

Inbreeding in Danish Dairy Cattle Breeds

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ABSTRACT

The purpose of this study was to monitor current and predict future rates of inbreeding in the Danish dairy breeds. Calves born from 1999 until 2003 and registered as Danish Holstein (1,883,983), Danish Jersey (336,966), or Danish Red (261,047) were reference populations. Average complete generation equivalent was approximately 7. For calves born in 2003, average inbreeding was 3.9, 3.4, and 1.4% for Holstein, Jersey, and Danish Red, respectively. In recent years, effective population sizes were 49, 53, and 47, respectively. Based on coancestry statistics, future effective population sizes will be 43, 42, and 51, respectively. The effective number of founders, effective number of ancestors, and effective number of founder genomes were calculated. These measures of genetic diversity were all low for Holstein and Jersey and somewhat larger for Danish Red. The most important ancestors of Danish Holstein were Elevation (13.8%), Chief (10.9%), and Bell (8.5%). The most important ancestor of Danish Red was Momentum (9.4%), a Red Holstein-Friesian. The most important ancestor for Danish Jersey was FYN Lemvig (12.1%) with a large number of progeny in the reference population. The results of this study indicate the necessity for active management of the rate of inbreeding in the future.

(Key words: inbreeding, effective population size, genetic diversity, pedigree analysis)

INTRODUCTION

The breeding strategies currently applied in dairy cattle breeding are effective in generating genetic gain. However, the reproductive technologies used have increased the focus on the few superior animals, especially bulls, and the advanced methods of breeding value estimation have increased the accuracy of predic-

tion by using information on all available relatives. Both of these advancements in animal breeding will increase the probability of generating inbred animals (Verrier et al., 1993; de Boer and van Arendonk, 1994). Associated with inbreeding is the decline in performance usually known as inbreeding depression (e.g., Smith et al., 1998). Moreover, an increased rate of inbreeding also means an increased risk of the breeding program in terms of the variance of genetic gain (Meuwissen, 1991) and a reduced additive genetic variance is expected (Falconer and Mackay, 1996). Inbreeding is therefore an important parameter to monitor and control in a breeding program.

The population structure determines the development in inbreeding. Danish Holstein has undergone repeated backcrossing to North American Holstein since 1965, so that now more than 93% of the Danish Holstein genes are of North American origin. Danish Holstein is the largest of the breeds with 300 young bulls progeny tested every year. Danish Jersey and Danish Red are smaller breeds with 60 young bulls each starting for progeny testing every year. Danish Jersey has imported US Jersey breeding material and has now around 35% US genes. Robertson and Mason (1954) predicted that Danish Red would meet inbreeding problems, as a few ancestors contributed very heavily (~18%) to the gene pool of breeding bulls, and Danish Red suffered from inbreeding depression in the 1970s. The breeders, therefore, chose to import genes from US Brown Swiss and later from Red Holstein. In the 1990s, an import from Swedish Red and White started. Due to this ongoing introduction of new genes, Danish Red is expected to show a different trend in inbreeding than the other 2 breeds. For all breeds, the importation of semen is ongoing, with approximately 7% of inseminations being performed with imported semen. The objective of this paper was to monitor current trends and predict future trends in inbreeding and to assess the genetic diversity in Danish Holstein, Danish Jersey, and Danish Red.

MATERIALS AND METHODS

Data

Three dairy breeds were studied: Danish Holstein, Danish Red, and Danish Jersey. For each breed, a refer-

Received November 9, 2004.

Accepted January 18, 2005.

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Table 1. Number of animals in reference population and entire pedigree. Average pedigree completeness index and average complete generation equivalents for individuals in the reference population. Average birth year of founders with known birth year and percentage of founders with known birth year.

