55th Annual Meeting of European Association for Animal Production
Bled, Slovenia, 5 – 8 SEPT 2004
Commission on Animal Genetics G3.9

Inbreeding in Danish dairy cattle breeds

Anders Christian Sørensen[a,b], Morten Kargo Sørensen[a], Peer Berg[a]

[a] Department of Animal Breeding and Genetics, Danish Institute of Agricultural Science, P.O. Box 50, DK-8830 Tjele, Denmark. E-mail: AndersC.Sorensen@agrsci.dk
[b] Department of Large Animal Sciences, Royal Veterinary and Agricultural University, Ridebanevej 12, DK-1870 Frederiksberg C, Denmark

---

Abstract

Inbreeding depression poses a potential threat to dairy cattle breeding. Therefore, inbreeding should be monitored. Calves born from 1999 until 2003 and registered as Danish Holstein (DH; 2,238,349), Danish Jersey (DJ; 383,414) or Danish Red (DR; 292,395) were reference populations in this study. For calves born in 2003, average inbreeding was 3.4% for DH, 3.1% for DJ and 1.3% for DR. Since 1983, the effective population sizes have been 70 for DH, 98 for DJ and 274 for DR.

For DH, 8 ancestors contributed 50% to the reference population. The most important ancestors were Elevation (13.5%), Chief (10.7%), and Bell (8.3%). The genetic basis is very narrow as illustrated by an effective number of founders of 73. The effective number of ancestors is 22. The difference in numbers reflects unequal use of ancestors between founders and reference population.

For DR, 13 ancestors contributed 50% to the reference population. The 4 most important ancestors contributed 26%. They belong to 4 different breeds: Red Holstein Friesian, Swedish Red and White, Brown Swiss, and original DR. This highlights the synthetic character of the DR population. The effective number of founders in DR is 214 and the effective number of ancestors is 35.

These data provide material for estimation of inbreeding depression in dairy cattle.

Introduction

The breeding strategies currently applied in dairy cattle breeding are very effective in generating genetic gain. However, the reproductive technologies have increased the focus on a small number of superior animals, especially bulls, and the advanced methods of breeding value estimation have increased the accuracy of prediction by using information on all available relatives. Both of these advancements in animal breeding have increased the probability of generating inbred animals. Associated with inbreeding is the decline in performance usually known as inbreeding depression. Moreover, an increased rate of inbreeding also means an increased risk of the breeding program in terms of the variance of genetic gain. Inbreeding is therefore an important parameter to monitor and control in a breeding program.

The population structure determines the development in inbreeding. The Danish Holstein has undergone repeated backcrossing to North American Holstein since 1965, so that now more than 93 % of the genes are North American. The Danish Jersey has imported from US Jersey and has now around 35 % US genes. These populations are expected to show similar patterns in the development of inbreeding with Jersey showing a lag relative to Holstein. Danish Red suffered from inbreeding depression in the 1970’s and chose to import genes from US Brown Swiss and later from Red Holstein. In the 1990’s 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 two other breeds.

This paper shows that the increase in inbreeding in the Danish Holstein and Danish Jersey is substantial, and that the increase in inbreeding in Danish Red is smaller. Furthermore, this study suggests that the pedigree information is sufficiently complete to estimate inbreeding depression.

Materials and Methods

DATA

Three dairy breeds were studied: Danish Holstein, Danish Red, and Danish Jersey. For each breed, a reference population was defined as the calves born in Denmark in 1999 until 2003, representing approximately an entire generation. For all animals of the reference populations, the pedigree was traced as far back as possible in the electronic database, and all ancestors found were included in the analysis. The numbers of animals for each breed are shown in Table 1.

Table 1. Number of animals in reference population and entire pedigree

	Danish Holstein	Danish Jersey	Danish Red
Reference population	2,238,349	383,414	292,395
Pedigree file	4,168,761	704,597	608,349

METHODS

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:

$$PEC_{animal} = \frac{4C_{sire}C_{dam}}{C_{sire} + C_{dam}}$$

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

$$C = \left(d \sum_{i=1}^{d} a_i \right)^{-1}$$

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, five generations are considered ($d = 5$).

