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Running title: Effect of sire mating patterns on future genetic structures

Effect of sire mating patterns on future genetic merit and inbreeding in a closed beef cattle population

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Keywords

beef cattle; genetic merit; inbreeding; mating frequency; number of sires; service period; simulation.

Summary

Alternative breeding strategies were simulated based on the population structure of the Tajima strain of Japanese Black cattle. An analysis of the population structure revealed that some sires up to 20 years of age have been used in Tajima. In addition, 95% of newborn calves were the progeny of only 20 sires, and their mating frequencies were significantly skewed. The current average inbreeding coefficient and founder genome equivalents of the strain were estimated to be 0.199 and 2.25. Average inbreeding coefficient is expected to reach 0.394 within 27 years. Thus, different breeding strategies were assessed for their effect on the level of inbreeding and average genetic merit. We compared strategies that 1) halve the sire service period, 2) double the number of mating sires, and 3) lower the skewed sire mating frequency and optimize the frequency for weighted genetic merit and diversity. Reducing the service period yielded a 7.0 to 12.0% reduction in the rate of inbreeding while maintaining almost the same genetic gain. Increasing the number of sires resulted in a 19.3 to 21.3% reduction in inbreeding with a corresponding 1.6 to 8.4% reduction in gain. The rates of inbreeding from the optimized strategies decreased as the weight on genetic diversity increased. However, a strategy that emphasized only genetic gain yielded lower gain than other strategies because the strategy allowed only one sire to mate and resulted in reduced genetic variance and low accuracy of genetic evaluation. In contrast, a strategy with no emphasis on genetic gain when determining mating frequency resulted in reductions of 16.0% and 63.2% in genetic gain and inbreeding. The strategies examined here are easily applicable and can be expected to reduce immediate loss of genetic diversity.

Introduction

The balance between genetic response and the rate of inbreeding must be considered in most breeding plans. It is relatively easy to focus on only one factor - however, factors can conflict and make planning very difficult. Possible solutions have been proposed by many authors. Some solutions employ in the breeding value prediction the use of higher heritability than the estimated one (Grundy *et al.* 1994), non-random mating (Sonesson & Meuwissen 2002), and parental contributions that consider the future inbreeding level with discrete generations (Wray & Goddard 1994; Brisbane & Gibson 1995) and with overlapping generations (Meuwissen & Sonesson 1998; Grundy *et al.* 2000). While the effectiveness of such sophisticated methods has been confirmed through simulation, actual populations are often larger than simulated ones and have complex relationships due to past selection. Thus, each method's impact on the existing population is an interesting subject for research.

Japanese Black cattle, one of the four Wagyu breeds, is the most common beef breed in Japan, with a population of 0.6 million breeding females. Breeding of Japanese Black is usually conducted within each local subpopulation along with some genetic migration from other subpopulations. A subpopulation called the Tajima strain consists of 12,000 breeding females and has supplied a considerable amount of breeding stock throughout Japan due to its prominent feature of beef marbling (Mukai *et al.* 1989). However, Tajima has not allowed any migration from other subpopulations for more than 100 years. Moreover intensive use of a few sires resulted in high inbreeding in Tajima and Honda *et al.* (2001) warned of the rapid decline of its genetic diversity. The Japanese Black population has scarce genetic resources outside of Japan, and thus a similar decline is expected throughout the breed. Action must be taken to prevent the decline.

The present study attempts to forecast the future of Tajima under the current breeding

structure and examine the effect of alternative sire mating patterns on genetic diversity through a stochastic simulation. The sire mating patterns here include the number of individuals, service period, and mating frequency. We compared these strategies with optimal selection, optimally balancing genetic gain and diversity based on the approach by Wray & Goddard (1994).

Materials and methods

Analysis of the breeding structure

All available parturition and pedigree records of Tajima were extracted from the Wagyu Registry Association database. The records covered 147,812 parturitions of 25,454 cows from December 1984 to March 2002. The number of calvings, selection intensity, number of service sires, and service periods of Tajima were then analyzed and incorporated into the simulation.

Lifetime calf production of cows. Only the cows that had already been culled, should be used to obtain basic information on lifetime calf production. The culling dates were not recorded for Japanese Black, and thus we used records from cows born before 1984. The 18,787 parturition records from 2,246 cows met the conditions, and the number of calvings in a lifetime were counted for the cows. The analysis showed that 39 % of all the cows calved nine to twelve times in their lifetime (Fig. 1). Although presently existing cows may be used differently, we assumed that the data in Fig. 1 reflects the current situation - recent data will become available only when all the existing cows have been culled.

Number of service sires. All Tajima calves are produced by artificial insemination and therefore the number of service sires is limited. The most frequently used 5, 10, 15, and 20 sires in each year account for 71%, 88%, 93%, and 95% of the total calf production on average over the past five years. Increasing the number did not significantly affect the proportions, and thus we assumed that 20 sires were used at a time in the simulation study. The frequency of usage of the 20 sires was stretched by multiplying the frequency value by 1.053 (= 100/95) to bring the total to 100%; this is indicated by the closed bar ("highly skewed") in Fig. 2. The frequencies were extremely skewed, and the top sire accounted for 22% of the total number of calves. The amount of beef marbling strongly determines the carcass price in Japan, and it is likely that those 20 sires are genetically superior for marbling. There is no doubt that the skewed frequencies have rapidly narrowed the genetic diversity of the breed.

