

Inbreeding trends and pedigree analysis of Irish dairy and beef cattle populations

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ABSTRACT: The objective of this study was to determine the inbreeding levels and to analyze the pedigree of Irish purebred populations of Charolais, Limousin, Hereford, Angus, and Simmental beef cattle, as well as the Holstein-Friesian dairy breed. Pedigree analyses included quantifying the depth of known pedigree, average generation intervals, effective population size, the effective number of founders, ancestors, and founder genomes, as well as identifying the most influential animals within the current population of each breed. The annual rate of increase in inbreeding over the past decade was 0.13% ($P < 0.001$) in the Hereford, 0.06% ($P < 0.001$) in the Simmental, and 0.10% ($P < 0.001$) in the Holstein-Friesian breeds. Inbreeding in the other breeds remained relatively constant over the past decade. Herefords had the greatest mean inbreeding in 2004, at 2.19%, whereas Charolais had the lowest, at

0.54%. Over half of each purebred population in 2004 was inbred to some degree; the population with the greatest proportion of animals inbred was the Hereford breed (85%). All 6 breeds displayed a generation interval of approximately 6 yr in recent years. In the purebred females born in 2004, the 3 most influential animals contributed between 11% (Limousin) and 24% (Hereford) of the genes. Effective population size was estimated for the Hereford, Simmental, and Holstein-Friesian only, and was 64, 127, and 75, respectively. The effective number of founders varied from 55 (Simmental) to 357 (Charolais), whereas the effective number of ancestors varied from 35 (Simmental and Hereford) to 82 (Limousin). Thus, despite the majority of animals being inbred, the inbreeding level across breeds is low but rising at a slow rate in the Hereford, Simmental, and Holstein-Friesian.

Key words: beef cattle, dairy cattle, inbreeding, pedigree analysis

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INTRODUCTION

Inbreeding is defined as the probability that 2 alleles at any locus are identical by descent (Malécot, 1948) and occurs when related individuals are mated to each other. In recent years, selection intensity, a contributing factor to level of inbreeding (Weigel, 2001), has intensified in line with the progress in reproductive technologies, such as embryo transfer and in vitro fertilization, both of which result in the use of fewer parents to provide the next generation of breeding animals. The possibility of coselecting related animals is also enhanced through the statistical methods employed by animal breeders, such as BLUP animal models (Weigel, 2001).

The practice of inbreeding results in inbreeding depression, which is described as the decline in performance of inbred animals, particularly in the areas of reproduction (Wall et al., 2005) and health (Miglior et al., 1995). Inbreeding also impairs performance in growth, lactation, and survival (Weigel, 2001), thus reducing farm profitability (Weigel and Lin, 2002). Inbreeding depression was expressed as a reduction in postweaning gain of 240 g per percentage increase in inbreeding in the US Limousin population (Gengler et al., 1998) and as a reduction in peak milk yield of 0.06 to 0.12 kg per day per percent increase in inbreeding in US Holsteins (Cassell et al., 2003). Nevertheless, levels of inbreeding have not been examined, nor have thorough pedigree analyses been undertaken, in Irish beef and dairy cattle populations.

Therefore, the objective of this study was to determine levels of and trends in inbreeding and to ascertain the depth of pedigree known, average generation intervals, the effective number of founders, ancestors, and

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founder genomes, as well as the most influential animals within each of the 5 largest purebred populations of beef cattle and the largest dairy cattle population in Ireland.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from the existing Irish Cattle Breeding Federation database, Bandon, Co. Cork, Ireland.

Data Edits

Pedigree information on 8,803,155 Irish cattle was obtained from the Irish Cattle Breeding Federation database. Data on breed fraction, recorded in increments of 1/32, were available for most animals. Information on the 5 largest beef breeds, the Charolais, Limousin, Simmental, Hereford, and Angus, was extracted. Up to the mid 1980s the predominant breed of dairy cattle in Ireland was the British Friesian. Over the last 20 yr in the United Kingdom and Ireland, the use of North American Holstein Friesian genetics has dominated, increasing in sires used from 10% in 1977 to 80% in 1998 (Simm, 1998). Therefore, in the current study, no differentiation was made between British and North American genetics, although pedigree analyses of purebred Holstein and purebred Friesians were undertaken for comparative purposes. The methodology used is described herein for the Charolais population. However, identical procedures were used for the other beef and dairy breeds, unless otherwise stated.

Primarily animals with any proportion of Charolais and those with an unknown breed fraction were extracted from the main database. The base year was set to 1960 for each of the 5 beef populations because only a small number of recorded births were observed before 1960, and these animals were treated as unrelated founder animals. An earlier base year of 1950 was set for the dairy population because 1,509 Holstein-Friesian animals were born between 1950 and 1960. Founder animals (animals with unknown parents) were assumed to be unrelated and have an inbreeding coefficient of zero.

Year of birth for animals with no recorded birth year was estimated as the birth year of their earliest progeny less 2. This was iterated 10 times, leaving a much reduced number of animals missing birth years for each population.

Data Sets

Three separate data sets were created from the reordered pedigree file: 1) all animals with some proportion of the Charolais breed, 2) only purebred Charolais animals with a recorded or estimated birth year, and 3) all purebred Charolais animals. Purebred Charolais were defined as $\geq 28/32$ Charolais. Only 2 data sets were cre-

ated to analyze the Holstein-Friesian pedigree. Data set 1 included all crosses between the Holstein and Friesian breeds, including all 32/32 Holsteins and 32/32 Friesians. Data set 2 contained only those animals included in data set 1 with a recorded or estimated birth year. Furthermore, data sets were created including any purebred Holstein (i.e., $\geq 28/32$ Holstein; $n = 775,713$) or purebred Friesian (i.e., $\geq 28/32$ Friesian; $n = 329,557$) for comparative purposes.

