,734	49.2

polymorphic state for some neutral autosomal gene and its evolution over time. Pedigree analyses focused on inbreeding and relationship on one hand, and on probabilities of gene origin on the other hand. They were carried out with the software Pedig (Boichard, 2002).

Demographic Analyses

For each subpopulation, demographic analyses were carried out to characterize gene flows between countries and generation intervals (**GI**). For each subpopulation, incoming gene flows were estimated as the proportion of calves sired by bulls originating from each country of first registration. Generation intervals were computed as the average age of the parents at the birth of their offspring. They were calculated on the 4 gametic pathways, considering only useful offspring (i.e., offspring kept for breeding). The mean GI was obtained as the mean of GI estimated on each gametic pathway.

Pedigree Completeness Level

Pedigree knowledge was assessed by the number of complete generation equivalents (**CGE**), which summarizes the quantity of genealogical information known in a pedigree. For a given animal, it was calculated as the sum of proportions of known ancestors over all traced generations (Boichard et al., 1997). The proportion of known ancestors per generation was also estimated to compare the depth of pedigree in each subpopulation.

Genetic Diversity Within Populations

Effective Population Size via Increase in Inbreeding. The rate of increase in inbreeding (ΔF) is widely used to evaluate the genetic diversity of a population. Indeed, an increase in inbreeding reduces the population heterozygosity and therefore allows the importance of random allele losses attributable to across-family selection and drift to be quantified (Falconer and Mackay, 1996). In this study, individual inbreeding coefficients (F_i) were calculated with the algorithm by Meuwissen and Luo (1992). The annual ΔF (ΔF_a) was estimated from F_i by regressing $\log(1 - F_i)$ on the birth year of calves, with the regression coefficient being equal to $\log(1 - \Delta F_a)$ (Perez-Enciso, 1995). This regression was carried out by considering all calves born between 1999 and 2008 and with at least 3 CGE in the pedigree. The parameter ΔF_a was then converted to an effective population size (N_e), which corresponds to the size of a virtual population that would undergo the same amount of genetic change via random union of gametes as the actual population (Wright, 1969). It was calculated with the formula $N_e = 1/(2GI \times \Delta F_a)$ (Falconer and Mackay, 1996).

Probabilities of Gene Origin. Investigations of the genetic structure of populations were also carried out by using statistics derived from probabilities of gene origin (Boichard et al., 1997) to assess how an

original gene pool has been maintained over generations. In this approach, founders are defined as ancestors without known parents and are not supposed to be inbred and related. The total number of founders (N_f) poorly reflects the original genetic diversity of a population because founders may be related and may have unbalanced genetic contributions to the current population. Therefore, genetic diversity within each population was assessed using 3 statistics: the effective numbers of founders (f_e), ancestors (f_a), and founder genomes (f_g). They were computed from the expected genetic contributions as described by Boichard et al. (1997). To limit calculation requirements, f_a was approximated by bounding using marginal genetic contributions of the first 10,000 main ancestors. The parameter f_g was estimated by a gene-dropping procedure (McCluer et al., 1986) using 1,000 Monte-Carlo simulation replicates for each population. Within a country, analyzing the ratios f_a/f_e and f_g/f_a and their relative evolution over time permitted detection of the occurrence and magnitude of bottlenecks and genetic drift in each population, respectively (Boichard et al., 1997). All analyses were carried out for calf populations with both known parents that were born during 3 successive time periods: 1994 to 1998, 1998 to 2003, and 2004 to 2008.

Genetic Diversity Between Subpopulations

Different indicators and measures were used to assess genetic diversity among European CHA and LIM populations using both relationship and probabilities of gene origin approaches.

Relationship Between Subpopulations and Wright's F -Statistics. The average relationship coefficient between 2 individuals was calculated as twice the coancestry coefficient defined by Malécot (1948). The average relationship coefficient (f_{ij}) between subpopulations i and j was estimated as the average of all pair-wise relationship coefficients between animals belonging to populations i and j . The degree of genetic differentiation between subpopulations was estimated using Wright's F -statistics (F_{ST} ; Wright, 1969). Supposing that genetic diversity can be defined as the heterozygosity expected under Hardy-Weinberg equilibrium, F_{ST} can be expressed as the ratio of expected heterozygosities between subpopulations (GD_B) and within the whole metapopulation ($GD_T = GD_B + GD_W$, where GD_W is the expected heterozygosity within a population):

$$F_{ST} = \frac{GD_B}{GD_T} = 1 - \frac{GD_W}{GD_T}$$

(Nei, 1977). In a model in which all founders are assumed to have 2 unique alleles at a neutral autosomal locus, the expected homozygosity of a population is equivalent to the mean coefficient of coancestry defined

by Malécot (1948). Therefore, according to Caballero and Toro (2002), $GD_T = 1 - \bar{f}$, $GD_W = 1 - \tilde{f}$, $GD_B = \bar{f} - \tilde{f}$, and $F_{ST} = \tilde{f} - \bar{f} / 1 - \bar{f}$, where \bar{f} and \tilde{f} are the average coancestry coefficients in the whole metapopulation and within subpopulations, respectively. The average coancestry coefficient in the metapopulation was calculated as

$$\bar{f} = \sum_{i=1}^n \sum_{j=1}^n \frac{1}{N_T^2} f_{ij}$$

and the average coancestry coefficient within subpopulations was calculated as

$$\tilde{f} = \sum_{i=1}^n \frac{1}{N_T} f_{ii}$$

where f_{ij} is the coancestry coefficient between individuals of subpopulations i and j , and N_T is the total number of animals in the metapopulation (Toro and Caballero, 2005).