Simulation

Basic structure. Stochastic computer simulations modeled according to the Tajima strain were carried out to estimate the genetic gain and inbreeding for the near future. The simulation proceeded in units of 400 days based on the average calving interval of Japanese Black (Oyama *et al.* 2002). A unit is hereafter referred to as a cycle; we use C_i to indicate the *i*-th cycle. Actual service sires and 15,125 cows that had calved within the most recent two cycles were regarded as alive and were randomly mated with equal frequency to produce the base population, C_0.

We assumed that beef marbling was the target trait for genetic improvement and predicted breeding values (PBV) of the trait calculated in November 2002 were used as true breeding values for parents of C_0 in the simulation. The heritability was estimated

to be 0.56 in the evaluation. Progeny true breeding values were obtained by averaging the true breeding values of the parents plus Mendelian sampling terms, which were sampled from a normal distribution following $N(0, 0.5(1-\overline{F})\sigma_A^2)$, where $\overline{F}$ is the average inbreeding coefficient of parents and σ_A^2 is the additive genetic variance of the base population. The phenotypic record represented the sum of the true breeding value and the environmental component, which followed $N(0, \sigma_E^2)$, where σ_E^2 denotes the environmental variance. No inbreeding depression was assumed for the selected trait or fitness-related traits. The PBV were calculated by the animal model BLUP at each cycle.

Every year approximately 16 newborn bulls are chosen for performance tests in Tajima. Six to seven performance-tested bull calves then proceed to the progeny test. The bulls are added to the Tajima service sire list after the two tests. We chose six to seven newborn bulls at birth in each cycle for the simulation using the average PBV of the parents since the PBV of actual bulls become available only after progeny testing. Random selection was applied to heifers with a selected proportion of $p = 0.239$ at birth. The remaining newborn bulls and heifers were treated as feeder cattle. Phenotypes were assigned to feeder cattle three cycles old and used to calculate the PBV. Selected bulls and heifers became available for breeding when they reached the respective ages of three and two cycles. A more advanced age was assumed for bulls since in practice they need to be performance and progeny tested. Both sires and cows could breed up to the age of 18 cycles. However, this does not imply that all breeding animals continue to produce up to that age. Due to artificial insemination (frozen semen), all sires were assumed available until they were 18 cycles old, but only 20 sires with the highest PBV at a time were given the opportunity to breed. The service periods for cows were

randomly determined following the distribution presented in Fig. 1. Thus, the cows born in one cycle are culled gradually. Their days in the herd varied and overlapping generations were simulated. All dams in use were randomly mated to one of the 20 sires and delivered calves at each cycle.

Strategies for the number of sires. It is conceivable that the decline of genetic diversity can be reduced by simply increasing the number of service sires. We considered two situations in which 20 and 40 sires with the highest PBV (denoted as 20 and 40) could be used at a time.

Strategies for mating frequency. The frequencies indicated by the closed bar in Fig. 2 were the results of actual economic activities of cow-calf operators. We labeled the frequency with "H" since it was highly skewed. Reduction of the skewness is useful for maintaining diversity. Thus, we considered strategies in which the frequencies were equal or their distribution was only moderately skewed (labeled E and M). The frequencies of strategy M represent the averages of H and E. For example, the frequency of the top sire would be 0.135 for strategy M since the frequencies of strategies E and H were 0.05 and 0.22. Each frequency for 20 sires was equally split into two frequencies when 40 sires were used. Sires with higher PBV were assigned higher frequencies in strategies H and M.

In addition, we used a method similar to Wray & Goddard (1994) that simultaneously considers both genetic merit and diversity. Let **m, u,** and **1** denote the vectors of the mating frequency, the PBV, and ones, and subscripts S and D be sires and dams. Assuming one calf for all n_D dams, the expected average breeding value of their

progeny becomes

$$G = \frac{1}{2}\mathbf{m}_S'\mathbf{u}_S + \frac{1}{2n_D}\mathbf{1}_D'\mathbf{u}_D .$$

The average additive relationship (= twice the coancestry) among progeny can be expressed as

$$\begin{aligned}\bar{r} &= \frac{1}{4}\left[\mathbf{m}_S'\mathbf{A}_{SS}\mathbf{m}_S + 2\mathbf{m}_S'\mathbf{A}_{SD}\mathbf{m}_D + \mathbf{m}_D'\mathbf{A}_{DD}\mathbf{m}_D\right] \\ &= \frac{1}{4}\left[\mathbf{m}_S'\mathbf{A}_{SS}\mathbf{m}_S + \frac{2}{n_D}\mathbf{m}_S'\mathbf{A}_{SD}\mathbf{1}_D + \frac{1}{n_D^2}\mathbf{1}_D'\mathbf{A}_{DD}\mathbf{1}_D\right]\end{aligned}$$

