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Quantifying genetic contributions to a dairy cattle population using pedigree analysis

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Abstract

A variety of techniques were employed in the analysis of the change in genetic diversity of the UK Holstein–Friesian population over the last 30 years using the Holstein Friesian Society database (which has a base year of 1960). The parameters estimated were average inbreeding coefficient, average degree of relationship between cows, and two measures of genetic diversity, founder equivalent and founder ancestor number. The cow population was seen to change in founder origin from 96% British Friesian in 1967 to 24% British Friesian and 76% North American Holstein in 1997. The change in origin was seen to affect the rate of increase in inbreeding and to a lesser extent relationship, however the measures of genetic diversity were largely unaffected by the Holstein importation. In 1997 average relationship between cows had reached 1.34%, average inbreeding coefficient was 0.4% and the founder equivalent and founder ancestor number had converged at 93. The average inbreeding coefficient was seen to fall from 0.74% in 1982 to 0.38% in 1992 and to remain fairly constant up to 1997. The maternal structure of the cow population born in 1997 was also analysed. It was found that 93% of the cows were in maternal families of only one to four cows and only 0.5% of cows were in maternal families with more than 100 members, where a maternal family is a group of cows related only by maternal lineage. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Over the last 20 years there has been a rapid increase in the proportion of North American Holstein genes in the British black and white dairy cattle population. More recently genetics from European countries such as France and the Netherlands have been imported. However, these countries themselves have sourced most of their genetics from North America, so that we do not distinguish between North American and European genes in this study. This is not the first time that an importation has occurred in the UK dairy population. Robertson and Asker (1951) provided a brief history of the formation of the British Friesian herd tracing the effects that a variety of different importations had had. They document importations that occurred from Holland in the last century and the early part of this century and also a Canadian importation in 1946. The recent importation has certainly been the most significant

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due to the advances that have occurred in reproductive technology allowing a more rapid and widespread grading up of animals. Within this study the British Friesian population can be defined as those individuals registered with a British Friesian breed code in the database and foreign animals can be defined as other breed codes, those individuals being mostly of North American Holstein origin. The breed substitution has had an effect on the degree of relationship and level of inbreeding in the British dairy population, and the extent of this was investigated. Inbreeding trend has for many years been the preferred tool for the quantification of the rate of genetic drift but, as highlighted by Boichard et al. (1997), in order for the measure to be of relevance the population should conform to the rules specified by Wright (1931). It should be closed, unselected, panmictic and of finite size. It is quite obvious that the British dairy population does not satisfy these requirements. Boichard et al. (1997) proposed the use of measures of genetic variability more commonly used in conservation genetics. Lacy (1989) developed a 'founder equivalent' approach which combined the information of the founder animals contributing to the population under study and estimated the number of equally contributing ancestors that would provide the same level of genetic diversity. Caballero (personal communication) indicated that this parameter is directly related to group coancestry (Cockerham, 1967), the average pairwise coancestry of a group of individuals in a pedigree including reciprocals and self-coancestries. The parameter can also be related to genetic diversity defined as the expected frequency of heterozygotes by descent. This approach was taken further by Boichard et al. (1997) in the development of 'founder ancestor equivalent' which located the highest contributing ancestors to the population under study and used these animals to estimate the equivalent number of equally contributing ancestors that would provide the same level of genetic diversity. Bowman et al. (1978) studied the degree of relationship and average level of inbreeding in the British Friesian population. This current study is intended to update the information on the British dairy population and to investigate other properties of the dairy population by estimating parameters of genetic diversity.

2. Material and methods

2.1. Data

Data were extracted from the database of the Holstein Friesian Society of Great Britain and Ireland which has complete pedigree records, including grade-up animals, back to 1960. In this study grade-up animals are the progeny of non-pedigree cows that have been mated to pedigree bulls. This database also records the pedigree of all imported foreign cows and, if available, three generations of ancestors. In total the database holds about 5 million animals. Random samples, each of 2000 cows, were taken from cows born in specific years and the complete ancestry of these animals present in the database was traced. This pedigree file was then used for the various analyses. Ten samples were taken for 1997 births, which was essentially the year of interest. A further four samples per year were then taken going back in 5-year intervals including 1992, 1987, 1982, 1977, 1972, 1967. Five years was taken as being approximately the equivalent of a generation. The use of sampling rather than analysing the whole population was necessitated by a restriction on computing resources.

