Inbreeding and loss of founder alleles in four variations of a conservation programme using circular mating, for Danish Shorthorn Cattle

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Summary

The beef cattle breed Danish Shorthorn is used as a model for simulation of four variations of the circular mating scheme running for 50 years. Schemes 1 and 2 used a fixed exchange of bulls between female groups while schemes 3 and 4 used a random exchange of bulls between female groups. The number of bulls used in schemes 1 and 4 was 16 while the number of bulls used in schemes 2 and 3 was 8. Inbreeding levels were computed and gene dropping was applied to estimate the risk of founder allele loss. In the population of year 50 the inbreeding levels for the four mating schemes are not statistically different. The male founder alleles contribute strongly to the population of year 50. The female founder alleles are in greater risk of being lost than the male founder alleles.

Résumé

La race bovine à viande Danish Shorthorn est utilisée comme modèle pour la simulation de quatre variations du schéma circulaire d’accouplement au long de 50 ans. Les schémas 1 et 2 utilisent un échange fixe de taureaux dans des groupes de femelles. Le nombre de taureaux utilisés dans les schémas 1 et 4 a été de 16, tandis que le nombre de taureaux utilisés dans les schémas 2 et 3 était de 8. On a établi les niveaux de consanguinité et appliqué le comptage des gènes pour estimer le risque de perte d’alleles de base.

Key words: Gene dropping, Diversity, Beef cattle.

Introduction

Several methods for the conservation of animal genetic diversity have been developed. Cryogenic storage is a conservation method free from human interference which might bring about genetic change (Bodó, 1990). Though storage of frozen semen and embryos has been known and used for years, the most important and practical method of conserving genetic diversity now and in near future is to manage genetic variability in some small living populations (Smith, 1984; Wang et al., 1994). For most livestock breeds the conservation of a living population involves private breeders. Therefore it is necessary to have the support of the breeders if a conservation programme is to be a success (Rognoni & Finzi, 1984). This calls for breeding plans that are fairly easy for the breeders to implement in the population, e.g. breeding plans that fit the demographic structure of the population.
Many studies have been carried out on the topic of conserving small populations with a minimum of inbreeding (Kimura & Crow, 1963; Smith, 1984; Chevalet & Rochambeau, 1985; Bodó, 1990; Wang et al., 1994). The majority of the authors suggested dividing the population into breeding groups of females and a rotation of males among the groups in a circular mating scheme. Chevalet & Rochambeau (1985) compared three turnover rates of the males in a circular mating scheme implemented in a small dairy cattle breed by simulations. In the first and second systems the males were used for two years in each group of females; totally the males were used for 16 years. In the first system the bulls were replaced by a son. In the second system the programme was initiated by selection of eight bulls and one male offspring of each bull as a replacement male. When a bull was culled the replacement male became the new bull and one of the culled bulls sons was selected as a new replacement male. Thus, the second system prolonged the generation interval of the males as compared to the first. In the third system the males were only used for two years and only in one group of females. Chevalet & Rochambeau (1985) found that prolonging the generation interval of the males delayed the inbreeding, but the rapid turnover (system three) gave the lowest inbreeding level.

Not only is the inbreeding of concern in conservation genetics, attention has also been given to the founder representation in the population under study and to preventing loss of founder alleles in the future (Chevalet & Rochambeau, 1985; MacCluer et al., 1986; Lacy, 1989; Boichard et al., 1997). With fewer breeding males than females, as is the case in cattle populations, there is a tendency of loss of female founder alleles, but a rapid turnover of the males enables the population to keep alleles from the female founders (Chevalet & Rochambeau, 1985).

In the circular mating schemes outlined by other authors (Kimura & Crow, 1963; Chevalet & Rochambeau, 1985) a fixed scheme is used for the exchange of males between the groups of females. In practice breeders might find it difficult to follow such a strict plan for the use of the males.

In this paper the objectives are:
1. to test the hypothesis that a random exchange of males between the groups of females increases the inbreeding level compared to an exchange of males that follows a fixed scheme;
2. to test the hypothesis that increasing the number of males will result in a decrease in female founder alleles.

Materials and Methods

Data of the beef cattle breed Danish Shorthorn (figure 3), provided by The National Committee of Danish Cattle Husbandry, is used as a model for simulations of four variations of the circular mating scheme. The first generation in the simulation of the mating schemes is founded by the Danish Shorthorn population of 1997 which consisted of 96 females and 8 males (Trinderup et al., 1998). This year is referred to as year zero in the simulations.

Initially the females are divided into eight breeding groups, each of 12, referring to the original herds found in the data material. The number of females is fixed through the time period simulated to exclude the effect of fluctuations in population size.