To limit calculation requirements, only males born in 2008 in each subpopulation were considered in this study. As concerns the French CHA and LIM populations, the number of calves born in 2008 in the recorded population was too large to compute coancestry coefficients. Therefore, an average coancestry coefficient with other subpopulations was estimated from 5 samples of 2,000 calves born in seedstock breeder herds. A seedstock breeder herd was defined as a herd having sold at least 25 bulls to other herds with performance recording in the CHA breed and having sold at least 20 in the LIM breed (Bouquet et al., 2009). Male calves were sampled in nucleus herds because those herds were shown to be very influential in the genetic structure of the French CHA and LIM populations. Although these herds represent only 10% of herds with performance recording, they provide more than 70% of all natural service (NS) bulls used in the recorded population. They also provide approximately 65 and 95% of males entering the CHA and LIM breeding programs, respectively, of AI bulls (Bouquet et al., 2009). Thus, males born in nucleus herds were worth being analyzed because they were more likely to be exported abroad or to be used by AI in the whole metapopulation.

Genetic Similarity Between Populations from Gene-Dropping Analysis. To measure how close the different subpopulations were, a measure of genetic similarity between pairs of subpopulations was calculated by using the probabilities of gene origin. A pair of subpopulations was compared on the basis of differences in contributions of each 1 of the 2 N_f founder alleles they inherited. In this study, frequencies of each founder allele in calf populations with both known parents and born between 2004 and 2008 were estimated by gene dropping, as recommended by Sölkner et al.

(1998). Genetic similarity between subpopulations was assessed using the cosine similarity measure introduced by Bhattacharyya (1946). By representing 2 populations on the surface of a multidimensional hypersphere, Bhattacharyya (1946) measured the extent of differentiation between populations in terms of the angle θ between the 2 lines projecting from the origin to the 2 subpopulations on the hypersphere, whose coordinates are defined by the square root of frequencies of each founder allele (Nei, 1987). According to Bhattacharyya (1946), when there are 2 N_f alleles, a 2- N_f -dimensional hypersphere has to be considered and cosine θ is obtained with the formula

$$\cos \theta = \sum_{i=1}^{N_f} \sqrt{w_{Ai} w_{Bi}},$$

where w_{Ai} and w_{Bi} are allele frequencies of founder allele i in subpopulations A and B , respectively. This cosine can be considered a measure of genetic similarity between populations and takes a value between 0 and 1, with a value of 1 indicating perfect agreement in founder allele contributions. Genetic similarity within a subpopulation was also estimated by randomly splitting each population into 2 halves and measuring the genetic contributions of the founder alleles in those 2 halves, as described by Sölkner et al. (1998).

RESULTS AND DISCUSSION

Demographic Analyses: GI

Mean GI are presented in Table 2 for animals born in 2000. Generation intervals for the CHA and LIM populations are generally quite similar within a country. The greatest GI were found in IRL (>6.3) and the least were found in SWE (<5.1). Generation intervals found in both breeds were very consistent with those obtained by Mc Parland et al. (2007) in IRL and by Bouquet et al. (2009) in FRA. Thus, there are large variations in the renewal of breeding populations between countries, especially in the CHA metapopulation, which may affect the rate of reduction in genetic diversity.

Gene Flows Between Populations

In each subpopulation, gene flows were assessed by the calf proportion sired by bulls originating from each country of first registration (Figure 1). All the sires used in the French CHA and LIM herds were born in FRA, indicating that the French subpopulations were closed.

Since the early 1990s, gene flows between different recorded subpopulations have mostly been observed from FRA toward other countries (results not shown). In 2008, FRA still provided a large proportion of NS bulls or semen straws to the IRL CHA and LIM populations

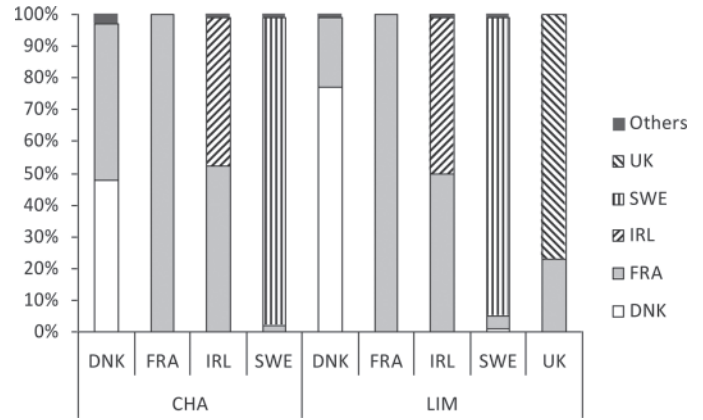
Table 2. Mean generation intervals (in years) estimated for animals born in 2000

Country	Charolais	Limousin
Denmark	5.5	5.4
France	5.7	6.1
Ireland	6.4	6.3
Sweden	4.6	5.1
United Kingdom	—	5.9

and the DNK CHA population. Exportations of French genetics were more moderate into the DNK and UK LIM populations and were negligible into SWE (Figure 1). Except for gene flows originating from FRA and some limited gene flows between DNK and SWE in the 1990s, bull and semen exchanges between European subpopulations were scarce, especially during the last decade. Cow and embryo flows between countries were much more limited than bull and semen flows (results not shown). Some bull flows were observed within recorded populations in DNK, SWE, and the UK. Such domestic gene flows were not detected in IRL from performance recording data. Those results are of primary importance for setting up an international genetic evaluation of beef cattle. Indeed, limited gene flows result in weak connectedness between European subpopulations, which may hamper the estimation accuracy of both genetic correlations between countries and breeding values (Venot et al., 2009).