2.2. Founder equivalent

Founder animals were taken as being ancestors having unknown parents. If only one parent was unknown the animal was treated as a half founder and its contribution to the population under consideration was halved. The formula for the calculation of the founder equivalent (FE) parameter is:

$$\mathrm{FE} = 1 \bigg/ \sum_{k=1}^{f} q_k^2$$

where q is the proportional contribution of a founder k (total number of founders is f), to the generation for which FE is being calculated. If all founders had contributed equally to the population then the FE would equal the actual number of founders. This provides a measure of the change in genetic diversity of the population over time.

2.3. Founder ancestor number

The FE parameter does not properly account for bottlenecks in the pedigree caused by the heavy use of AI in cattle populations. If a recent sire made a high contribution to the current population through AI then it would be more important, in respect to the loss of genetic diversity, than tracing all of the pathways that founder ancestors in the pedigree made through this individual. In order to account for this Boichard et al. (1997) proposed a second measure, founder ancestor number (FA), which treats all the ancestors in the same way regardless of whether they are founders. The highest contributing ancestor, termed a 'pseudo-founder' was identified, its contribution stored, and then it was removed from the pedigree so that no further contribution could be made through its pathway in the pedigree. The procedure was iterated, finding the highest marginal contribution at each cycle. At each round of iteration an upper and lower limit was imposed on FA. The upper limit (f_u) was determined by setting the remaining contribution to the population genome to be equally distributed across all remaining founders and calculating FA. The lower limit (f_l) was determined by considering that all remaining founders contribute the proportion of the genome equivalent to the last found pseudo founder. The upper and lower limits converge over iterations and a criterion for stopping can be imposed on this process using either a level of convergence or a given number of pseudo founders. In this study a stopping criteria of $f_u - f_l < 5$ was used.

2.4. Founder origin

The contribution of the founder animals to the average individual genome of the population was determined in order to show the influence that the importation of the North American genome has had over the last 30 years. This involved finding the earliest known ancestors of the cows in the sample and calculating their contribution to the current gene pool based on each parent contributing 50% of their offspring's genome. The information generated by the FE procedure was used for this analysis.

2.5. Inbreeding coefficient and average relationship

Inbreeding coefficient was determined using the methodology of Meuwissen and Luo (1992). This was based on the decomposition of the additive genetic relationship matrix **A**, as described by Henderson (1976): $\mathbf{A} = \mathbf{LDL}'$, where **L** is a lower triangular matrix containing the fraction of genes that animals derive from their ancestors, and **D** is a diagonal matrix containing the within family additive genetic variances of animals. **L** is calculated row by row in the algorithm. The results of the samples for a given year were pooled. Average coefficient of inbreeding was determined for the whole population and also for those individuals with a non-zero coefficient of inbreeding. The average relationship between all members of a given sample, born in the year of the sample, was determined using the recursive algorithm of Miglior et al. (1992).

2.6. Maternal family distribution

In addition to the nuclear genome the current distribution of the mitochondrial genome in the Holstein Friesian cow population was analysed using all cows born in 1997 as the study population. The earliest maternal ancestor for each of the Holstein Friesian cows born in 1997 was traced using the same database as the other analyses and this was taken as being the point of cytoplasmic origin. Mitochondrial DNA (mtDNA) is inherited almost exclusively maternally in mammalian species (Hutchinson et al., 1974) and as such all cows in a maternal family will have the same mtDNA as the cow that provides the cytoplasmic origin of that maternal family.