Pedigree Analysis

The software package Pedig (Boichard, 2002) was used to analyze the pedigree of each of the cattle populations.

Pedigree Completeness. Depth of pedigree known (i.e., used in the current study after the base year was set) was calculated for all purebred populations using data set 3, composed of all purebred animals. Pedigree depth in the current study was measured in complete generation equivalents (CGE). A CGE refers to the degree of pedigree information for an animal. It was computed as $\sum_{i=1}^{n_j} \frac{1}{2^{g_{ij}}}$, where n_j = the number of ancestors of animal j , and g_{ij} is the number of generations between individual j and its ancestor i (Sørensen et al., 2005).

Inbreeding Coefficients. Data set 1, including all animals with any proportion of the breed in question, was used to calculate inbreeding coefficients (**F**) using the Meuwissen and Luo (1992) algorithm. After the calculation of the inbreeding coefficients for all animals, the annual mean inbreeding of only the purebred animals was extracted. The annual rate of inbreeding was estimated by fitting a linear regression using PROC REG (SAS Inst. Inc., Cary, NC) through the time period from 1994 to 2004. Animals were also classified according to their level of inbreeding and were assigned to 1 of 5 groups: $F = 0$; $0 < F \leq 6.25$; $6.25 < F \leq 12.5$; $12.5 < F \leq 25$; or $F > 25$. Furthermore, the level of inbreeding for inbred animals (i.e., animals with $F > 0$) by year of birth was determined.

Generation Intervals. Data set 2, consisting of only purebred animals with a recorded or estimated year of birth, was used to calculate generation intervals for each population separately. Generation intervals were calculated along the 4 selection pathways: sire to male offspring, sire to female offspring, dam to male offspring, and dam to female offspring. The average generation interval, weighted by the number of animals within each pathway, was subsequently calculated.

Effective Population Size. The effective population size (N_e) is defined as the number of breeding animals that would lead to the actual increase in inbreeding if they contributed equally to the next generation (Wright, 1923). It was calculated for purebred animals only as $N_e = \frac{1}{2\Delta F_y \times L}$, where ΔF_y is the annual rate of inbreeding in the population, and L is the generation interval (Hill, 1972).

Table 1. The number of Charolais (CH), Limousin (LM), Simmental (SM), Hereford (HE), Angus (AA), and Holstein-Friesian cross (HOXFR) animals included in each data set for analysis

Data set ¹	CH	LM	SM	HE	AA	HOXFR
1	1,037,308	883,470	550,591	862,343	1,105,168	2,653,390
2	149,326	83,204	63,023	47,753	39,742	1,076,350
3	149,772	83,478	63,363	48,081	40,451	—

¹Data set 1 = all animals with any proportion of the breed in question; data set 2 = only purebred animals with a recorded or estimated birth year; and data set 3 = all purebred animals (purebred = $\geq 28/32$).

Marginal Genetic Contribution. The marginal contribution of the top 1,000 ancestors within each breed to the reference population of females born in 2004 was calculated. The marginal contribution of an individual quantifies its contribution to the reference population, which has not previously been explained by greater contributing individuals.

Effective Number of Founders, Ancestors, and Founder Genomes. Founder animals were defined for the purpose of this study as those animals with unknown parents. The effective number of founders (Lacy, 1989) is the number of equally contributing founders that would be expected to produce identical genetic diversity to that observed in a reference population. The effective number of founders equals the actual number of founders if all founders contribute equally to the reference population; otherwise the former is smaller but increases as the contribution among founders is more balanced. Nonetheless, the effective number of founders does not account for bottlenecks in a pedigree. For this reason the effective number of ancestors (Boichard et al., 1997), which is the minimum number of ancestors (including founders and nonfounders) required to explain the genetic diversity of the reference population, was also calculated. Finally, the effective number of founder genomes (MacCluer et al., 1986; Lacy, 1989), which is the number of equally contributing founders with no random loss of founder alleles in the offspring that would be expected to produce a level of genetic diversity identical to that observed in the reference population, was calculated. Across all 3 analyses, the reference population consisted of females born in the year 2004.

RESULTS

The number of purebred Charolais, Limousin, Simmental, Hereford, and Angus animals included in the analyses are summarized in Table 1. The number of purebred animals born in 2004 for the Charolais, Limousin, Simmental, Hereford, and Angus was 14,620, 9,732, 3,739, 3,411, and 3,467, respectively. The number of Holstein-Friesian animals included in the analyses was 2,653,390, whereas the number of Holstein-Friesian animals born in 2004 was 233,386.

The mean number of progeny born to date, per purebred sire born between 1990 and 1995 was 31, 45, 27,

31, 28, and 134 for the Charolais, Limousin, Simmental, Hereford, Angus, and Holstein-Friesian, respectively. The numbers of sires used during this period were 1,424, 638, 559, 487, 530, and 5,770, respectively.

Complete generation equivalents by year of birth are illustrated in Figure 1 for the 6 breeds. All breeds followed the same trend of pedigree completeness, increasing over time; however, the absolute levels varied. In 2004, Herefords had the deepest pedigree with a CGE of greater than 6. Simmentals had the shallowest pedigree of all the beef breeds with pedigree completeness less than 4 CGE. Of the purebred Herefords born in 2004, 84% had full information on 4 generations; however, only 3.5% of Simmentals had this degree of pedigree information. The Holstein-Friesian had information on 5 CGE in 2004, yet only 48% of animals had full information on their dam and sire.