Pedigree Knowledge

In the performance file, the percentage of calves with an unknown sire was low (<5%) in all countries and in all breeds (results not shown), except in DNK for the CHA breed (16.2% in 2008). Hence, the proportion of calves discarded for carrying out pedigree analyses was small. The rate of unknown paternal grandsires was uniformly low whatever the breed (<2% in 2008). However, the proportion of calves with both parents known but with an unknown maternal grandsire varied across countries (Table 3). In 2008, this proportion was the least in the UK and SWE, intermediate in DNK, and the greatest in FRA and IRL. In FRA and IRL, the greater rates of unknown maternal grandsires can be

**Figure 1.** Proportion of calves sired by bulls registered at birth in different subpopulations for each Charolais (CHA) and Limousin (LIM) recorded population born in 2008. UK = United Kingdom; SWE = Sweden; IRL = Ireland; FRA = France; DNK = Denmark.

explained by the rather large number of herds joining the performance recording system in the last few years. In those herds, parents of cows born before subscription to the performance recording are generally not recognized. Pedigree knowledge is then generally less on the maternal side than on the paternal side.

Complete generation equivalents are presented in Table 4 for calves born between 2004 and 2008 in each European subpopulation. Pedigree knowledge was good in all countries and was almost exhaustive in the first 3 generations for animals recorded in DNK, SWE, and the UK (results not shown). Whatever the breed, accounting for all European genealogies did not improve the pedigree knowledge of French calves because there were no gene importations in the FRA population. In other countries, taking into account French genealogies markedly improved pedigree knowledge, up to 2.8 and 1.7 CGE for the CHA and LIM breeds, respectively (results not shown). However, the improvement in pedigree knowledge was detected from the fourth generation in IRL and the fifth generation in SWE, DNK, and the UK, indicating that the French pedigree file mainly provided old genealogical information. Accounting for all European genealogies, pedigree knowledge became better for LIM animals born in DNK, SWE, and the UK than for those born in FRA. It should nevertheless be mentioned that pedigree knowledge is heterogeneous

Table 3. Percentage of calves born in 1989, 1998, and 2008 from unknown maternal grandsires but with both parents known in the Charolais and Limousin reference populations

Country	Charolais			Limousin		
	1989	1998	2008	1989	1998	2008
Denmark	11.0	6.3	7.9	3.3	1.7	5.2
France	12.2	17.5	11.1	13.7	18.0	10.7
Ireland	0.0	0.0	15.0	1.8	0.0	9.9
Sweden	1.8	0.7	1.8	1.3	3.2	0.6
United Kingdom	—	—	—	0.0	0.0	0.0

Table 4. Complete generation equivalents calculated for the reference population of calves born between 2004 and 2008

Country	Charolais	Limousin
Denmark	8.5	7.3
France	9.3	6.9
Ireland	9.1	6.5
Sweden	8.3	7.5
United Kingdom	—	7.5

in the French population: the pedigree knowledge of calves born in nucleus breeder herds is generally 1 CGE greater than the one in commercial herds (Bouquet et al., 2009). Pedigree knowledge in the DNK, SWE, and UK populations was therefore comparable with that in the French nucleus breeder herds.

Genetic Contribution of the French Populations

The genetic contribution of French founders to each European calf population born between 1989 and 2008 is presented in Figure 2. All founders of the FRA CHA and LIM calf populations were of French origin, confirming that French populations are closed. In the UK, the proportion of FRA LIM founders remained quite stable and high. In IRL, it remained stable and high until 2005 (about 90 to 95%) but declined by approximately 10% in 2005. The contribution of French founders to the DNK population increased from 61 to 85% and from 76 to 89% in the CHA and LIM breeds, respectively. Thus, in DNK, IRL, and the UK, a substantial part of the founder genes stemmed from FRA, and most of the non-French founders were born in their respective countries. This also highlights the good pedigree knowledge that allows genealogies to be traced back to the French population.

The situation was different in the SWE population, in which the proportion of French founders decreased from 80 to 38% and from 85 to 71% in the CHA and LIM reference populations born between 1989 and 2008, respectively (Figure 2). Similarly, the genetic contribution of DNK founders decreased from approximately 15% in the early 1990s to approximately 8 to 10% in 2008 in both breeds (results not shown). Inversely, the genetic contribution of North American founders has increased since the late 1990s (approximately 5 to 10%), reaching 49 and 15% in 2008 in the CHA and LIM breeds, respectively (results not shown). This is explained by the use of North American CHA and LIM breeding animals in breeding programs to introgress the polled gene (J.-Å. Eriksson, personal communication).

Another implication for establishing the international beef cattle genetic evaluation concerns the heterogeneity of founder origins among countries. Indeed, different founder origins suggest genetic heterogeneity among the founder population, which has to be accounted for

via genetic groups to avoid estimating potentially biased breeding values (Quaas, 1988).

Genetic Diversity Within Populations

Inbreeding and Effective Size of Populations.

Mean inbreeding coefficients are presented in Table 5 along with the rates of increase in inbreeding estimated between 1999 and 2008 and the effective sizes of each subpopulation. Although the proportion of inbred animals was high in each CHA and LIM subpopulation (>80%), inbreeding proportions estimated in the present study were low. However, it should be mentioned that inbreeding coefficients were estimated with the algorithm by Meuwissen and Luo (1992), which assumes that founders are not related. Although it may lead to underestimating inbreeding coefficients, ignoring average relationships between founders does not affect the estimated ΔF much (Lutaaya et al., 1999), which is regarded as a better criterion for assessing genetic diversity because it is less dependent on the pedigree completeness (Boichard et al., 1997). Inbreeding values estimated in this study for the IRL population were much greater than those found by Mc Parland et al. (2007) in both the CHA and LIM breeds (approximately 0.5%). This difference can be explained by the better pedigree knowledge in the present study than in the one by Mc Parland et al. (2007).