	Danish Holstein	Danish Jersey	Danish Red
Total number of calves born 1999–2003	2,238,349	383,414	292,395
Reference population	1,883,983	336,966	261,047
Entire pedigree	3,702,136	639,704	558,212
Pedigree completeness index	0.94	0.95	0.93
Complete generation equivalent	7.20	7.36	6.77
Average birth year of founders	1982	1978	1976
Founders with known birth year, %	10	10	12

ence population was defined as the calves born in Denmark in 1999 until 2003 with a minimum completeness of pedigree of 0.6 (see below). The length of the reference period was chosen such that it represented approximately an entire generation. For all animals in the reference populations, the pedigrees were traced as far back as possible in the Danish Cattle Database (Bundgaard and Høj, 2000), and all ancestors found were included in the analysis. The total number of animals for each breed is shown in Table 1. The average birth year of founders with known birth year was around 1980 for all 3 breeds (Table 1). Figure 1a shows the proportion of founders within birth years. The number of animals included in the analysis is shown in Figure 1b per birth year. The increase in numbers from 1998 to 1999 in all breeds is due to the inclusion of bull calves

in the reference population. In earlier years, most animals are females. The calves born late in 2003 were not included. This explains the small drop in numbers from 2002 to 2003.

Pedigree completeness. The degree of completeness of pedigrees was assessed by the index proposed by MacCluer et al. (1983). They set up a coefficient for pedigree completeness (PEC) to quantify the possibilities for detecting inbreeding in the pedigree:

$$PEC_{animal} = \frac{2C_{sire}C_{dam}}{C_{sire} + C_{dam}}$$

where C_{sire} and C_{dam} are contributions from the paternal and maternal lines respectively:

$$C = \frac{1}{d} \sum_{i=1}^d a_i$$

where a_i is the proportion of known ancestors in generation i ; and d is the number of generations that is taken into account. In this study, 5 generations are considered ($d = 5$). This index is ad hoc in the sense that a specific value cannot be translated into an expected bias in the calculated coefficient of inbreeding. However, being a harmonic mean, the index has a value of zero if one parent is unknown no matter how much pedigree is known for the other parent. There were no substantial differences between breeds in the completeness of pedigrees (Table 1 and Figure 2). Hence, the results are comparable across breeds. More than half of the reference population has pedigree completeness for 5 generations above 0.9.

In addition, for each individual j , the number of complete generation equivalents was computed as

$$\sum_{i=1}^{n_j} \frac{1}{2^{g_{ij}}}$$

where n_j is the number of ancestors of individual j , and g_{ij} is the number of generations between individual j

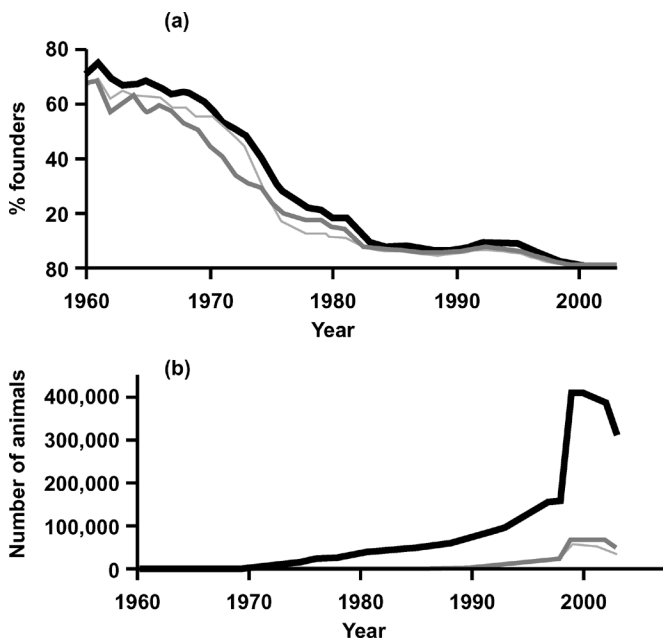


Figure 1. (a) Percentage of founders within each birth year, and (b) total number of animals born against year of birth for Danish Holstein (thick line), Danish Jersey (gray line), and Danish Red (thin line).