Mean annual inbreeding by year of birth is shown in Figure 2 for purebred beef animals and Holstein-Friesians born between 1975 and 2004. The Hereford breed had the greatest recorded level at 2.19% in 2004, rising consistently at 0.13% ($P < 0.001$) per annum between 1994 and 2004. The Holstein-Friesian breed had an average inbreeding coefficient of 1.49% in 2004, also increasing by 0.10% ($P < 0.001$) per annum. The level of inbreeding in the Holstein-Friesian in 2004 is lower than that of the purebred Holstein (2.15%) and Friesian (1.61%) populations in 2004. Inbreeding level within the Simmental population has also been rising, with an annual increase of 0.06% ($P < 0.001$) between the years 1994 and 2004, reaching an inbreeding level of 1.35% in 2004. Level of inbreeding in the Angus population was 1.31% in 2004 and decreased at a rate of -0.02% ($P < 0.05$) between the years 1994 and 2004. Inbreeding level in the Limousin and Charolais populations was 0.57 and 0.54% in 2004, respectively, and has remained relatively stable over the past decade.

Figure 3 shows the proportion of inbred animals in each of the 6 populations. The proportion inbred rose consistently throughout the 1980s and 1990s but started to plateau in 2000 for all breeds with the exception of the Charolais and Simmental. Over 50% of animals born in 2004 across breeds were inbred; the breed with the greatest proportion of inbred animals born in 2004 was the Hereford with over 85% inbred. The average level of inbreeding of inbred animals born in 2004 was 0.91, 1.08, 2.21, 2.56, and 1.91% for the Charo-

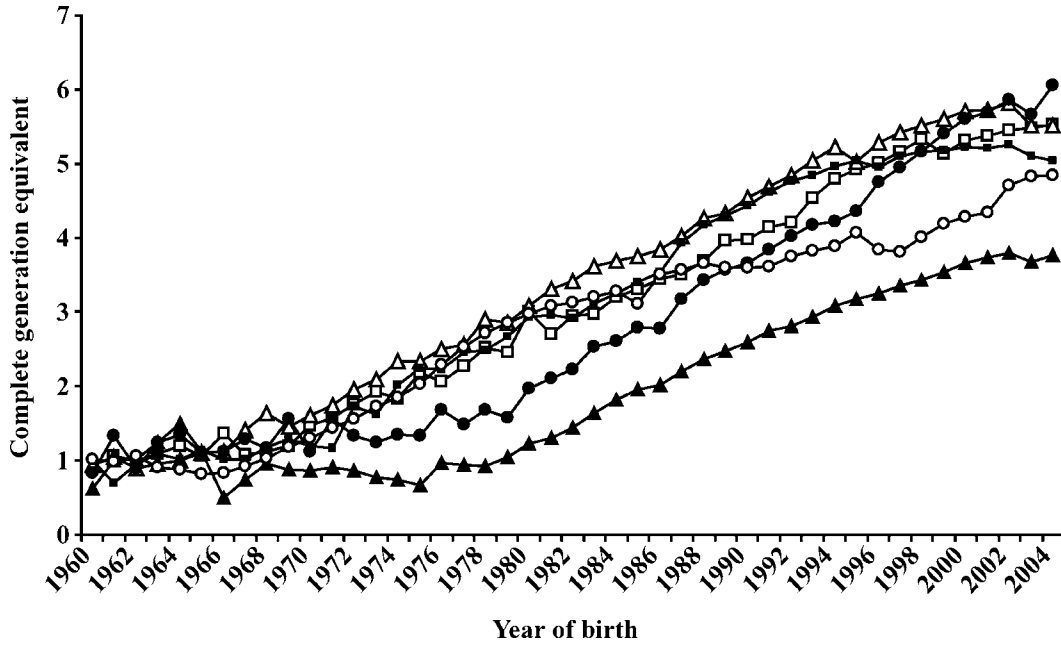


Figure 1. Level of pedigree completeness for the Charolais (-△-), Limousin (-■-), Hereford (-●-), Angus (-□-), Simmental (-▲-), and Holstein-Friesian (-○-) breeds across year of birth.

lais, Limousin, Simmental, Hereford, and Angus beef breeds, respectively. In the Holstein-Friesian, the level of inbreeding in inbred animals born in 2004 was 2.45%, whereas inbred purebred Holsteins and purebred Friesians had coefficients of 3.05 and 2.00%, respectively.

Table 2 shows the distribution of inbreeding coefficients within each population. The maximum inbreed-

ing coefficient for a single animal in 2004 was recorded in the Limousin breed at 37.69%. All breeds had animals with inbreeding coefficients of greater than 25%, whereas the proportion of animals with an inbreeding coefficient greater than 12.5% varied from 0.8% (Angus and Holstein-Friesian) to 2.3% (Hereford).