Rates of inbreeding estimated in the present study were small in both breeds and corresponded to large N_e (Table 5). The N_e of a population is not estimable when ΔF is close to 0 or negative. Therefore, N_e was not estimated for the SWE Charolais and the SWE

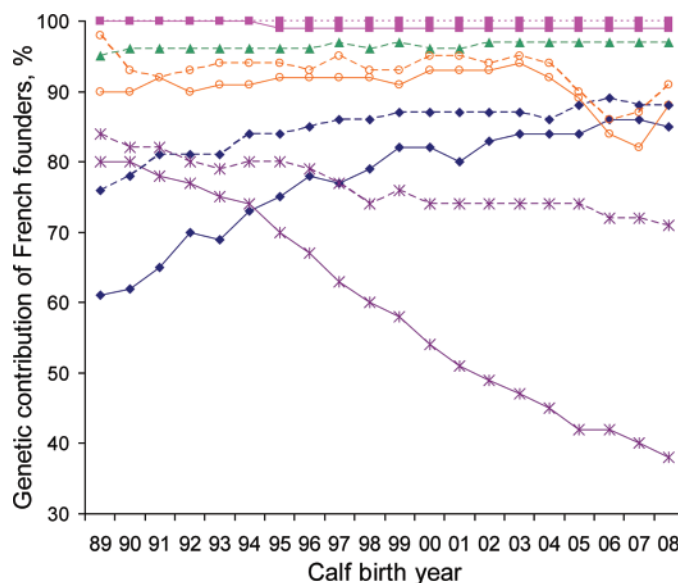


Figure 2. Genetic contribution of French founders in the pedigree of Charolais (solid line) and Limousin (dotted line) calf populations born in Denmark (♦), France (■), Ireland (○), Sweden (*), and the United Kingdom (▲) between 1989 (89) and 2008 (08). Color version available in the online PDF.

Table 5. Mean inbreeding coefficients (F) for calves born in 2008, annual rate of inbreeding (ΔF_a) over the last decade, and effective size (N_e) of each European sub-population

Breed	Country	F, %	ΔF_a , %	N_e
Charolais	Denmark	1.04	0.016	558
	France	0.67	0.018	493
	Ireland	0.99	0.032	244
	Sweden	0.92	0.000	—
Limousin	Denmark	1.02	0.006	1,667
	France	0.71	0.003	2,459
	Ireland	0.79	0.023	345
	Sweden	1.08	-0.022	—
	United Kingdom	1.13	-0.009	—

and UK Limousin populations (Table 5). The low rate of inbreeding estimated for the SWE CHA population could result from the recent use of polled bulls with North American origins, whose pedigree knowledge was less than for the other bulls used. This could also explain, to a certain extent, the flat inbreeding trend estimated in the SWE LIM population in the last decade. However, it should be mentioned that the inbreeding rate estimated in this population was erratic over time, which was probably related to its limited size. Finally, no clear evidence was found to explain the negative ΔF estimated in the UK LIM population. Actually, inbreeding increased at a steady rate (+0.04%/yr) between 1989 and 1999 and has been stagnating since 2001. This could result from the reduction in the AI rate observed from the late 1990s (results not shown).

Given the amount of pedigree knowledge in these populations for the first generations, the risk of overestimating N_e should be limited. Such large N_e estimates were also found by Márquez et al. (2010) in the American Red Angus population. However, effective sizes estimated in other studies concerning beef and dual-purpose cattle populations (Sölkner et al. 1998; Cleveland et al., 2005) and dairy cattle populations (Sørensen et al., 2005; Mattalia et al., 2006; Mc Parland et al., 2007) are generally less. For example, effective sizes of the 3 largest French dairy cattle populations, which are comparable in size and pedigree knowledge with the main French beef cattle populations, comprised between 34 and 61 (Mattalia et al., 2006). Differences in N_e estimated in the present study and in other studies are probably related to the large use of NS in those beef cattle populations.

According to FAO (1998), ΔF should be less than 1% per generation to avoid inbreeding depression. This corresponds to an effective size of 50 breeding stock for a population whose GI is equal to 5 yr. Therefore, indicators derived from the study of inbreeding show that the decay in genetic diversity is relatively slow in each of the CHA and LIM European subpopulations.

Effective sizes of the entire CHA and LIM metapopulations were not derived from ΔF estimated in metapopulations because mating cannot be supposed

to be random in a subdivided population (Wang and Caballero, 1999). The effects of subdivision were studied in the frame of theoretical models generally assuming simplistic hypothesis such as equal subpopulation sizes, migration rates between populations, and discrete generations (Wang and Caballero, 1999), which cannot hold in the case of beef cattle metapopulations. The main findings of these studies indicated that subdivision results in an increase in N_e when contributions from individuals within populations are balanced and populations contribute equally to the next generation. On the contrary, when the reproductive success of an animal varies considerably within and between subpopulations, subdivision provokes a decrease in the effective size of the metapopulation (Whitlock and Barton, 1997). As stressed by Toro and Caballero (2005), the subdivision of selected or conserved populations is more likely to result in a decrease than an increase in N_e because populations do not contribute equally to the next generations and the variance in family size is generally large, especially in beef cattle populations, because of the use of both NS and AI.

Genetic Contributions of Founders and Ancestors. Table 6 presents statistics concerning the probability of gene origin in each European CHA and LIM subpopulation of calves born between 2004 and 2008, respectively. In each population, the number of f_e is much less than the N_f , indicating that the genetic contributions of founders are unbalanced. However, in both breeds, f_e and f_a remained large, especially in comparison with dairy cattle populations. For example, the f_a parameter for the 3 largest French dairy cattle populations comprised between 20 and 25 (Mattalia et al., 2006).