3. Results

3.1. Samples

For all parameters estimated the samples provided consistent results within the year sampled. For example in 1997 the mean and standard deviation of the sample results was 0.43±0.057 for average inbreeding coefficient, 1.34±0.09 for average degree of relationship and 93±4.26 for FE. The results presented are a mean of the sample results for each year. Table 1 gives details of the sample pedigrees and shows that the 'depth' of pedigree information changed in the early 1990's indicative of the change to North American Holstein genome origin, which has less ancestral information stored on the database.

3.2. Founder origin

The change in the origin of the average genome over time (Table 2) clearly demonstrates the influence of the North American Holstein breed on the British Friesian population. The change in origin was most clearly seen over the last 10 years when male Holstein origin rose to the same level of influence as British Friesian females had had 25 years ago. Holstein female origin had risen to 20% in 1997 but the rate of increase was seen to fall to only 2% (0.4%/year) between 1992 and 1997. In all four origins, except for the Holstein female, the rate of change did not appear to have stabilised by 1997. It is important to note that the completeness of the pedigree information has an influence on the male:female contribution ratio. For example consider a simple scenario of a cow with pedigree information available on the sire and dam and the paternal grandsire and granddam only. If base animals are taken as being animals with unknown parents then 75% (50% dam, 25% paternal granddam) of the genome is traced to female origin and 25% (25% paternal grandsire) to male origin.

3.3. Average inbreeding coefficient

The base population of the pedigree samples used in this analysis was 1960. The samples from 1967 were, therefore, not very deep in pedigree structure (Table 1) and, as can be seen in Fig. 1 and Table 3, calculated inbreeding had risen little above zero at this time. Bowman et al. (1978) calculated average inbreeding coefficient of cows in the British Friesian population between 1955 and 1972, tracing animals

Table 1
Average information about pedigrees for 10 samples of 2000 cows

Year of birth	Number of founders in sample pedigree	Number of ancestors in sample pedigree	Average number of ancestors per individual
1967	2535	2785	2
1972	3523	7492	53
1977	4349	11 842	254
1982	8635	33 210	872
1987	8414	31 361	1321
1992	6090	22 284	796
1997	6640[a]	26 434[b]	646

[a] SD between 1997 samples 134.
[b] SD between 1997 samples 454.

Table 2
Origin of nuclear genome of the British Holstein–Friesian population

Year of birth	British female (%)	Male (%)	Foreign female (%)	Male (%)
1967	72	24	2	2
1972	55	37	4	4
1977	53	34	6	7
1982	48	31	9	12
1987	36	28	14	22
1992	22	20	18	40
1997	13	11	20	56

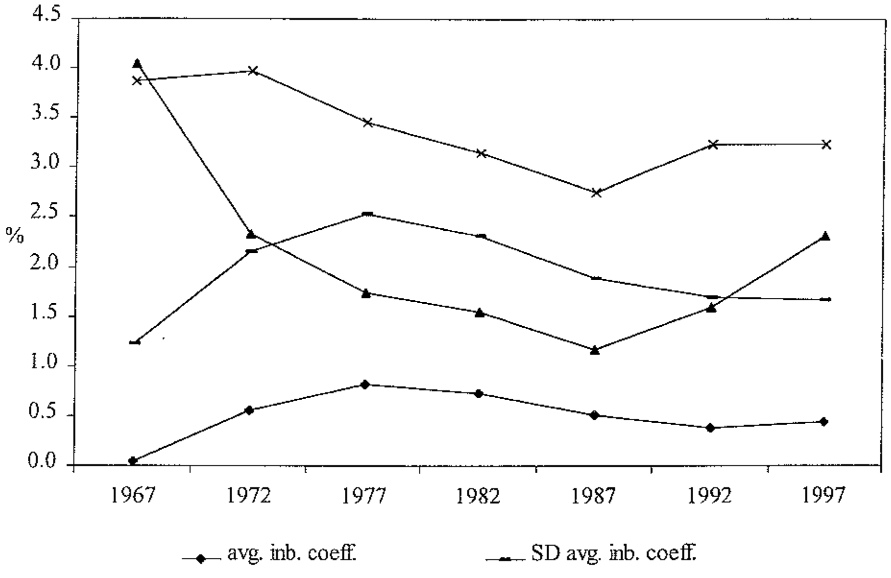

Fig. 1. Average and non-zero average inbreeding coefficient of cows of the UK dairy population born between 1967–1997.