The software package Pedig by Boichard (2002) was used to calculate generation intervals, effective number of founders, effective number of ancestors, and marginal contributions of ancestors according to Boichard *et al*. (1997).

The software package Inbred by Berg (2003) was used to calculate coefficients of inbreeding, using the algorithm of Meuwissen & Luo (1992), and pedigree completeness indices according to MacCluer *et al.* (1983).

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

All animals with both parents unknown are regarded as founders in this 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 only tells a little of how wide the genetic basis for the population is. Firstly, founders are assumed to be unrelated, because nothing is known of their parentage. 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 remain constant, no matter what happens to the population afterwards. The genetic contributions are expected to have converged after 5 to 7 generations (Bijma & Woolliams, 1999). E.g. 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.

The effective number of ancestors, f_a, has been defined in order 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 the 1000 ancestors with the largest genetic contributions. The genetic contributions of founders are independent. That is not the case for genetic contributions of ancestors. E.g. the dam of a highly used sire is at least half the contribution of her son, because the same genes are represented in both generations. What is important is the marginal contribution. The ancestors contributing most to the reference population are considered one at the time in a recursive process. For each round of the recursion an ancestor is chosen based on the highest contribution, 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 part of the genetic contribution from an individual that is independent of other ancestors already considered in the recursive process. Otherwise, the effective number of ancestors is calculated as f_e:

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

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.

Results

RATE OF INBREEDING

The trend in inbreeding (Figure 1) shows that Danish Holstein and Danish Jersey increased the most during the last two decades. The trend for Danish Holstein is very smooth, while the trend 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. Danish Holstein had the smallest effective population sizes of the three breeds and Danish Red had the largest (Table 2).

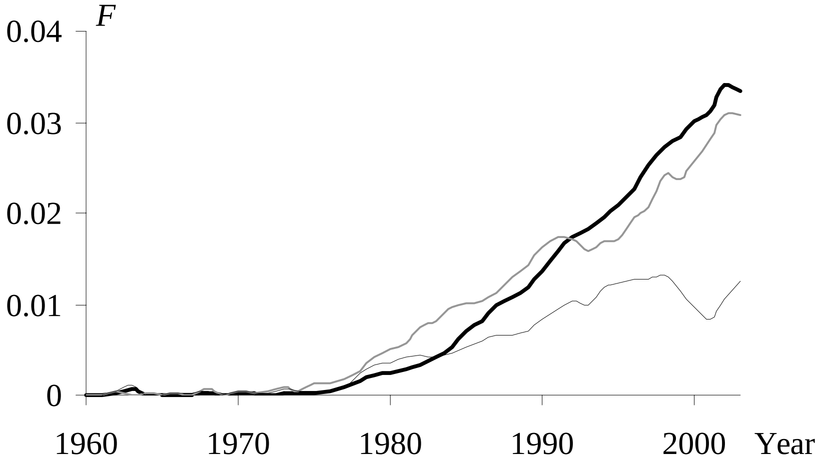

Figure 1. Average coefficient of inbreeding (F) for each birth cohort plotted against year of birth for Danish Holstein (thick line), Danish Jersey (grey line), and Danish red (thin line).

Table 2. Summary statistics of pedigree analysis in Danish dairy breeds.

	Danish Holstein	Danish Jersey	Danish Red
Effective population size	70	98	274
Effective number of founders	73.2	119.0	214.2
Effective number of ancestors	21.6	24.3	35.6
Ancestors to give 50 %	8	9	13
Ancestors to give 75 %	37	27	39
Ancestors to give 90 %	393	89	141
% explained by 1000 ancestors	91.4	94.4	94.6
Generation interval, years	4.62	4.70	4.83

GENETIC CONTRIBUTIONS

The effective number of founders (Table 2) is of the same magnitude as the effective population size for all three breeds and show large differences between breeds. The effective number of ancestors (Table 2) are smaller and more equal for the three breeds.

The five ancestors with the largest marginal genetic contributions account for almost 41 % in DH (Table 3). In DR the comparable number is less than 29 %. The 4 most important ancestors of DR belong to 4 different breeds: Red and White Holstein Friesian (Momentum), Swedish Red and White (Tor Bruno), Brown Swiss (Improver), and original DR (FYN Rosen). This highlights the synthetic character of the DR population.