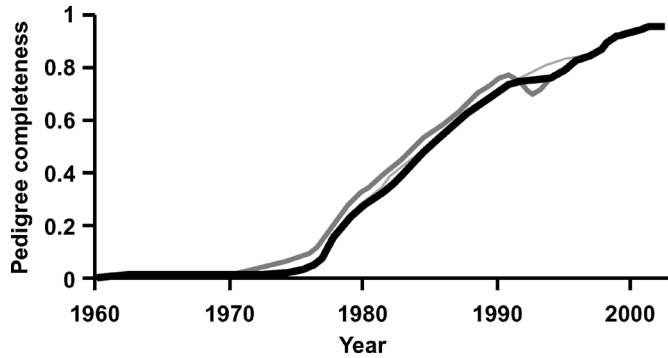


Figure 2. Average pedigree completeness index for 5 generations for each birth cohort plotted against year of birth for Danish Holstein (thick line), Danish Jersey (gray line), and Danish Red (thin line).

and its ancestor i (Sölkner et al., 1998). In that way, one-half is added for each known parent, one-fourth is added for each known grandparent, and so on. The complete generation equivalent quantifies how many generations have been traced. This number is around 7 for all 3 breeds (Table 1).

The correlation between the pedigree completeness index and complete generation equivalents was between 0.94 and 0.96 for the 3 breeds, indicating that they assess more or less the same.

Methodology

Effective population size. The effective population size, N_e , was calculated from the rate of inbreeding per generation, obtained by multiplying the annual rate of inbreeding, ΔF_y , with the generation interval, L ,

$$N_e = \frac{1}{2\Delta F_y \cdot L} \tag{1}$$

The effective population size was calculated for time intervals in which the trend in inbreeding was approximately linear. This was assessed by visual inspection of the trends in Figure 3a.

The average coancestry of animals in a population forecasts the average coefficient of inbreeding in the following generation (Falconer and Mackay, 1996). Hence, the rate of increase in coancestry per year, Δf_y , can be interpreted as the future rate of inbreeding per year. Therefore, the expected future effective population size can be calculated by replacing ΔF_y in [1] with Δf_y . The expected future effective population size was calculated for the same time intervals as the historical effective population size above assuming constant generation interval.

Effective number of founders. All animals with both parents unknown are regarded as founders in this

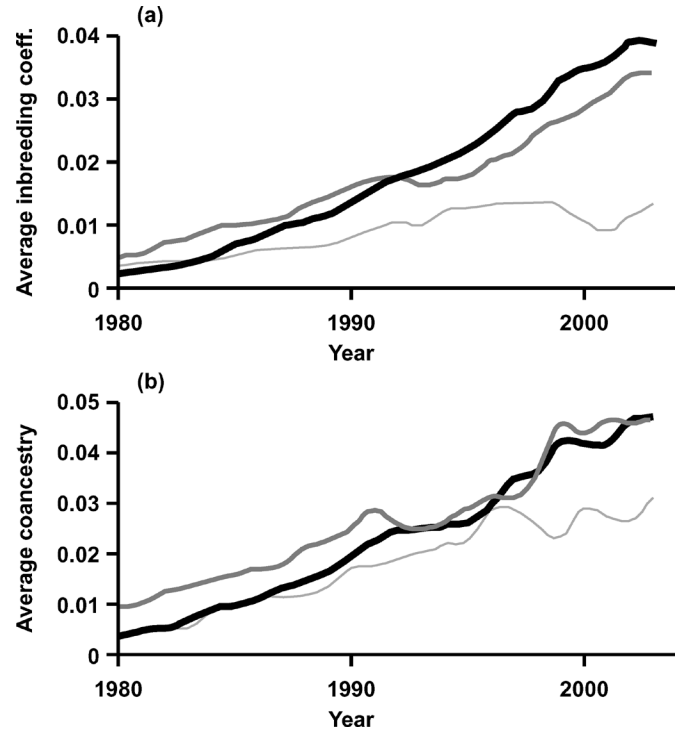


Figure 3. (a) Average coefficient of inbreeding, and (b) average coancestry within cohorts for each birth cohort plotted against year of birth for Danish Holstein (thick line), Danish Jersey (gray line), and Danish Red (thin line).