back to the 1914 herd book. They used the sampling techniques described by Wright and McPhee (1925), that involve using three generations of complete pedigree information and then a sampling technique to establish common ancestors prior to these generations. In 1960, the base year in this current study, they estimated an average coefficient of inbreeding of 2.28%. The rate of increase in average coefficient of inbreeding in the study of Bowman et al. (1978) between 1965 and 1972 was very similar to that seen in the current study in which the level of inbreeding in the population followed a fairly steady increase between 1967 and 1982, over which time the origins of the population were in a steady state (Table 2). However, between 1982 and 1987 a steady fall was seen in the average inbreeding coefficient and this fall continued until 1992. From 1992 to 1997 a slight rise of 0.05% was seen, though when the years between 1992 and 1997 were analysed (results not shown) the samples were seen to differ little from 0.4%. More interesting were the results of the non-zero average inbreeding coefficients and the distribution of the inbred individuals. The year 1967 can be discounted as being too close to the base population to have had a significant level of inbreeding with only 1% of the population inbred, but by 1972 24% of the population was inbred and this rose to nearly 50% in 1977 and 1982. By 1987 the

Table 3
Average inbreeding coefficient (%) of the British Holstein–Friesian population[a]

Year of birth	Avg. inb. coeff.	SD avg. inb. coeff.	Non-zero avg. inb. coeff.	SD non-zero avg. inb. coeff.	Proportion inbred (%)
1967	0.05	1.22	4.05	3.87	1
1972	0.55	2.16	2.33	3.97	24
1977	0.82	2.54	1.75	3.46	47
1982	0.74	2.31	1.55	3.15	48
1987	0.52	1.90	1.17	2.76	42
1992	0.38	1.70	1.60	3.24	23
1997	0.43	1.67	2.32	3.24	19

[a] Base population 1960.

proportion of inbred animals had fallen to 42% and this proportion continued to fall until 1997. It was evident when the distribution of the inbred individuals was examined that the 1997 results were very similar to the 1972 results with only the proportion of individuals more than 12% and less than 1% inbred being lower in 1997. This similarity is not surprising given that essentially the base population of the 1997 animals had changed, as demonstrated in Table 2, to the imported Holstein population, a population with less depth of pedigree available. The distribution of non-zero inbreeding coefficients across all years appears to be an exponential distribution with a high frequency close to zero and a long thin tail up to 25%.

3.4. Average degree of relationship

The average degree of relationship (Fig. 2, Table 4) has been less affected by the breed grade-up than the average inbreeding coefficient. Though the parameter fell in 1987 the drop was soon halted with a stable average degree of relationship between 1987 and 1992. After 1992 the level was seen to increase at a rate close to the magnitude of the rate prior to 1982. However, what is more interesting is that the

Table 4
Average pair-wise relationship of the British Holstein–Friesian population

Year of birth	Avg. rel. (%) (%)	SD avg. rel.	Non-zero avg. rel. (%)	SD non-zero avg. rel.	Non-zero proportion (%)
1967	0.16	3.94	1.83	1.17	9
1972	0.52	2.62	1.08	1.90	48
1977	0.90	2.46	1.14	2.22	79
1982	1.25	2.64	1.46	2.50	85
1987	1.02	2.47	1.28	2.26	80
1992	1.03	2.94	1.52	2.50	60
1997	1.34	2.87	1.80	2.59	93