Generation intervals across the alternative selection pathways have generally been increasing over time,

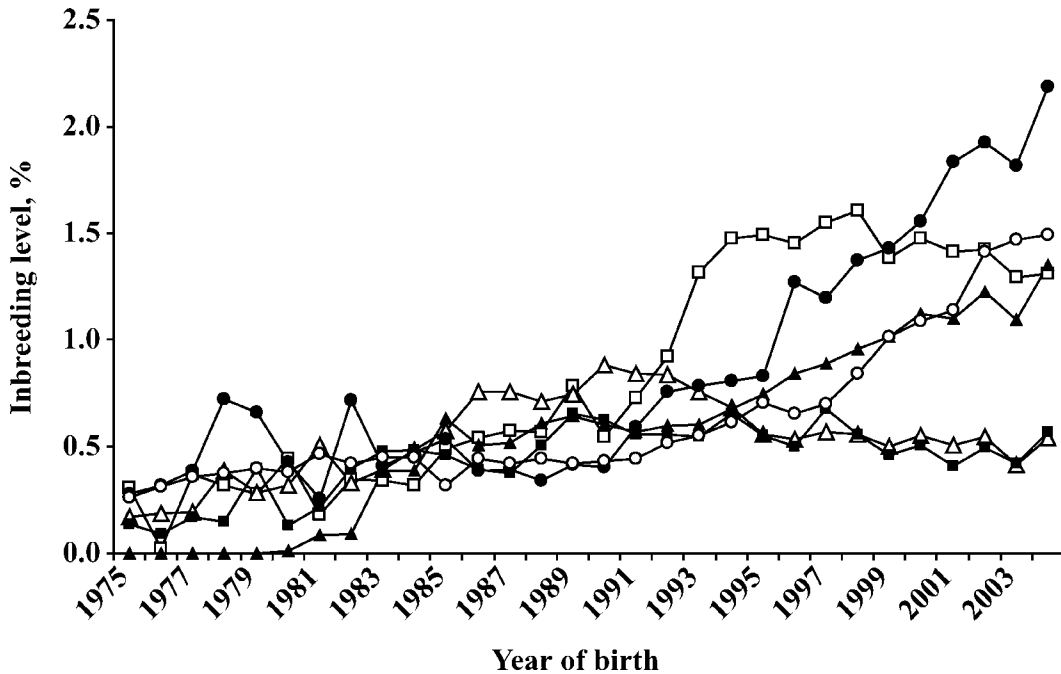


Figure 2. Trend in level of inbreeding for the Charolais (-△-), Limousin (-■-), Hereford (-●-), Angus (-□-), Simmental (-▲-), and Holstein-Friesian (-○-) breeds across year of birth.

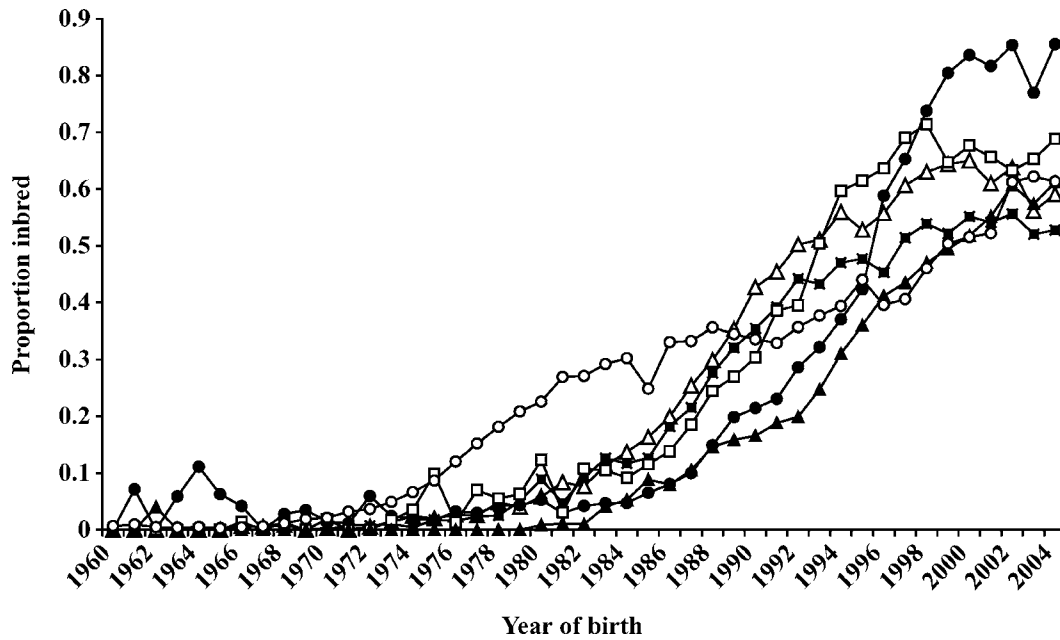


Figure 3. Proportion of the purebred populations of Charolais ($-\Delta-$), Limousin ($-\blacksquare-$), Hereford ($-\bullet-$), Angus ($-\square-$), Simmental ($-\blacktriangle-$), and Holstein-Friesian ($-\circ-$) that are inbred, across year of birth.

although at a declining rate. Generation intervals for the alternative pathways across the different breeds are summarized in Table 3 for progeny born in 2004. The average age of parents of progeny born in 2004 was 6.17, 6.71, 6.03, 6.09, 6.54, and 6.66 yr for Charolais, Limousin, Hereford, Angus, Simmental, and Holstein-Friesian, respectively. Based on the reported rate of increase in inbreeding and generation intervals, the effective population size for the Hereford, Simmental, and Holstein-Friesian breeds was calculated as 64, 127, and 75, respectively. As the effective population size is calculated using the rate of increase in inbreeding per generation, no effective population size could be estimated for the Charolais, Limousin, and Angus where negative inbreeding changes occurred.