Studying the ratio f_a/f_e allows evaluation of the extent to which the genetic variability available in the founder population has been reduced because of bottlenecks (Boichard et al., 1997). In both breeds, the ratio f_a/f_e has been decreasing since the early 1990s, indicating that bottlenecks have occurred in the last 2 decades (results not shown). In the CHA metapopulation, the ratio f_a/f_e for calves born between 2004 and 2008 was the largest in FRA (39%) and was relatively small in the

Table 6. Statistics derived from probabilities of gene origin estimated in the Charolais and Limousin breeds for reference calf populations born between 2004 and 2008

Breed	Country	Reference population	Number of founders	f_e^1	f_a^2	f_g^3	C_{\max}^4	C_{10}^5	N50 ⁶
Charolais	Denmark	898	4,401	512	107	53	3.2	23	39
	France	369,353	85,200	547	212	95	2.6	16	101
	Ireland	2,165	6,357	475	75	43	5.9	30	30
	Sweden	9,143	4,663	371	99	53	3.2	23	35
Limousin	Denmark	3,360	2,495	310	92	48	4.5	25	37
	France	217,606	43,064	468	156	89	3.4	20	81
	Ireland	1,745	3,261	395	110	60	5.8	23	41
	Sweden	2,213	1,520	274	77	39	3.9	27	28
	United Kingdom	13,237	4,098	232	86	48	6.5	26	45

¹Effective number of founders.

²Effective number of ancestors.

³Effective number of founder genomes.

⁴Maximal marginal genetic contribution (%).

⁵Marginal genetic contribution cumulated for the 10 major ancestors (%).

⁶Number of ancestors explaining 50% of the gene origins.

other 3 subpopulations (20, 18, and 27% for the DNK, IRL, and SWE populations, respectively). The loss of genetic variability attributable to bottlenecks is therefore the largest for those latter populations. However, the rate of decrease in f_a/f_e over the last decade was larger for the FRA subpopulation (14%) than for other European subpopulations (<9%; results not shown). This indicates that recent bottlenecks had larger effects in FRA. In the LIM metapopulation, the ratio f_a/f_e is relatively homogeneous between European subpopulations and comprises between 28% (IRL) and 37% (UK) of the subpopulations. The evolution of this ratio is also similar between subpopulations, with a decrease of 12 to 13% between calf populations born between 1994 to 1998 and 2004 to 2008.

The consequences of bottlenecks are illustrated in Table 6 by the marginal contributions of the main ancestor and the first 10 ancestors (C_{10}) in each population. Both variables have been increasing during the last decade. The contributions of the first 10 ancestors ranged between 16 and 30% and between 20 and 27% among the CHA and LIM subpopulations, respectively. At the same time, the number of main ancestors explaining 50% of the gene origin has been diminishing in the last decade. However, as a comparison point, the number of main ancestors explaining 50% of the gene origin was less than 10 in the 3 largest French dairy cattle populations (Mattalia et al., 2006). Few main ancestors diffused in several different countries. This generally concerned popular French AI bulls or very old French base founders, which diffused a large amount via their offspring and grandoffspring. However, a substantial proportion of main ancestors contributing to the DNK, IRL, and UK populations were born in FRA. They were generally French bulls exported to be used in breeder herds or by AI. For example, in IRL, 29 and 35 out of the respectively 30 and 40 CHA and LIM ancestors explaining 50% of gene origins were born in FRA (results not shown).

Studying the f_g/f_a ratio allows evaluation of the effects of genetic drift not related to bottlenecks, but only to the random sampling of alleles in a population of finite size. Smaller values indicate a larger loss of genetic variability because of genetic drift. The evolution of the f_g/f_a ratio for reference calf populations born between 1999 to 2003 and 2004 to 2008 is different according to the country. As expected, this ratio remained constant in the largest populations: the FRA and SWE subpopulations in the CHA breed and the FRA and UK subpopulations in the LIM breed. Although the IRL CHA and LIM populations were of small size, the f_g/f_a ratio remained stable. As stated by Mc Parland et al. (2007), this result can be explained by the relatively large importations of bulls and semen from FRA, which allowed a certain level of genetic diversity to be maintained. Finally, the effects of genetic drift appeared to be stronger in the DNK CHA and LIM populations and in the SWE LIM population because they are either of small size (DNK CHA population) or they import few genetics from foreign populations, using mostly bulls bred in their own respective countries.

Thus, those results derived from probabilities of gene origin indicate that the genetic diversity within each subpopulation is still relatively large, especially compared with dairy cattle populations. However, it follows a slightly declining trend, as already suggested by the analysis of inbreeding trends. In FRA, bottlenecks became larger because of the increasing use of AI in the 1990s and a more intensive selection of AI bulls across families, especially in the CHA breed (Bouquet et al., 2009). To better control rates of inbreeding in future generations, it would then be advisable to balance the genetic contributions of sires used to procreate the cohorts of males recruited for the breeding programs of AI bulls. This could be achieved by following recommendations from optimal contribution selection (Meuwissen, 1997).

Table 7. Relationship coefficients (in %) within (on diagonal) and between populations (above diagonal) along with Wright's F_{ST} (Wright, 1969) between pairs of populations (below diagonal) of Charolais and Limousin male calves born in 2008

Breed	Country	Denmark	France	Ireland	Sweden	United Kingdom
Charolais	Denmark	1.1	0.5	0.5	0.1	—
	France	0.13	0.7	0.6	0.1	—
	Ireland	0.12	0.10	1.3	0.1	—
	Sweden	0.25	0.20	0.28	1.1	—
Limousin	Denmark	1.1	0.5	0.5	0.4	0.3
	France	0.10	0.7	0.6	0.3	0.5
	Ireland	0.13	0.05	0.9	0.2	0.5
	Sweden	0.20	0.08	0.23	1.3	0.2
	United Kingdom	0.19	0.09	0.11	0.24	1.0