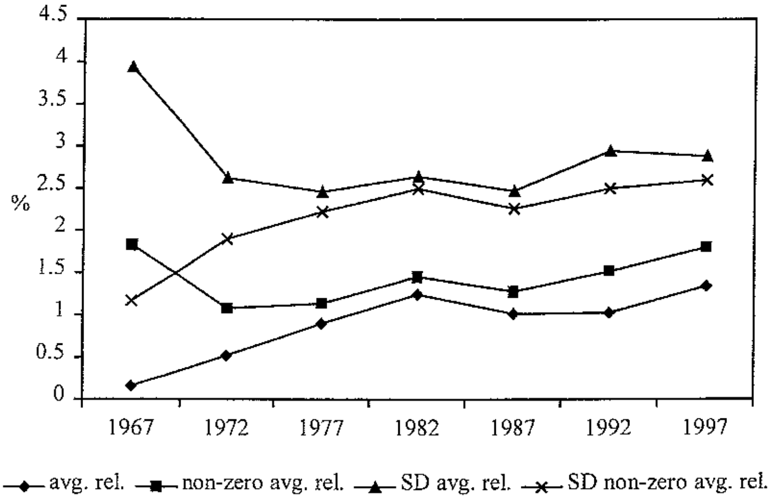

Fig. 2. Average and non-zero average degree of relationship between cows in the UK Holstein–Friesian population born between 1967 and 1997.

proportion of inbred individuals fell in 1987 and 1992 but by 1997 the figure had risen, with 93% of the population showing a non-zero degree of relationship.

3.5. Founder and ancestor equivalent number

The FE and FA parameter estimates for the samples (Table 5) illustrate the fall in genetic diversity over the last 30 years. The values shown for FA were actually the upper limits given the convergence criterion that $f_u - f_l >= 5$, and therefore potentially over-estimated by five. The trend in FE and FA shows that the fall in genetic diversity of the population was greatest in the years close to the base population. From 1977 to 1987 the FE parameter fell very little and the FA parameter, which estimated variability based on the highest contributing ancestors remained constant from 1977 until 1992. In 1997 both parameters had fallen to the same value of about 90. The convergence of these parameters in 1997 is indicative of the change in the founder population to the imported Holstein population with few selected sires being used to grade the population up. These few, but highly influential, founder individuals were also identified as being the highest contributing ancestors and hence the two parameters were seen to converge. To further illustrate the effect of few highly selected sires being extensively used, Table 6 shows the highest ancestor contributions to the years investigated. The highest contributing ancestor in 1997, To-Mar Blackstar, was responsible for 5% of the average nuclear genome in the population, more than double the level seen in 1967. Hanoverhill Starbuck made the second highest contribution, of 4.6% of the nuclear genome, in 1997, three times the contribution of the second highest contributing ancestor in 1967. The top 50 ancestors in 1997 were responsible for 50% of the nuclear genome, more than three times the 1967 level.

Table 5
Parameters of genetic diversity of the British Holstein–Friesian population[a,b]

Year of birth	Number of founders	FE	FA	FE as proportion of founders (%)	FA as proportion of founders (%)
1967	2535	1353	702	53	28
1972	3523	586	276	17	8
1977	4349	337	175	8	4
1982	8635	237	169	3	2
1987	8414	227	163	3	2
1992	6090	151	144	2	2
1997	6640	93	93	1	1

[a] FA is the founder ancestor equivalent number.

[b] FE is the founder equivalent number.

Table 6
Most important ancestor contributions

	1967	1972	1977	1982	1987	1992	1997
First ancestor[a]	0.023	0.032	0.033	0.026	0.028	0.041	0.051
Second ancestor[a]	0.017	0.028	0.030	0.025	0.022	0.034	0.046
Third ancestor[a]	0.007	0.013	0.023	0.024	0.021	0.025	0.030
First 10 ancestors[a]	0.080	0.140	0.165	0.201	0.185	0.197	0.282
First 50 ancestors[a]	0.165	0.301	0.359	0.409	0.440	0.427	0.501

[a] Proportion of alleles contributed by… …

Table 7
Distribution of Holstein–Friesian cows born in 1997, across maternal families