The number of founders, as well as the effective number of founders, effective number of ancestors, and effective number of founder genomes, is detailed in Table 4 for all populations. The effective number of founders was lower than the actual number of founders in all cases. Large variation in the effective number of found-

ers was found across breeds, ranging from 55 (Simmental) to 357 (Charolais). The variation among breeds was reduced for the effective number of ancestors and the effective number of founder genomes across populations, with the exception of the Limousin, where both statistics were considerably larger than in other populations.

The cumulative marginal genetic contributions of the top 100 contributing ancestors to the females born in 2004 are shown in Figure 4. The cumulative marginal genetic contributions of the top 100 ancestors in the Simmental and Angus breeds accounted for 87% of the genes of purebred females born in 2004 for these 2 breeds, whereas it accounted for 81, 78, 77, and 72% of the genes of purebred females born in 2004 for the Hereford, Limousin, Charolais, and Holstein-Friesian populations, respectively.

The single greatest contributing animal to a purebred population was Standard Lad 93J, an Irish Hereford bull born in 1977, who contributed 11% of the genes of purebred female Herefords born in 2004. Over 92% of

Table 2. Percentage of purebred Charolais (CH), Limousin (LM), Hereford (HE), Angus (AA), Simmental (SM), and Holstein-Friesian cross (HOXFR) animals within different inbreeding levels¹

Inbreeding class, %	CH	LM	HE	AA	SM	HOXFR
0	44.5	48.5	14.6	32.6	38.7	40.0
0 < F ≤ 6.25	53.1	49.2	78.5	64.3	56.5	57.1
6.25 < F ≤ 12.50	1.3	1.1	4.6	2.3	3.4	2.1
12.50 < F ≤ 25.00	0.8	0.8	1.7	0.6	1.2	0.5
>25.00	0.3	0.4	0.6	0.2	0.2	0.3

¹Includes only animals born in 2004. F = inbreeding coefficient.

Table 3. Generation intervals across 4 selection pathways and the weighted average for populations of purebred Charolais (CH), Limousin (LM), Hereford (HE), Angus (AA), Simmental (SM), and Holstein-Friesian cross (HOXFR) animals¹

Pathway	CH	LM	HE	AA	SM	HOXFR
Dam to sons	5.75	5.73	6.03	5.52	5.95	3.99
Dam to daughters	5.64	5.70	5.83	5.44	5.74	3.97
Sire to sons	6.68	7.70	6.05	6.54	7.18	8.25
Sire to daughters	6.69	7.65	6.23	6.86	7.25	8.14
Weighted average	6.17	6.71	6.03	6.09	6.54	6.66

¹Data for animals in 2004.

the purebred Herefords born in 2004 were descendants of this single bull. Figure 5 shows the proportion of purebred Herefords, by year of birth, that were descendants of Standard Lad 93J, as well as the number of generations of descent from Standard Lad 93J (i.e., generation 1 are Standard Lad's direct descendants, generation 2 are his grand-progeny, etc.). In contrast to this, the greatest contributing animal to the purebred female Limousins born in 2004, Ferry, contributed only 4% of their genes (Figure 6).

DISCUSSION

Despite the numerous international studies on pedigree analysis of Holsteins (Miglior and Burnside, 1995; Maltecca et al., 2002; Kearney et al., 2004) and other dairy or dual purpose breeds (Miglior et al., 1992; Boichard et al., 1997; Sørensen et al., 2005), few published studies have analyzed the pedigree of beef populations (Boichard et al., 1997; Gutiérrez et al., 2003; Cleveland et al., 2005). To date no pedigree analysis of Irish cattle has been undertaken with the exception of 1 study documenting the inbreeding trend of the indigenous Kerry breed in Ireland (Olori and Wickham, 2004). Because beef is of major economic importance to Ireland (Central Statistics Office, 2006) and the Holstein-Friesian is the most prevalent dairy breed in Ireland (Irish Cattle Breeding Federation, 2005), a comprehensive knowledge of the pedigree of these breeds is valuable. Therefore, the objective of this study was to assess the levels and trends of inbreeding and to analyze the pedigree of the largest dairy and beef breed populations in Ireland. In summary, results from this study indicate that despite the majority of animals born in 2004 being in-

bred to some degree, the current level of inbreeding in the major cattle breeds in Ireland is low, although it is rising slowly in the Hereford, Simmental, and Holstein-Friesian.

The level of inbreeding within a breed is dependent upon the pedigree completeness of that breed (Lutaaya et al., 1999; Cassell et al., 2003). A large fraction of missing parents in a pedigree may cause serious underestimation of the inbreeding level and the associated losses arising from inbreeding (Lutaaya et al., 1999). In the current study, the level of pedigree completeness was much greater for the beef breeds than for the Holstein-Friesian, with the exception of the Simmental beef breed. Such differences existed because only purebred beef animals, which are predominantly born in pedigree herds that traditionally keep good records for animal registration purposes, were included in the analyses. On the other hand, the Holstein-Friesian animals included in the analysis were from pedigree and nonpedigree herds. In Ireland, compulsory recording of the dam of the animal was only introduced in Holstein-Friesians in 1996, while to date the farmer is currently under no legal obligation to record the sire; sire was recorded for 84% of all Holstein-Friesian animals born in 2004.

The degree of pedigree completeness was lower in the Irish Limousin population than in the French Limousin population, with only 43% of the Irish Limousins having information on 4 generations, compared with 73% in French Limousins (Boichard et al., 1997). Nonetheless, the level of pedigree completeness in the Irish breeds was considerably greater than in the Spanish breeds (Gutiérrez et al., 2003), where average complete generation equivalents ranged from 0.81 to 2.97.