analysis. In addition, if an animal has one known and one unknown parent, the unknown parent is regarded as a founder. The total number of founders contains limited information on the genetic basis for the population. Firstly, founders are assumed to be unrelated, because their parentage is unknown. However, this is most probably not the case. Secondly, some founders have been used more intensely and therefore contribute more to the current population than other founders. The effective number of founders, f_e , has been designed to correct for this second shortcoming. It is defined as the number of equally contributing founders that would be expected to generate a similar amount of genetic diversity as the studied population (Lacy, 1989). It can be calculated from the genetic contributions of the N_f founders:

$$f_e = \left[\sum_{i=1}^{N_f} q_i^2 \right]^{-1}$$

where q_i is the genetic contribution of the i th founder to the reference population. When founders contribute unequally, the effective number of founders is smaller

than the actual number. The effective number of founders has a limited usefulness; because once the contributions of the founders have converged, the effective number of founders remains constant, no matter what happens to the population afterwards. The genetic contributions are expected to have converged after 5 to 7 generations (Bijma and Woolliams, 1999). For example, a population where animals have deep pedigrees (more than 7 generations) can be characterized with a high effective number of founders even after a severe, recent bottleneck. Hence, in isolation, the effective number of founders is not a good measure of genetic diversity. However, it provides a basis for comparison of the effective population size and the effective number of ancestors (see below). The effective number of founders is expected to be one-half the effective population size in a population with minimum inbreeding. If the effective number of founders is different from this, it shows that the breeding structure has been changed since the founder generation.

Effective number of ancestors. The effective number of ancestors, f_a , has been defined to supplement the effective number of founders (Boichard et al., 1997). Instead of using genetic contributions of founders only, the effective number of ancestors is calculated from the genetic contributions of ancestors with the largest marginal genetic contributions. The genetic contributions of founders are independent and sum to one. That is not the case for genetic contributions of ancestors. For example, the dam of a highly used sire has at least half the contribution of her son, because the same genes are represented in both generations. Boichard et al. (1997) therefore introduced the marginal contribution. The ancestors contributing most to the reference population are considered one at a time in a recursive process. For each round of the recursion the ancestor with the highest contribution is chosen, and the contributions of all others are calculated conditional on the contribution of the chosen ancestor. Then, based on these marginal contributions another ancestor is chosen and the process continues. So the marginal contribution is the genetic contribution from an individual after correcting for contributions of other ancestors already considered in the recursive process. Thus, the sum of marginal contributions of all ancestors is one. Ancestors only have a large marginal contribution to the reference population if their genes have passed through many descendants, e.g., a sire of sons with many sons selected. The effective number of ancestors is calculated as

$$f_a = \left[\sum_{i=1}^{1000} p_i^2 \right]^{-1}$$

where p_i is the marginal genetic contribution of ancestor i . Calculated this way, the effective number of ancestors is a measure of genetic diversity that accounts for recent bottlenecks, and thus account partly for the loss of allelic diversity since the foundation population. The marginal contribution is not counted for all ancestors, but for a given number of ancestors the upper and lower limits to the effective number of ancestors. In this study, we used 1000 ancestors, in which case the upper and lower limits does not show any difference for 2 decimal digits.

The effective number of ancestors is an ad hoc measure in the sense that it does not fit into the theory of long-term genetic contributions (Wray and Thompson, 1990; Woolliams and Thompson, 1994). In this theory, the rate of inbreeding and loss of genetic diversity is a function of total genetic contributions and not of marginal genetic contributions. In essence, the marginal genetic contributions ignore the generational structure of the population, and a number of highly contributing ancestors are treated as founders when calculating the effective number of ancestors. Thus, the effective number of ancestors does not tell the full story of the genetic diversity and is also somewhat dependent on the depth of pedigrees. However, it is useful in comparison with the effective number of founders. The ratio of the 2 is an indication of the importance of bottlenecks in the development of the population. If the ratio is close to unity, the population has been stable in terms of numbers of effectively contributing animals. If the effective number of founders is larger than the effective number of ancestors, bottlenecks have played a role in population formation.