Based on the age distribution of the females found in the data the replacement rates over age classes were computed (table 1). These replacement rates were used as culling probabilities for the cows in the simulations. As can be seen in table 1, the maximum age of females was set to 12 years in the simulations. The females were at least two years before they were mated for the first time. Once a cow was mated it was assumed that she gave birth to one calf of random sex each year until she was culled. To prevent loss of female founder alleles and to reduce variation in female family size the first choice of a replacement heifer was a daughter of the culled cow. A cow’s offspring were kept in the population until she was replaced in order to maximize the possibility of having a daughter for
replacement. Otherwise a heifer from the same breeding group or herd was randomly selected.

The difference between the four mating schemes was the way the breeding bulls were used in the population as illustrated in figure 1 and outlined in the following.

**Scheme 1**

Each of the eight bulls were assigned to one of the eight herds in year 0. Each bull was mated to all the females of his herd in year 0 and one son was randomly selected. Each of the eight selected young bulls were sent from the \( j \)’th herd to the \( j+1 \)’th herd, except for the 8’th herd where the young bull was sent to the first herd. After year 0 the ‘old’ bulls were mated to the cows and the ‘young’ bulls were mated to the heifers. The following year, after a new rotation of young bulls, the ‘old’ bulls were culled and replaced by the ‘young’ bulls, who now were mated to the cows, and the new ‘young’ bulls were mated to the heifers. Thus, each breeding bull was used in two years. The rotation of bulls follows a fixed system which ensures that the male descendant of a certain bull returns to the herd with the female descendants after eight rotations. This scheme doubles the number of males from the original eight to sixteen.

**Scheme 2**

This scheme was similar to scheme one, except that here was only one bull per herd. This bull was mated to both heifers and cows. The bulls were only used for one year before they were replaced by one of their sons and the number of bulls was kept at the original eight.

**Scheme 3**

As scheme 2, but here the bulls were randomly assigned to a herd. This means that a bull was allowed to breed in the herd that he was born in.

**Scheme 4**

As scheme 1, except that the ‘young’ bulls were randomly selected among all the bull calves born and all living, non-breeding bulls up to 10 years of age. As in scheme 1 the breeding bulls were culled after two years. The selected bulls were not assigned to any herd, but could be mated to all cows and heifers in the population just like bulls from artificial insemination centres (A.I.-bulls). PASCAL programmes were written to simulate the circular mating schemes. Each simulation of a mating scheme had a time span of 50 years or approximately 12 generations and were repeated 200 times.

The inbreeding coefficient for each animal was computed as proposed by Quaas (1976). The base animals for the inbreeding coefficient computation were the animals with unknown parents found in the data of Danish Shorthorn (Trinderup et al., 1998). The founders of the circular mating schemes, the Danish Shorthorn population of 1997, were therefore not unrelated animals as defined by other authors (e.g. Lacy, 1989), but the animals entering the circular mating schemes (Foose, 1986; Falconer & Mackay, 1996). The founders of the circular mating schemes were the reference generation of a gene dropping (MacCluer et al., 1986) which was conducted in order to estimate the founder representation after 50 years of breeding.

**Results**

Figure 2 shows the change in mean inbreeding coefficient over time in the four circular mating schemes. The inbreeding coefficients were highest in the schemes with random exchange of bulls in the first seven years of the simulations. But for animals born after year eight the inbreeding coefficients were almost the same in all four mating schemes.

Table 2 shows the inbreeding levels and trends with the standard deviation for the animals in the population of year 50. To reduce the confounding of the year of birth and the number of ancestral generations the
Inbreeding and loss of alleles in Danish Shorthorn cattle

Figure 1. Illustration of the differences between the four mating schemes.

Figure 2. Average inbreeding levels per year of birth.
inbreeding trends should be tabulated for animals with more than seven ancestral generations (Te Braake et al., 1994). Thus, the inbreeding trends were tabulated from the two last generations in the simulations. The schemes with random exchange of bulls had the largest inbreeding trend and thus the smallest effective population size. Though scheme 4 (16 bulls) had the second highest inbreeding trend, this scheme resulted in the lowest mean inbreeding trend in the population of year 50. Scheme 1 (16 bulls) had the lowest inbreeding trend and the second lowest mean inbreeding levels at the end of the simulations. However, the standard deviations indicate that there is no statistical difference between the four mating schemes in rate of inbreeding and mean inbreeding level in the population of year 50.

Table 3 shows the result of the gene dropping. The criteria used here were the average contribution of alleles from each male and female founder, the total male and female founder allele contribution and the minimum and maximum percentage of the 200 replicates in which the alleles of a male or female founder was lost. The mating schemes using 16 bulls (i.e. schemes 1 and 2) resulted in the largest individual and total contribution of male founder alleles and the smallest minimum values of percent replicates with male founder allele loss. In all four mating schemes the maximum and minimum percent replicates with male founder allele loss were lower than the percent replicates with female allele loss. The percentages of replicates where the alleles of a female founder were lost were very much the same for all four mating schemes, due to the fact that the replacement strategy was identical in all four mating schemes.