Table 4. Number of founders, effective number of founders, effective number of ancestors, and effective number of founder genomes for populations of purebred Charolais (CH), Limousin (LM), Hereford (HE), Angus (AA), Simmental (SM), and Holstein-Friesian cross (HOXFR) animals

Item	CH	LM	SM	HE	AA	HOXFR
No. of founders	4,194	2,293	1,248	1,680	1,081	60,474
Effective No. of founders	357	316	55	150	160	112
Effective No. of ancestors	58	82	35	35	40	40
Effective No. of founder genomes	42	58	25	24	26	24

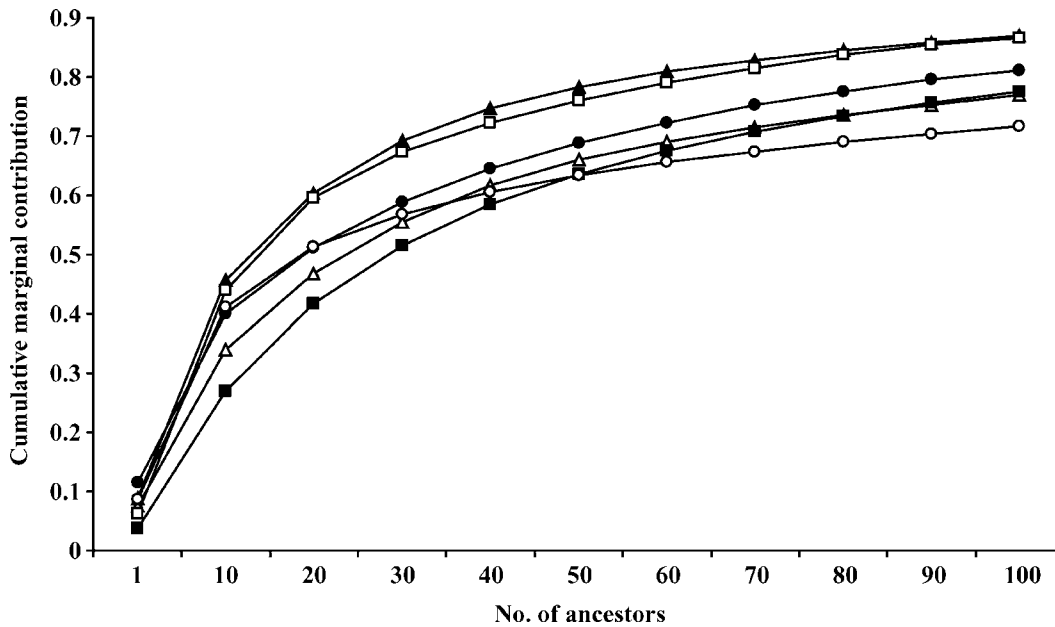


Figure 4. Cumulative marginal contribution for the purebred populations of Charolais (-△-), Limousin (-■-), Hereford (-●-), Angus (-□-), Simmental (-▲-), and Holstein-Friesian (-○-), up to 100 ancestors.

The shorter generation intervals of the dam-offspring pathways compared with the sire-offspring pathways across breeds in the current study is in contrast with reports in Asturian and Spanish beef cattle (Cañon et al., 1994; Gutiérrez et al., 2003), where dam-offspring generation intervals were longer. In recent years only slight differences in generation intervals between pathways were observed in the Irish Hereford breed, whereas the sire-offspring pathway was 2 yr greater

than the dam-offspring pathway in the Limousin. This indicates that proven sire semen is used longer in some beef breeds than in others. The sire-offspring generation interval was over 4 yr longer than the dam-offspring pathway in the Holstein-Friesian, suggesting a more extensive use of artificial insemination within the dairy industry than within the beef industry in Ireland. Generation intervals for the Irish purebred Holstein population were similar to those of populations of