Analysis of Genetic Diversity Between Populations

Kinship Between Subpopulations. The average relationship coefficients estimated within and between each male calf population born in 2008 are presented in Table 7 for both breeds. As expected, kinship was always greater within than between subpopulations. The mean relationship coefficient within a subpopulation was the least in the French CHA and LIM breeder populations (0.7%). Because all males recorded at weaning were accounted for in the analysis, discarding females should not bias relationship coefficient estimates. However, in both breeds, it should be noted that AI use was slightly less in French nucleus herds than in the rest of the recorded population (Bouquet et al., 2009). This could have led to a small underestimation of within-subpopulation relationship coefficients. Genetic relationships within subpopulations were low in each country (<1.3%) as well as between countries (<0.6%). As expected, the relationship between the SWE CHA population and other European CHA populations was the least. This was due to the negligible importations of foreign genetics from other European countries and to the use in breeding programs of North American sires, which are poorly related to the European population. This low kinship was first due to the insufficient pedigree knowledge to trace back to a common ancestry. Indeed, according to Bougler et al. (1973), most of the CHA cattle in North America stemmed from a few breeding stock imported from FRA via Mexico in the late 1930s. However, owing to sanitation rules preventing the importation of animals or semen from FRA until the mid-1960s (Bougler et al., 1973), North American CHA breeders decided to expand the breed by a 5-generation breeding-up program to meet the demand in CHA breeding stock by considering animals with at least 31/32 CHA blood as purebred. Through this breeding-up program, in which other polled breeds were used, polled CHA emerged. Thus, the North American as well as the SWE CHA populations may be genetically different from full French purebred CHA cattle because of the initial founder effect, genetic drift, and the admixture with other breeds. Because of the

recurrent use of purebred sires in North American CHA populations during the last decades, the influence of other breeds should be limited in genetic diversity when estimated at the genome level. However, because of selection for the polled phenotype, chromosomal segments around genes involved in the polled phenotype might still originate from other breeds.

Measures of Genetic Differentiation Between Subpopulations. To gain deeper insight into the effect of subdivision on the genetic differentiation of populations, Wright's F_{ST} (Wright, 1969) was estimated within each metapopulation and between pairs of subpopulations. Estimates of F_{ST} for the entire CHA and LIM metapopulations were equal to 0.27 and 0.24%, respectively. Table 7 presents F_{ST} estimates between pairs of countries. In each breed, the genetic differentiation is the greatest between the SWE population and other European subpopulations, which is consistent with previous results. However, F_{ST} estimates were low, which indicated that subpopulations within each breed are differentiated very little, mainly because coancestry coefficients within subpopulations estimated from pedigree are very low and not far from coancestry coefficients estimated in the whole metapopulation.

As highlighted by Excoffier (2007), the convenient definition of F_{ST} given by Nei (1977) as functions of expected and observed heterozygosities within or among populations hides the fact that subpopulation contributions to the total diversity should have to be given weights. In the calculation of \bar{f} and \tilde{f} , Caballero and Toro (2002) initially proposed to weigh coancestry coefficients within and between populations proportionally to their contribution to the metapopulation size. This assumption led us to assess no genetic differentiation between groups in the case of populations of unbalanced size (results not shown). Because within-subpopulation analyses showed that genetic diversity was not proportional to the population size, \bar{f} and \tilde{f} were estimated by assigning an equal weight to each subpopulation, as described by Toro and Caballero (2005).

Another question asked by Toro and Caballero (2005) concerns assigning weights to within vs. between diver-

sity when assessing the diversity of a metapopulation. This topic has been largely debated by conservation geneticists, but a consensus has not yet been reached. In this study, equal weight was given to within- and between-population diversity, as described by Caballero and Toro (2002). Indeed, giving equal weights to within and between diversity seems to be a reasonable compromise between an overemphasis on between-population diversity, which may result in ignoring most of the global diversity, and an overemphasis on within-population diversity, which may favor the largest population (Toro and Caballero, 2005). Other approaches published in the literature have proposed very different weights to within and between diversity in conservation purposes: Weitzman's diversity function ignored genetic diversity within populations (Thaon d'Arnoldi et al., 1998); Ollivier and Foulley (2005) proposed an aggregate diversity measure, with weights given to within and between diversity depending on the F_{ST} parameter; and finally, Piyasatian and Kinghorn (2003) gave 5 times more weight to between-population diversity on the basis of the speed of genetic change achieved by AI vs. NS across populations.

Measures of Genetic Similarity Between Subpopulations. Results concerning the cosine measure of genetic similarity between subpopulations are presented in Table 8 for the CHA and LIM breeds. A large cosine value means that the analyzed populations have inherited similar genetic contributions from an identical pool of founders. Genetic similarity within a subpopulation was found to be high, comprising between 0.89 and 1.00. The genetic similarity within IRL populations may be due to their small sizes and to sampling error, because only 1 replicate was carried out in this study. The similarity measures between the DNK, FRA, and IRL CHA populations comprised between 0.65 and 0.73 and indicated that those populations were deriving from a quite similar founder population. The Swedish CHA population was found to be more divergent from other populations. This was consistent with the low relationship coefficients estimated between SWE and other subpopulations and can easily be explained by the use of polled bulls from North America in the last 2 decades.

Similarity measures estimated between LIM populations were greater than those between CHA populations. Although within-population analyses showed that

the main ancestors were mostly different in each subpopulation, those results suggest that the DNK, FRA, IRL, and UK populations are relatively homogeneous, deriving from the same gene pool defined by a founder population, which has relatively similar contributions in each subpopulation. This is in good agreement with the large genetic contributions of French founders estimated into those 4 populations of recorded calves born between 2004 and 2008 (Figure 2). The SWE LIM population is more genetically distant from those latter 4 populations but is still not greatly differentiated, based on the analysis of founder genetic contributions.