Effective number of founder genomes. The effective number of founder genomes, f_g , accounts for both unequal contributions of founders, bottlenecks, and random loss of alleles due to genetic drift (Lacy, 1989, 1995). It is defined similar to the effective number of founders with the difference that the genetic contribution of the i 'th founder to the reference population, q_i , is modified by the proportion of the founder's genes that are found in the reference population, r_i . As $(1-r_i)$ quantifies the proportion of alleles from the founder that are not expected to be present in the reference population, f_g takes account of random loss of alleles during bottlenecks. The effective number of founder genomes is calculated as

$$f_g = \left[\sum_{i=1}^{N_f} \frac{q_i^2}{r_i} \right]^{-1}$$

With this definition, the interpretation is the number of equally contributing founders with no loss of founder

Table 2. Generation interval, rate of inbreeding, and rate of increase in coancestry per generation of 3 Danish dairy breeds. Historical effective population size (N_e) calculated based on the rate of inbreeding, and expected future effective population size (Future N_e) calculated based on the rate of coancestry.

	Period	Generation interval	Rate of inbreeding per generation, %	Rate of coancestry per generation, %	N_e	Future N_e
Danish Holstein	1983–1992	5.0	0.74	0.97	68	51
	1993–2003	4.6	1.03	1.15	49	43
Danish Jersey	1977–1991	5.2	0.57	0.86	87	58
	1993–2003	4.7	0.94	1.18	53	42
Danish Red	1977–1998	5.0	0.32	0.71	157	71
	2001–2003	4.8	1.07	0.97	47	51

alleles that would be expected to produce the same amount of diversity as in the reference population (Lacy, 1995). Even in the case of minimum inbreeding, the effective number of founder genomes is smaller than the effective number of founders and the effective number of ancestors and smaller than half the effective population size. The degree to which the effective number of founder genomes is smaller is an indication of the degree of random loss of alleles. As alleles are lost every generation, the effective number of founder genomes decreases every generation and is therefore sensitive to depth of pedigree.

In this study, the effective number of founder genomes is calculated using the software package Pedig by Boichard (2002). It follows the genedrop procedure described by Boichard et al. (1997), and calculates the average of the inverse of the summations from each genedrop simulation. However, the program was modified according to the suggestions of Caballero and Toro (2000), so that it takes the inverse of the average of summations instead. The difference between the 2 methods of calculation is small.

Software. The software package Pedig by Boichard (2002) was used to calculate generation intervals, effective number of founders, effective number of ancestors, effective number of founder genomes, and marginal contributions of ancestors. The software package Inbred by Berg (2003) was used to calculate coefficients of inbreeding, using the algorithm of Meuwissen and Luo (1992), pedigree completeness indices, number of complete generation equivalents, and average coancestry within birth cohorts.

RESULTS

The trend in inbreeding (Figure 3a) shows that Danish Holstein and Danish Jersey increased the most during the last 2 decades. The trend for Danish Holstein is very smooth, whereas that for Danish Jersey is less smooth. For Danish Red, the trend is less steep and is

broken in 1998 and starting to increase again in 2001. All 3 breeds have low effective population size for the most recent years (Table 2). The trends in coancestry (Figure 3b) are more similar for the 3 breeds, but less stable from year to year. This is due to a large sensitivity of the average coancestry of single year to the number and size of half-sib families. Based on the increase of coancestry, the effective population size is expected to decrease for Danish Holstein and Danish Jersey, whereas it is more stable for Danish Red with a tendency toward an increase (Table 2).

The generation interval has dropped for all breeds from earlier to later time periods (Table 2). This is partly due to a slightly changed breeding structure where proven bulls are no longer used for such long periods. The drop may also be affected by the fact that the earlier cohorts only included the age of parents of animals that reproduce, whereas the last cohorts included the age of parents of all animals because it is unknown whether they will reproduce.

The effective numbers of founders (Table 3) show large differences between breeds. It is largest for Danish Red and smallest for Danish Holstein. The effective numbers of ancestors are smaller and more equal for the 3 breeds. The effective numbers of founder genomes are very small for Danish Holstein and Danish Jersey. The number is somewhat larger for Danish Red.