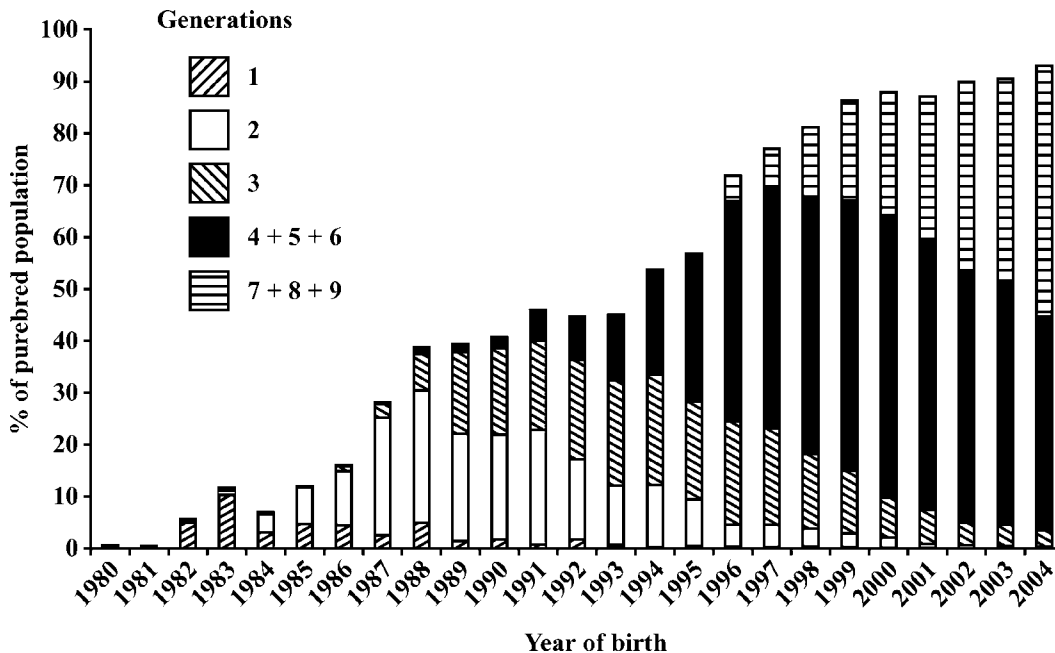


Figure 5. Descendants of Standard Lad 93J across 9 generations as a percentage of the purebred population of Herefords.

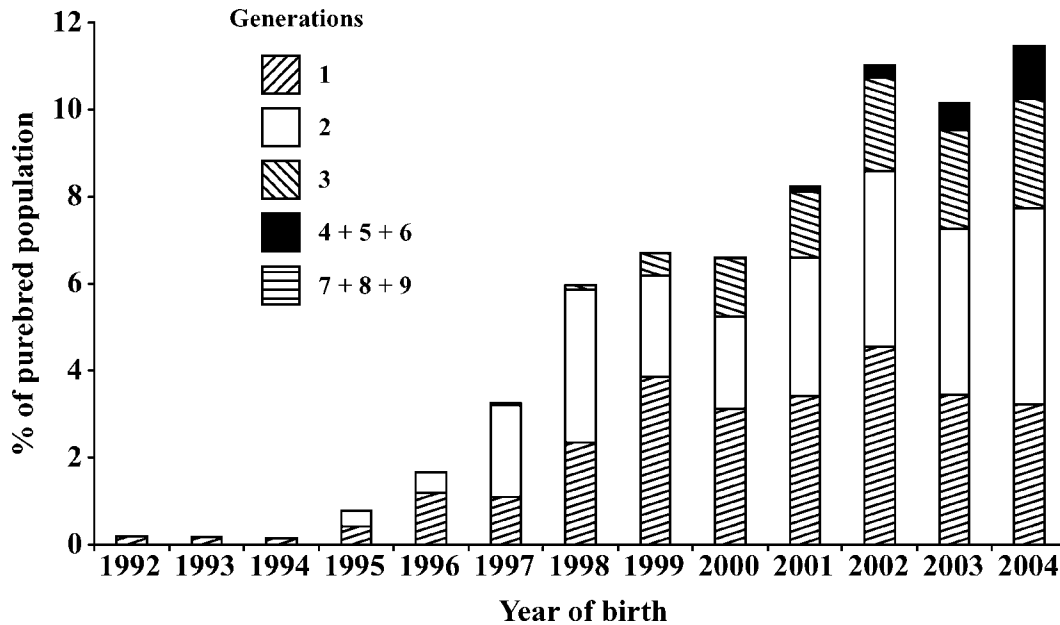


Figure 6. Descendants of Ferry across 5 generations as a percentage of the purebred population of Limousins.

French, German, Italian, and Dutch Holsteins, which all averaged 6 yr (Maltecca et al., 2002), longer than in Danish Holsteins (Sørensen et al., 2005), and shorter than in Japanese Black cattle (Nomura et al., 2001). The average generation interval of the beef cattle reported in the current study was similar to that of the Casina and Carreñana Asturianan beef breeds (Cañon et al., 1994) but greater than in US Herefords (Cleveland et al., 2005) and most Spanish beef breeds (Gutiérrez et al., 2003) with the exception of the Pirenaica.

The inbreeding coefficient for an individual is very sensitive to the quality of available pedigree information (Boichard et al., 1997); thus, absolute inbreeding levels provide less information for comparative purposes than the average rate of increase per generation. Additionally, level of inbreeding will depend on the base year defined (Young and Seykora, 1996), as well as the methodology used to estimate inbreeding coefficients (Van Doormaal et al., 2005). Nevertheless, the level of inbreeding across breeds represented in the current study was low. Reported inbreeding coefficients for the Limousin in the current study were lower than inbreeding levels reported in the US Limousin population (Gengler et al., 1998), whereas inbreeding levels for Hereford and Charolais in Ireland were greater than reported in Canada and America (Duangjinda et al., 2001). Level of inbreeding in Irish purebred Holsteins of 2.15% is slightly lower than that reported in UK Holsteins of >2.5% for animals born in 2002 (Kearney et al., 2004). Differences in the base year may have contributed to this greater level of inbreeding.

According to FAO guidelines, an increase in the rate of inbreeding of >1% (corresponding to an effective population size of 50) per generation should be avoided in order to maintain fitness in a breed (FAO, 1998). None

of the 6 breeds included in this study exceeded this level. The Hereford had the greatest rate of increase at 0.78% per generation. Based on the data provided by Olori and Wickham (2004) for the Kerry breed and assuming a generation interval similar to the other Irish beef breeds (i.e., 6 yr), the average increase in rate of inbreeding for the Kerry would be 1.68% per generation, exceeding the recommended maximum.

The annual increase in inbreeding of 0.12% for US Herefords born between 1990 and 2001 (Cleveland et al., 2005) was the same as the rate of increase observed in this study on Irish Herefords during the same time period, despite the much greater mean inbreeding level of 9.8% in the US population in 2001 (Cleveland et al., 2005). The discrepancy in the level of inbreeding is attributed to differences in the depth of the pedigree available between studies.