Family size (no. of cows)	No. of families	No. of cows	Proportion of cows (%)	Average no. of generations to origin
1	69 575	69 575	32.1	3.3
2–5	36 009	96 212	44.4	4.7
6–10	3743	27 277	12.6	6.0
11–20	1017	13 986	6.5	6.4
21–30	150	3721	1.6	6.8
31–40	56	1932	0.9	6.8
41–100	49	3046	1.4	7.4
101–150	5	574	0.3	7.7
151–220	2	383	0.2	9.0
Total	110 607	216 706	100	7.6

3.6. Maternal family distribution

The distribution of cows across maternal families can be seen in Table 7. Most of the cows are seen in families of less than five cows. The average family size was two with a standard deviation of 2.75 and nearly 70% of the families had only one cow. These single cow families represent 32% of the registered cows born in 1997 and traced on average three generations to their cytoplasmic origin, with about 70% tracing to grade-up cows. When the range of family size was increased to families of one to four cows 93% of the families were accounted for containing 71% of the cows. Only seven families were greater than 100 cows, with one having 217 members.

4. Discussion

In this study it has been shown that by treating the Holstein population as unrelated to the Friesian population, a decrease in inbreeding level was seen over the last 10 years. The same trend was also evident in the Dutch black and white dairy population between 1980 and 1985 (Te Braake et. al., 1994). Te Braake et. al. used a similar methodology in the calculation of average inbreeding coefficient and the population they were studying had undergone a similar introgression of North American Holstein genomes. Given the proportion of the British black and white cattle genome that is Holstein in origin at the present time, the relationship between the two breeds will soon be of little relevance. If this logic is followed it is not unreasonable to hypothesise that the rate of increase in the average level of inbreeding will soon return to the rate seen prior to the Holstein importation or indeed to a higher rate. In comparison, work done estimating inbreeding coefficients in the United States (VanRaden, 1992; Wiggans et al., 1995) and Canada (Miglior and Burnside, 1995) has consistently shown higher levels of inbreeding than has been seen in the British Holstein–Friesian population. VanRaden (1992) and Wiggans et al. (1995) using the same population of US Holsteins with a 1960 base population calculated the average inbreeding coefficients as 0.4, 1, 2 and 2.6%, respectively, for 1970, 1980, 1987 and 1990. Miglior and Burnside (1995) using a base population of 1950 estimated an average inbreeding coefficient of 1.7% between 1986 and 1990. They showed a plateau from the late 1970's until the late 1980's due to the heavy use of US Holstein sires in the Canadian population.

The average degree of relationship parameter would appear to have been less sensitive to the introduction of Holstein genes than the level of inbreeding. Indeed given the steady increase in average relationship and the introgression of North American Holsteins across most of Europe, it is inevitable that the average inbreeding coefficient will increase in the future. In the study of Bowman et al. (1978) the degree of relationship estimated for 1960 was 1.45% but was seen to have risen to 3.19% by 1972, with the rate of increase between 1965 and 1972 almost identical to that estimated by this current study.

As has previously been discussed the recent change in breed origin resulted in both the rate of increase in average inbreeding coefficient and average degree of relationship to be lowered considerably and indeed a decrease in the inbreeding parameter was seen during the late 1980s and early 1990s. These parameters are not therefore able to provide a good estimate of the genetic diversity of the British black and white dairy population over recent years. FE and FA were used to illustrated the change in genetic diversity over time, whilst the population was undergoing a major grade-up, which was not possible using the average inbreeding coefficient. These parameters provided a useful means of describing the change in genetic diversity but as indicated by Boichard et al. (1997) they cannot be used as predictors of future variability. In previous studies using FE and FA (Boichard et al., 1997; Sölkner et al., 1998) whole populations have been used. In this study samples from the population were used and whilst the parameters provided a description of the change over time they did not necessarily accurately estimate the magnitude of the population parameters. However, given the nature of these parameters, i.e. that they are heavily dependent on the proportional contribution of the top few, highest contributing founders/ancestors, it can be argued that the estimates provide a close approximation. The identity and magnitude of the contribution, of the highest contributing ancestors, was found to be consistent across the samples for given years, and this further validated the accuracy of the sample result. Young and Seykora (1996) estimated the ancestors with the highest contribution to the 1990 US Holstein females. Two of the three bulls with the highest contribution to the US female genome in 1990 were the same two bulls that made the highest contribution to the British Holstein–Friesian female genome in 1992. Round Oak Rag Apple Elevation contributed 12.2 and 3.4% and SWD Valiant contributed 9.6 and 4.1% to the US and UK female populations, respectively.