Table 3. Marginal genetic contributions of most important ancestors, %.

	Danish Holstein		Danish Jersey		Danish Red	
1.	13.5	Elevation	12.0	FYN Lemvig	9.4	Momentum
2.	10.7	Arli Chief	8.9	SKÆ Hede	6.8	Tor Bruno
3.	8.3	Bell	6.3	Top Brass	4.9	Improver
4.	4.4	Dam of SWD Valiant	5.7	FYN Tanic	4.8	FYN Rosen
5.	3.9	Blackstar	5.4	FYN Haug	3.6	MRS Abru
All	40.8		38.2		29.4	

The cumulated marginal contributions show different patterns for the three breeds (Figure 2). In DH 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, DR is less influenced by a few ancestors, but there are a smaller total number of ancestors accounting for the rest. The DJ follows DH for the most important ancestors and follows DR for the ancestors with small contributions.

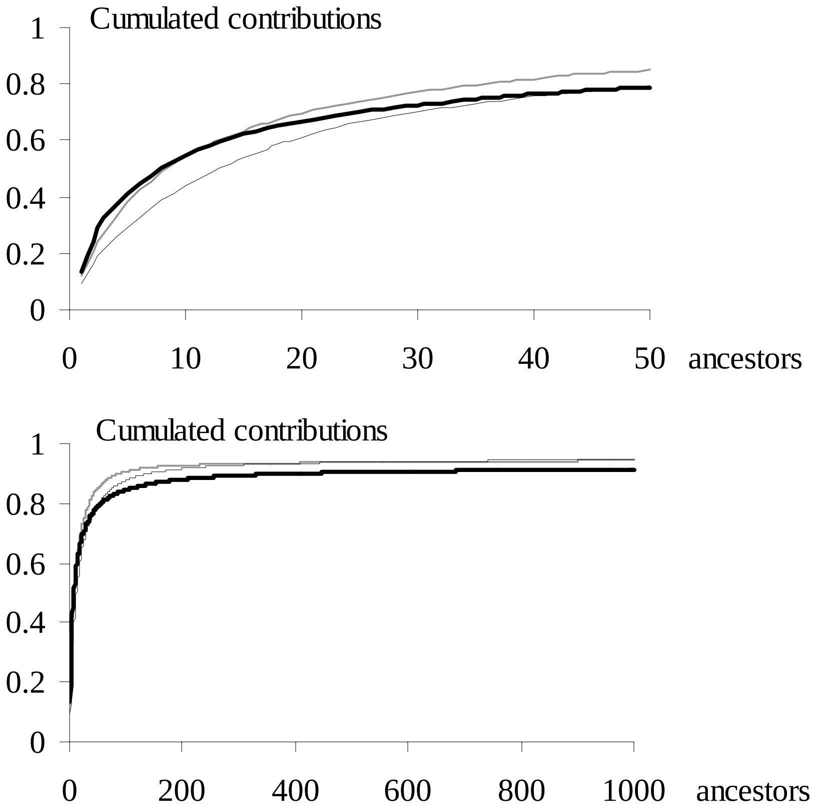

Figure 2. Cumulated marginal genetic contributions for Danish Holstein (thick line), Danish Jersey (grey line), and Danish red (thin line) up to 50 and 1000 ancestors.

COMPLETENESS OF PEDIGREES

There were no substantial differences between breeds in the completeness of pedigrees (Figure 3). Hence, the results are comparable across breeds. More than half of the reference population have pedigree completeness for five generations above 0.9, which indicates that there is sufficient pedigree information for estimation of inbreeding depression.

Discussion

The results presented in this paper highlight the impact of the current breeding programs on genetic diversity. Inbreeding has increased at a rate of 0.5 to 0.7 % per generation for Danish Jersey and Danish Holstein. The other diversity measures confirm that the current gene pool has been derived from a small number of individuals.