The downward trend in the level of inbreeding observed in the French Limousin population (−0.05% per annum; Boichard et al., 1997) is similar to, albeit steeper than, the decreasing trend in the Irish Limousin population (−0.01% per annum). The similarity in trends is largely attributed to the importation of French Limousin germplasm into Ireland, based on country of origin of animals recorded in the pedigree file. Up until 1994, almost 100% of recorded purebred Limousins in the Irish population were of French origin. However, the importation of French germplasm into Ireland is declining from year to year.

The parameters derived from the probabilities of gene origin, as described by Boichard et al. (1997), are useful tools in measuring genetic variability within breeds after a small number of generations, compared with inbreeding coefficients and effective population sizes, which are useful to monitor genetic variability over a

longer time period. Furthermore, probability of gene origin statistics is less sensitive to missing pedigree than estimated inbreeding coefficients. Although each statistic in Table 4 has its merit (Boichard et al., 1997), comparisons between ratios are also useful in identifying the previous existence of bottlenecks, as well as relative differences in degree of genetic drift, within the different populations. Therefore, whereas estimates of the effective population size are useful in predicting future changes in genetic variability, probability of gene origins are useful in identifying changes in the genetic variability after a recent change in the breeding program. The effective population size is an indication of the rate of loss of genetic diversity over a reference time period. The effective population sizes of the Hereford (64), Simmental (127), and Holstein-Friesian (75) breeds are above the recommended threshold, as well as being greater than reported effective population sizes in Danish dairy cattle breeds (47 to 53; Sørensen et al., 2005), US Holstein (39) and Jersey (30) cattle (Weigel, 2001), and Japanese Black cattle (Nomura et al., 2001). Nonetheless, the effective population size of the Hereford breed is approaching the minimum threshold, and thus, evasive action should be considered to maintain genetic diversity.

The number of founder animals for each population is proportional to the size of the purebred population for all breeds. This is the same as the pattern across 8 Spanish beef breeds (Gutiérrez et al., 2003). Despite the larger population size, the small effective number of founders relative to the other beef breeds suggests that the Holstein-Friesian population in Ireland was derived from a relatively smaller number of animals. This is consistent with reports from Weigel (2001) that, of the more than 5,000 Holstein young sires progeny tested annually around the world, approximately half are offspring of the 10 most popular sires.

Of the 3 breeds for which an effective population size was calculated, only the Simmental had an effective population size double its effective number of ancestors, suggesting minimum inbreeding in its population (Sørensen et al., 2005). The greater effective number of founders relative to the effective number of ancestors across all breeds indicates the presence of bottlenecks, the major cause of gene loss (Boichard et al., 1997), in the development of the Irish populations. The greater ratio of effective number of founders to the effective number of ancestors in the Irish Limousin population (4) as compared with the French Limousin population (2) indicates that there was a narrower bottleneck in the Irish population (Boichard et al., 1997). Bottlenecks were less important in determining the genetic stock of the Simmental breed but of greater importance in the Charolais breed. The development of a bottleneck in the Charolais breed most likely occurred in the 1980s as inbreeding levels increased. The ratio of the effective number of founder genomes to effective number of founders was lowest in the Charolais and greatest in the Simmental breeds, the difference being partly at-

tributed to the difference in pedigree depth between breeds. Nonetheless, it indicates that genetic drift was greater in the Simmental population, despite the relatively lower amount of historical pedigree information. However, most gene losses occur in the early generations after the predefined base year (Boichard et al., 1997).

The 2 largest breeds, the Holstein-Friesian and the Charolais, had a large cumulative marginal genetic contribution from the first 10 ancestors, similar to the other breeds in the study, but had the 2 lowest figures for the marginal contribution from their top 100 ancestors. This result is similar to that observed in Spanish beef breeds, where in the largest breeds, some ancestors accounted for a large proportion of the population, but the rest of the population was accounted for by many others (Gutiérrez et al., 2003).

The population with the greatest cumulative contribution from its top 3 ancestors was the Hereford. This was also the population with the greatest level of inbreeding in 2004. The 2 breeds with the lowest cumulative genetic contribution from the top 3 ancestors were the Limousin and the Charolais, which also recorded the lowest level of inbreeding. The results of the greatest and lowest contributing breeds are in stark contrast to one another because only 11.5% of the purebred Limousins born in 2004 were descendants of Ferry (the greatest contributor to the gene pool of Limousin females born in 2004), whereas nearly 93% of purebred Herefords born in 2004 were descendants of Standard Lad 93J (the greatest contributor to the gene pool of Hereford females born in 2004).

IMPLICATIONS

The lower level of inbreeding in the current study compared with international estimates is partly attributed to greater importation of germplasm into Ireland due to lack of a national breeding program. Ireland's beef sector is comprised mainly of crossbred cattle. Thus, the level of inbreeding on most commercial farms will, on average, be lower than in the purebred populations documented in this study. Nevertheless, the consistent rise in inbreeding level within the Hereford, Simmental, and Holstein-Friesian breeds, although within acceptable limits, may be reason for concern if inbreeding continues to intensify. A faster rate of increase in inbreeding levels is anticipated if selection for lowly heritable traits is pursued due to the increased emphasis on family information to identify genetically superior animals, although such broader selection indexes may also identify novel family lines. Future studies will attempt to quantify the effect of inbreeding depression on economically important traits in Ireland.

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