The use of long-term founder contributions is similar to the approach taken by Woolliams and Mantysaari (1995) in the Finnish Ayrshire population, however they related this contribution to the rate of inbreeding using the methodology of Wray and Thompson (1990).

The use of founder equivalent as a measure of genetic diversity can be criticised due to the nature of long-term founder contributions. Over a number of generations the proportionate contributions of founder individuals will stabilise to the same across all contemporary individuals (Wray et al., 1994) and hence the founder equivalent parameter will become fixed. Caballero (personal communication) states that minimising coancestries is a more effective way of maintaining genetic variability than trying to equalise founder contributions. This minimises the variances of contributions from ancestors to descendants in all previous generations to the current one, i.e. maximising the effective population size.

Rate of increase in average inbreeding coefficient has been used frequently as a measure of genetic diversity (e.g. Goddard, 1992; Wang, 1997). However, it is a measure that is sensitive to changes in population structure and crossbreeding. One method to avoid this problem was proposed by VanRaden (1992). He suggested that given that Holstein and Friesian populations will have a common base at some point in the past, then it is possible to assign an average relationship between Friesian and Holstein individuals based on several assumptions utilising earliest known ancestor information. The genetic diversity parameter FA estimated in this study is less sensitive to a change in origin and reflects the level of contribution being made by few very influential individuals to the whole population. Such information could also be used to identify families that have high influence and provide extra information to be used in future selection strategies. These measures of founder representation are used by conservation biologists in order to retain genetic variation of captivity bred 'wild' populations (Lacy, 1989). As FE and FA decrease so the level of inbreeding will increase with the general increase in similarity of the genome. The present study estimated the genetic diversity parameters to be of very similar magnitude to those estimated by Boichard et al. (1997) and Sölkner et al. (1998) for dairy breeds. However, the FA and FE parameters converged in 1997 in the British Holstein–Friesian population. This was attributable to the fact that the imported Holstein sires formed the new founder base population and, at the same time, these few, heavily used sires made a large contribution to the average genome of the population. This again illustrates the robustness of the FA parameter, which does not rely on distant relationships to the same level that the other parameters do. The measure of FE in small conservation populations is used as a standard by which genetic diversity can be maintained. Here the populations are not being actively selected and the objective is to attain an equal representation of all founders across generations. In livestock improvement the objective is very different but if we are looking towards long term effective improvement then preservation of the variability of the genetic base is important. Goddard (1992), considering the global black and white population and using N_e as the measure of genetic diversity calculated the optimal effective size using discounting to estimate future gains. Such a calculation is dependent on several assumptions regarding objectives and differences between countries. Goddard (1992) hypothesised that differences between countries in both environment and objectives will lead to the development of isolated strains, which originate from the same founding animals, i.e. North American Holsteins. What is not certain at present is the degree of exchange of genes that will continue to occur between these 'isolated' populations.

When the mitochondrial genome was considered, using 1960 as the population of cytoplasmic origin, a very different level of diversity was seen. Due to the nature of the transmission of the mitochondrial genome, i.e. it is almost exclusively maternally inherited; the heavy use of foreign sires has had no impact on its diversity. This study provided an under estimation of maternal family size for two reasons. Firstly, pedigree information prior to 1960 was not used and secondly many of the single cow families were a first generation grade-up cow with no information on the non-pedigree dam. It would appear that the level of diversity remaining between mitochondrial genomes is still high or at least has not been reduced greatly by selection over the last 30 years.

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