**Discussion**

It was expected that if there were any differences in inbreeding trends among the four mating schemes they would be small, because the same replacement strategy for the females were used in all the mating schemes, the difference in population size was very small and there were only small variations in the generation length for the males. In the simulations there was no significant difference in inbreeding trend or in inbreeding level after 50 years. In the first few years there seems to be a difference between the schemes using random exchange of males and the schemes using a fixed plan for exchange of males. This confirms the hypothesis that random use of males results in an instantly higher inbreeding level, but the difference is not permanent. When the first rotation of males is completed, the inbreeding increases in the schemes with fixed exchange of males to the level of the schemes with random exchange of males after which the rate of inbreeding is fairly similar in all four mating schemes.

Concerning the inbreeding level and trend it can be concluded that it is not important that the breeders follow a strict plan for the exchange of males as long as they follow the guidelines used in these simulations: minimising the variation of family size within sires and dams and avoid fluctuations of population size. The size of inbreeding trend found in these simulations of about 0.5% is acceptable in any breeding plan, because with such a low increase in inbreeding it is possible to select the animals showing the least inbreeding depression (Adalsteinsson et al., 1994).

The distribution of male and female alleles in the founder population (year 0) is 7.7% male founder (8 bulls among 104 animals) alleles versus 92.3% female founder alleles (96 cows among 104 animals). The total contribution to the population of year 50 found in schemes 2 and 3, using eight bulls, was 20% male founder alleles and 80% female founder alleles (table 3), as found by Chevalet & Rochambeau (1985) in a simulation study running over 40 years. The change in the contribution of male and female founder alleles over years is due to the more intense use of bulls. Hence the male founder alleles are over-contributing to the population of year 50, whereas the schemes fail to some extent to keep the female founder alleles segregating.
Table 1. Replacement probabilities for female age classes.

<table>
<thead>
<tr>
<th>Age, years</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
</tr>
</thead>
<tbody>
<tr>
<td>Probability</td>
<td>0.178</td>
<td>0.159</td>
<td>0.209</td>
<td>0.137</td>
<td>0.267</td>
<td>0.189</td>
<td>0.267</td>
<td>0.318</td>
<td>0.333</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Table 2. Mean inbreeding and inbreeding trend with standard deviation in the population of year 50.

<table>
<thead>
<tr>
<th>Mating scheme</th>
<th>Inbreeding trend a)</th>
<th>$N_e$ b)</th>
<th>Mean inbreeding c)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%</td>
<td>S.D.</td>
<td>%</td>
</tr>
<tr>
<td>1</td>
<td>0.47</td>
<td>0.22</td>
<td>106</td>
</tr>
<tr>
<td>2</td>
<td>0.52</td>
<td>0.19</td>
<td>97</td>
</tr>
<tr>
<td>3</td>
<td>0.62</td>
<td>0.37</td>
<td>81</td>
</tr>
<tr>
<td>4</td>
<td>0.55</td>
<td>0.32</td>
<td>91</td>
</tr>
</tbody>
</table>

a) Computed from the last two generations and averaged over the 200 replicates.
b) Calculated by the equation: $N_e = 1/(2*\Delta F)$.
c) Mean inbreeding coefficient of the last generation averaged over the 200 replicates.

Table 3. Founder contribution to the population of year 50 and risk of allele loss.

<table>
<thead>
<tr>
<th>Mating scheme</th>
<th>Individual contribution of the two sexes, %</th>
<th>Total contribution of the two sexes, %</th>
<th>Replicates with founder allele loss, %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>males</td>
<td>females</td>
<td>males</td>
</tr>
<tr>
<td>1</td>
<td>3.07</td>
<td>0.79</td>
<td>24.52</td>
</tr>
<tr>
<td>2</td>
<td>2.44</td>
<td>0.84</td>
<td>19.54</td>
</tr>
<tr>
<td>3</td>
<td>2.54</td>
<td>0.83</td>
<td>20.31</td>
</tr>
<tr>
<td>4</td>
<td>3.04</td>
<td>0.79</td>
<td>24.34</td>
</tr>
</tbody>
</table>

Our simulations indicate that in a conservation programme using a circular mating scheme it can be up to the individual breeders to manage the exchange of bulls among the groups of females. The over contribution of founder sire alleles found in this investigation indicates that the initiating sires of a conservation programme should be selected carefully. A method to ensure that the founder sires of a conservation programme are of the type of interest is the gene dropping method as shown by Trinderup et al. (1998). The observed small differences between the four mating schemes indicate that other factors, such as economy, should be considered in the choice of conservation programme.
References


Inbreeding and loss of alleles in Danish Shorthorn cattle