The 10 ancestors with the largest marginal genetic contributions account for almost 56% in Danish Holstein (Table 4). In Danish Red, the comparable number is less than 45%. The 4 most important ancestors of Danish Red belong to 4 different breeds: Red and White Holstein Friesian (Momentum), Swedish Red and White (Tor Bruno), Brown Swiss (Improver), and original Danish Red (FYN Rosen). This highlights the synthetic character of the Danish Red population. In Danish Jersey, the most important ancestor is FYN Lemvig (12.1%). This is a very recent bull, whose large contribution is due to a large number of his offspring in the reference population, because he was heavily used as

Table 3. Summary statistics of pedigree analysis in Danish dairy breeds.

	Danish Holstein	Danish Jersey	Danish Red
Average coefficient of inbreeding, calves born 2003	0.039	0.034	0.014
Average coefficient of coancestry, calves born 2003	0.047	0.047	0.032
Effective number of founders	70.0	115.7	207.2
Effective number of ancestors	20.6	23.8	34.6
Effective number of founder genomes	11.9	11.4	21.7
Ancestors to explain 50% of gene pool	8	9	13
Ancestors to explain 75% of gene pool	32	26	37
Ancestors to explain 90% of gene pool	193	73	126
Percentage of gene pool explained by 1000 ancestors	93.6	95.7	96.2

a proven bull in a rather small population. In the future, his contribution can easily be changed either upwards or downwards.

The cumulated marginal contributions show different patterns for the 3 breeds (Figure 4). In Danish Holstein, a small number of ancestors contribute heavily to the reference population, but the rest of the genes are derived from a large number of ancestors each with a very small contribution. On the other hand, Danish Red is less influenced by a few ancestors, but there are a smaller total number of ancestors accounting for the rest. The Danish Jersey follows Danish Holstein for the most important ancestors and follows Danish Red for the ancestors with small contributions.

DISCUSSION

The results presented in this paper highlight the impact of the current breeding programs on genetic diversity. In recent years, inbreeding has increased at a rate of 0.9 to 1.1% per generation for the Danish dairy breeds. For Danish Holstein and Danish Jersey, the rate of inbreeding is expected to increase according to the rate of increase of coancestry. The other diversity measures confirm that the current gene pool for Danish

Holstein and Danish Jersey has been derived from a small number of individuals. For Danish Red, the effective number of ancestors indicates that the number of individuals contributing to the gene pool is only slightly higher than for the other breeds, and inbreeding has increased over the last 2 yr.

In animal breeding, the recommendation is to maintain an effective population size of at least 50 to 100 (FAO, 1998; Bijma, 2000). All 3 breeds fall within or below this interval, and so breeders should be concerned of controlling inbreeding in their breeding programs. This recommendation is by no means a magic number, but has been derived from theoretical arguments, where natural selection counteracts inbreeding depression. An effective population size of at least 500 is needed if genetic variation in the long term should not decrease (see Franklin and Frankham, 1998). This argument is the basis for the recommendation from associations of zoos (Wheater et al., 1993).

The different measures of diversity assess different aspects of diversity. The most important is the rate of increase of coancestry as it holds all currently available information on the future rate of inbreeding. Tools designed to balance the rate of gain and the rate of inbreeding in the future (Wray and Goddard, 1994; Meu-

Table 4. Total and marginal genetic contributions (%) of 10 ancestors with the largest marginal genetic contributions within each breed.