Finally, it should be noted that those analyses of genetic differentiation are based on only a small fraction of European CHA and LIM populations. Although the purpose of this study was to study the genetic diversity of recorded animals subjected to genetic evaluation and likely to be selected in European CHA and LIM breeding programs, it should be kept in mind that those statistics could be different if a larger fraction of the populations was accounted for.

Pedigree vs. Molecular Information to Assess Genetic Diversity. All those pedigree-based measures of genetic differentiation are highly dependent on the assumption that each individual in the founder population has 2 unique alleles on each locus. Even if the pedigree provides considerable information on how allele frequencies evolve over generations relative to the base population, it does not allow the real heterozygosity level of a population to be stated. Therefore, taking advantage of molecular information could provide more insight into estimating genetic diversity within and between those beef cattle populations.

An extensive amount of literature has been developed around the estimation of genetic diversity from molecular markers, with applications in the management of natural, selected, and conserved populations. As reviewed by Toro and Caballero (2005) and Excoffier (2007), different methodologies were proposed to assess genetic diversity from genetic markers and also in the case of subdivided populations. However, it should be kept in mind that the amount of molecular information used to estimate accurate parameters must be relatively large (Eding and Meuwissen, 2001; Baumung and Sölkner, 2003; McKay et al., 2008). The availability of dense marker panels of biallelic markers is likely to offer new opportunities for the study of ge-

Table 8. Bhattacharya's genetic similarity measure (Bhattacharya, 1946) estimated for the Charolais and Limousin (Charolais/Limousin) metapopulation both within (on diagonal) and between subpopulations (off-diagonal terms)

Country	Denmark	France	Ireland	Sweden	United Kingdom
Denmark	0.95/0.98	0.88	0.83	0.74	0.82
France	0.65	0.94/1.00	0.96	0.65	0.93
Ireland	0.68	0.73	0.89/0.89	0.62	0.96
Sweden	0.32	0.35	0.34	0.95/0.99	0.60
United Kingdom	—	—	—	—	—/1.00

netic diversity (Meuwissen, 2009). Despite their limited informativeness, biallelic markers are powerful tools for analyzing the genome because of their high density and the low genotyping cost per marker, which should enable one to sample more individuals and therefore reduce estimation bias (Weir et al., 2006). Thus, the huge amount of information provided by dense marker panels should allow the estimation of more accurate genetic diversity parameters than the ones estimated from pedigree information. Furthermore, as stated by Meuwissen (2009), it should enable one to measure diversity per chromosome region instead of genome wide, which would make it possible to relate phenotypic differences between breeds or populations to certain divergent chromosomal regions.

To conclude, this study provides an overview of the genetic diversity of each European purebred CHA and LIM cattle metapopulation by using pedigree analyses. Because most of the founder genes come from the French population, the evolution of the genetic structure of each European population is mainly dependent on the offering of domestic AI bulls in each country and the importation of semen or breeding stock from FRA and from North America, in the case of SWE. Analyses within populations showed that genetic diversity was still large, although a decline was observed, mainly because of the occurrence of bottlenecks and eventually because of genetic drift in the smallest populations. In both breeds, pedigree analyses showed that coancestry coefficients between subpopulations were low, which emphasized the interest in an international genetic evaluation to enlarge the choice of bulls in each country to other foreign populations with different pedigrees. However, in both breeds, even if coancestry coefficients between populations were low, analyses of founder genetic contributions to different subpopulations showed that most European subpopulations were remotely deriving from a large unique founder population, with the exception of the SWE CHA population, in which North American sires were used to introgress the polled phenotype.