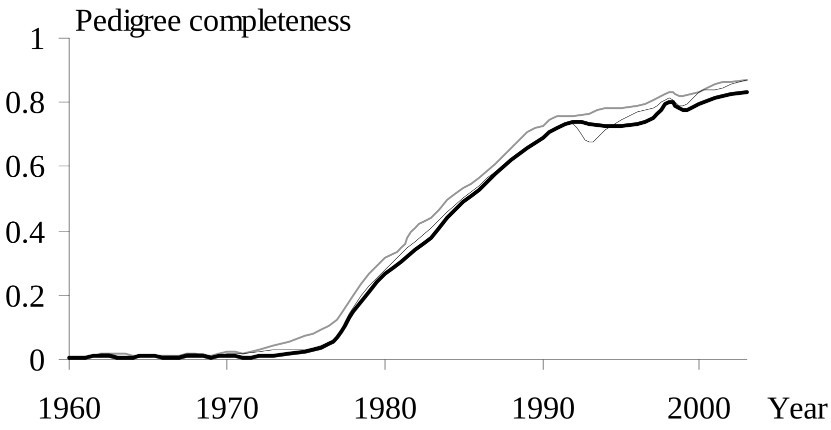

Figure 3. Average pedigree completeness index for five generations for each birth cohort plotted against year of birth for Danish Holstein (thick line), Danish Jersey (grey line), and Danish red (thin line).

For Danish Red, the importation strategy has resulted in a smaller rate of inbreeding than the other breeds. But 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. Therefore, DR needs to continue the importation from unrelated populations to keep the inbreeding trend at the current low level.

In animal breeding, the recommendation is to maintain an effective population size of at least 50-100 (Bijma, 2000). This is by no means a magic number, but is derived from theoretical arguments, where natural selection counteracts inbreeding depression. Anyway, DH and DJ both falls in this interval, and so should be concerned of controlling inbreeding in their breeding programs.

The different measures of diversity assess different aspect of diversity. The effective population size calculated from the trend in inbreeding is a historical measure with small predictive value as to what happens in the coming years. The effective number of founders is to an even higher degree a historical measure as this number is essentially insensitive to recent breeding strategies if pedigrees are reasonably deep, so contributions from founders can be expected to have converged. On the other hand, the effective number of ancestors measures the contributions of ancestors that can give rise to inbreeding in the future. This measure therefore has a higher predictive value. According to the effective number of ancestors, the three breeds are quite similar and therefore can be expected to have similar trends of inbreeding in the future. This assertion is based on the assumption that DR continues to work with the synthetic population of today. If they continue to import genetic material from foreign populations, they can keep inbreeding at low levels. The effective number of ancestors is only of predictive value if importation discontinues.

Conclusion

The breeding policies of the three Danish dairy breeds have resulted in different levels of genetic diversity within the breeds as well as different structures in the population. The Danish Holstein and Danish Jersey are very close to the minimum recommended effective population size, so tools are needed to monitor the selection process in order to control inbreeding in these populations. The Danish Red breed holds considerably more genetic diversity and is therefore less prone to inbreeding problems. However, this is only true if importations are continued.

References

Berg, P. 2003. *EVA version 1.4. Evolutionary algorithm for mate selection. User's guide.* Danish Institute of Agricultural Sciences, Foulum, Denmark.

Bijma, P. & Woolliams, J. A. 1999. Prediction of genetic contributions and generation intervals in populations with overlapping generations under selection. *Genetics* 151, 1197-1210.

Bijma, P. 2000. *Long-term genetic contributions. Prediction of rates of inbreeding and genetic gain in selected populations.* Ph.D. Thesis Wageningen University.

Boichard, D., Maignel, L. & Verrier, É. 1997. The value of using probabilities of gene origin to measure genetic variability in a population. *Genet. Sel. Evol.* 29, 5-23.

Boichard, D. 2002. Pedig: A fortran package for pedigree analysis suited for large populations. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production.* CD-ROM communication no. 28-13.

Lacy, R. C. 1989. Analysis of founder representations in pedigrees: Founder equivalents and founder genome equivalents. *Zoo Biology* 8, 111-123.

MacCluer, J. W., Boyce, A. J., Dyke, B., Weitkamp, L. R., Pfennig, D. W. & Parsons, C. J. 1983. Inbreeding and pedigree structure in Standardbred horses. *J. Hered.* 74, 394-399.

Meuwissen, T. H. E. & Luo, Z. 1992. Computing inbreeding coefficients in large populations. *Genet. Sel. Evol.* 24, 305-313.