	Danish Holstein			Danish Jersey			Danish Red		
	Ancestor	Total	Marginal	Ancestor	Total	Marginal	Ancestor	Total	Marginal
1	Elevation	13.8	13.8	FYN Lemvig	12.1	12.1	Momentum	9.4	9.4
2	Arlinda Chief	10.9	10.9	SKÆ Hede	12.0	9.0	Tor Bruno	6.9	6.9
3	Bell	8.5	8.5	Top Brass	6.3	6.3	Improver	5.0	5.0
4	Dam of SWD Valiant	4.5	4.5	FYN Tanic	5.7	5.7	FYN Rosen	4.9	4.9
5	Blackstar	6.3	4.0	FYN Haug	5.5	5.5	MRS Abru	3.7	3.7
6	Cleitus	6.3	3.9	Duncan	7.2	4.2	Elegant	3.4	3.4
7	Astronaut	3.2	3.2	Flower ¹	3.3	3.3	Emory	4.2	3.1
8	Ned Boy	2.7	2.7	ØJY Mikkell	3.2	3.2	Topper-Red	2.9	2.9
9	Ivanhoe	9.0	2.5	FYN Danny	3.0	3.0	Drøpstad	2.8	2.8
10	Leadman	5.0	1.9	Royal	3.0	3.0	Punch	2.5	2.5
All			55.9			55.3			44.6

¹Molly Brook Fascinator Flower is the dam of 5 Danish progeny-tested sons and of 2 US bulls of which semen was imported. Among these is Molly Brook Brass Major.

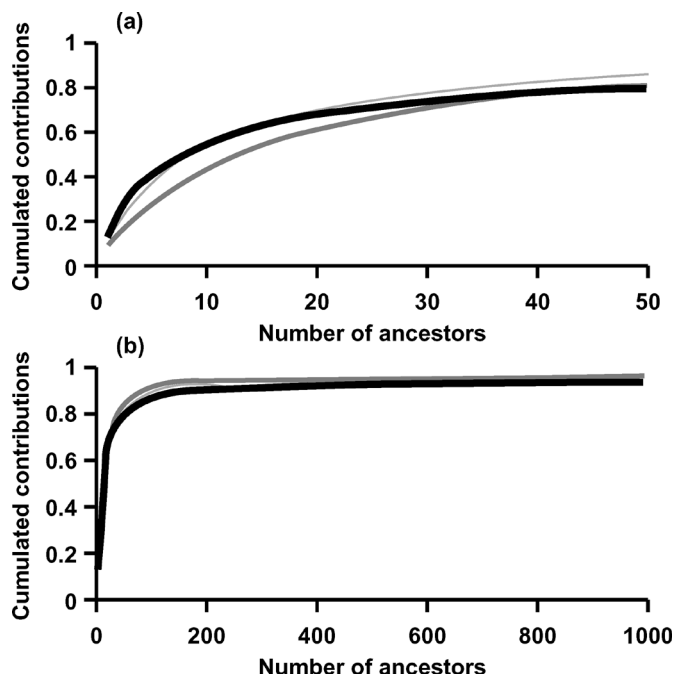


Figure 4. Cumulated marginal genetic contributions for Danish Holstein (thick line), Danish Jersey (gray line), and Danish red (thin line) up to (a) 50, and (b) 1000 ancestors.

wissen, 1997) constrain the rate of increase of coancestry when selecting animals. According to the results of this study, control of future rate of inbreeding is necessary for all breeds. These methods are currently being implemented for this purpose.

The other diversity measures are historical with limited predictive value. However, together they hold information on the history of population formation. The effective population size measures the rate of loss of genetic diversity that has occurred historically. For all breeds, their rate of loss has been large in the last decade. For all breeds, the difference between half the effective population size and the effective number of founders shows that drift has been accelerating since the founder generation, primarily due to increased selection pressure. Also for all breeds, the difference between the effective number of founders and the effective number of ancestors show that bottlenecks have occurred since the foundation of the population. According to the difference of half the effective population size and the effective number of founder genomes, random loss of founder alleles due to drift has been larger in Danish Holstein and Danish Jersey than in Danish Red.

This study illustrates that current breeding strategies can result in depletion of genetic diversity even in very large populations. All 3 breeds have considerable census sizes. However, their effective population sizes are small and decreasing. Despite the difference in

breeding strategy between the Danish Red and the other breeds, the loss of genetic diversity seems to occur at the same rate. For all breeds, active management of the future rate of inbreeding is necessary.

ACKNOWLEDGMENTS

The authors acknowledge an anonymous reviewer for useful comments that improved the paper.

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