LITERATURE CITED

- Baumung, R., and J. Sölkner. 2003. Pedigree and marker requirements to monitor genetic variability. *Genet. Sel. Evol.* 35:369–383.
- Bhattacharyya, A. 1946. On a measure of divergence between two multinomial populations. *Sankhya* 7:401–406.
- Blackburn, H., and D. Gollin. 2009. Animal genetic resource trade flows: The utilization of newly imported breeds and the gene flow of imported animals in the United States of America. *Livest. Sci.* 120:240–247.
- Boichard, D. 2002. Pedig: A Fortran package for pedigree analysis suited to large populations. CD-ROM Communication 28-13, 7th World Congr. Genet. Appl. Livest. Prod. INRA and CIRAD, Montpellier, France.
- Boichard, D., L. Maignel, and E. Verrier. 1997. The value of using probabilities of gene origin to measure genetic variability in a population. *Genet. Sel. Evol.* 29:5–23.
- Bougler, J., B. Coudurier, J. M. Duplan, H. Hocde, H. Le Liboux, R. Tondu, and B. Vissac. 1973. La race Charolaise—Résultats étrangers. INRA, Jouy-en-Josas, France.
- Bouquet, A., G. Renand, and F. Phocas. 2009. Evolution of the genetic diversity of French beef cattle populations from 1979 to 2008. *INRA Prod. Anim.* 22:317–330.
- Caballero, A., and M. A. Toro. 2002. Analysis of genetic diversity for the management of conserved subdivided populations. *Conserv. Genet.* 3:289–299.
- Cleveland, M. A., H. D. Blackburn, R. M. Enns, and D. J. Garrick. 2005. Changes in inbreeding of US Herefords during the twentieth century. *J. Anim. Sci.* 83:992–1001.
- Eding, H., and T. H. E. Meuwissen. 2001. Marker-based estimates of between and within population kinships for the conservation of genetic diversity. *J. Anim. Breed. Genet.* 118:141–159.
- Excoffier, L. 2007. Analysis of population subdivision. Pages 980–1020 in *Handbook of Statistical Genetics*. 3rd ed. D. J. Balding, M. Bishop, and C. Cannings, ed. Wiley, Chichester, West Sussex, UK.
- Falconer, D. S. and T. F. C. Mackay. 1996. *Introduction to Quantitative Genetics*. 4th ed. Longman Editors, Essex, UK.
- FAO (Food and Agriculture Organization). 1998. *Secondary Guidelines for Development of National Farm Animal Genetic Resources Management Plans: Management of Small Populations at Risk*. FAO, Rome, Italy.
- Lutaaya, E., I. Misztal, K. Bertrand, and J. W. Makey. 1999. Inbreeding in populations with incomplete pedigree. *J. Anim. Breed. Genet.* 116:475–480.
- Malécot, G. 1948. *Les mathématiques de l'hérédité*. Masson, Paris, France.
- Márquez, G. C., S. E. Speidel, R. M. Enns, and D. J. Garrick. 2010. Genetic diversity and population structure of American Red Angus cattle. *J. Anim. Sci.* 88:59–68.
- Mattalia, S., A. Barbat, C. Danchin-Burge, M. Brochard, P. Le Mezec, S. Minery, G. Jansen, B. Van Doormaal, and E. Verrier. 2006. The genetic variability within the main eight dairy cattle breeds: What evolutions over time, what international comparisons? Pages 239–246 in *Proc. 13th Rencontres Recherche Ruminants*, Paris, France.
- McCluer, J. W., J. L. Van de Berg, B. Read, and O. A. Ryder. 1986. Pedigree analysis by computer simulation. *Zoo Biol.* 5:147–160.
- McKay, S. D., R. D. Schnabel, B. M. Murdoch, L. K. Matukumalli, J. Aerts, W. Coppieters, D. Crews, E. Dias Neto, C. A. Gill, C. Gao, H. Mannen, Z. Wang, C. P. V. Tassell, J. L. Williams, J. F. Taylor, and S. S. Moore. 2008. An assessment of population structure in eight breeds of cattle using a whole genome SNP panel. *BMC Genet.* 9:37.
- McParland, S., J. F. Kearney, M. Rath, and D. P. Berry. 2007. Inbreeding trends and pedigree analysis of Irish dairy and beef cattle populations. *J. Anim. Sci.* 85:322–331.
- Meuwissen, T. H. E. 1997. Maximizing the response of selection with a predefined rate of inbreeding. *J. Anim. Sci.* 75:934–940.
- Meuwissen, T. H. E. 2009. Towards a consensus on how to measure neutral genetic diversity? *J. Anim. Breed. Genet.* 126:333–334.
- Meuwissen, T. H. E., and Z. Luo. 1992. Computing inbreeding coefficients in large populations. *Genet. Sel. Evol.* 24:305–313.
- Nei, M. 1977. *F*-statistics and analysis of gene diversity in subdivided populations. *Ann. Hum. Genet.* 41:225–233.
- Nei, M. 1987. *Molecular Evolutionary Genetics*. Columbia Univ. Press, New York, NY.
- Ollivier, L., and J.-L. Foulley. 2005. Aggregate diversity: New approach combining within- and between-breed genetic diversity. *Livest. Prod. Sci.* 95:247–254.
- Pabiou, T., E. Venot, and J. Guerrier. 2007. Data exchange for international beef evaluations. *Interbull Bull.* 36:49–56.
- Perez-Enciso, M. 1995. Use of the uncertain relationship matrix to compute effective population size. *J. Anim. Breed. Genet.* 112:327–332.

- Piyasatian, N., and B. P. Kinghorn. 2003. Balancing genetic diversity, genetic gain and population viability in conservation programmes. *J. Anim. Breed. Genet.* 120:137–149.
- Quaas, R. L. 1988. Additive genetic model with groups and relationships. *J. Dairy Sci.* 71:1338–1345.
- Sölkner, J., L. Filipcic, and N. Hampshire. 1998. Genetic variability of populations and similarity of subpopulations in Austrian cattle breeds determined by analysis of pedigrees. *Anim. Sci.* 67:249–256.
- Sørensen, A. C., M. K. Sørensen, and P. Berg. 2005. Inbreeding in Danish dairy cattle breed. *J. Dairy Sci.* 88:1865–1872.
- Thaon d'Arnoldi, C., J.-L. Foulley, and L. Ollivier. 1998. An overview of the Weitzman approach to diversity. *Genet. Sel. Evol.* 30:149–161.
- Toro, M. A., and A. Caballero. 2005. Characterization and conservation of genetic diversity in subdivided populations. *Phil. Trans. R. Soc. B Biol. Sci.* 360:1367–1378.
- Venot, E., M. N. Fouilloux, F. Forabosco, A. Fogh, T. Pabiou, K. Moore, J.-Å. Eriksson, G. Renand, and D. Laloë. 2009. Beef without borders: Genetic parameters for Charolais and Limousine Interbeef genetic evaluation of weaning weights. *Interbull Bull.* 40:55–60.
- Venot, E., T. Pabiou, M.-N. Fouilloux, M. Coffey, D. Laloë, J. Guerrier, A. Cromie, L. Journaux, J. Flynn, and B. Whickham. 2007. Interbeef in practice: Example of a joint genetic evaluation between France, Ireland and United Kingdom for purebred Limousin weaning weights. *Interbull Bull.* 36:41–47.
- Wang, J., and A. Caballero. 1999. Developments in predicting the effective size of subdivided populations. *Heredity* 82:212–226.
- Weir, B. S., A. D. Anderson, and A. B. Hepler. 2006. Genetic relatedness analysis: Modern data and new challenges. *Nat. Rev. Genet.* 7:771–780.
- Whitlock, M. C., and N. H. Barton. 1997. The effective size of a subdivided population. *Genetics* 146:427–441.
- Wright, S. 1969. *Evolution and the Genetics of Populations: The Theory of Gene Frequencies*. Univ. Chicago Press, Chicago, IL.