where **A** is the additive relationship matrix. Thus,

$$GD = 1 - \frac{\bar{r}}{2}$$

represents a measure of genetic diversity that accounts for unequal genetic contributions among the founders, genetic drift caused by Mendelian sampling, and bottlenecks (Caballero & Toro 2000). Our objective was to determine $\mathbf{m}_S$ for 20 sires, which maximizes

$$V = w \cdot GD + (1 - w) \cdot G$$

under the constraint of $\mathbf{m}_S'\mathbf{1}_S = 1$. With a LaGrange multiplier (λ), it is achieved by differentiating

$$V - \lambda(\mathbf{m}_S'\mathbf{1}_S - 1)$$

with respect to the unknown $\mathbf{m}_S'$ and equating the partial derivative to 0. Solving the equation gives the optimized $\mathbf{m}_S$ (labeled O) as

$$\begin{aligned}\mathbf{m}_S = &\frac{1}{\mathbf{1}_S'\mathbf{A}_{SS}^{-1}\mathbf{1}_S}\mathbf{A}_{SS}^{-1}\mathbf{1}_S + \frac{1}{n_D}\left(\frac{\mathbf{1}_S'\mathbf{A}_{SS}^{-1}\mathbf{A}_{SD}\mathbf{1}_D}{\mathbf{1}_S'\mathbf{A}_{SS}^{-1}\mathbf{1}_S}\mathbf{A}_{SS}^{-1}\mathbf{1}_S - \mathbf{A}_{SS}^{-1}\mathbf{A}_{SD}\mathbf{1}_D\right) \\ &+ \frac{2(1-w)}{w}\left(\mathbf{A}_{SS}^{-1}\mathbf{u}_S - \frac{\mathbf{1}_S'\mathbf{A}_{SS}^{-1}\mathbf{u}_S}{\mathbf{1}_S'\mathbf{A}_{SS}^{-1}\mathbf{1}_S}\mathbf{A}_{SS}^{-1}\mathbf{1}_S\right)\end{aligned}$$

for $0 < w \leq 1$. The first term of the right hand side can be obtained when only the contribution from male parents to the progeny, $\mathbf{m}_S' \mathbf{A}_{SS} \mathbf{m}_S$, is minimized. The second term is obtained by adding the relationship between male and female parents, $\mathbf{m}_S' \mathbf{A}_{SD} \mathbf{m}_D$, for minimization. The third term is attained by considering G for optimization. We cannot substitute 0 for w, but it is obvious from the definition of V that $w = 0$ indicates the use of only one sire with the highest PBV since it optimizes the genetic merit only. The expression may produce $\mathbf{m}_S$ with negative elements, *i.e.* negative mating frequencies. We removed the sire with the greatest negative frequency; this was repeated until all frequencies were non-negative (Meuwissen 1997). Wray & Goddard (1994) ignored $\mathbf{m}_S' \mathbf{A}_{SD} \mathbf{m}_D$ since they assumed that it was affected little by the choice of $\mathbf{m}_S$. It was left in the expression in our simulation to possibly determine a more efficient $\mathbf{m}_S$.

Strategies for the length of service period. An analysis of the population structure revealed that some sires in Tajima were used until they were approximately 20 years old, which is equivalent in age to 18 cycles. In addition to the superior genetic advantage of those sires, artificial insemination prolonged the service period. We assumed two different upper limits of the service period in the simulation, up to 18 or 9 cycles (labeled N and S), to investigate the effect of the service period. This does not necessarily signify that sires must be used until those ages. Only 20 or 40 sires with the highest PBV at a time had the opportunity to breed.

We examined three factors. A label was designated for each factor, and they were combined to express a strategy. For example, M40N denotes the strategy for a

moderately skewed frequency for 40 sires with a normal service period. Each strategy proceeded to C_{25}, which was equivalent to 27.4 years, and the results were the averages of 50 simulation replicates.

The rate of inbreeding was calculated as $\Delta F = (F_i - F_{i\text{-}1}) / (1 - F_{i\text{-}1})$ where F_i is the average inbreeding of animals born in C_i. Genetic diversity in the cycles was also measured using the founder genome equivalents:

$$d = \frac{1}{\bar{r}}$$

(Caballero & Toro 2000). In all strategies, d was estimated to be 2.25 at C_0, indicating that only genomes that originated from the two founders were left for the recent strain. Moreover, we defined the genetic gain divided by the rate of inbreeding as a measure of efficiency for each strategy. We performed the Wilcoxon's rank sum test implemented in JMP IN version 5 (SAS Institute) to examine the significance between the two strategies.

Results and discussion

Table 1 summarizes the results from all the strategies examined. We treated H20N, a strategy of highly skewed frequency for 20 sires with a normal service period, as the basis for comparison since it would best approximate what is happening in the actual breeding population. Changes in the average breeding value and cumulative inbreeding from H20N are illustrated in Fig. 3. The average inbreeding at C_0 was 0.199, which is considerably high. It would be doubled and reach 0.394 if H20N continued to C_{25}. The rate of inbreeding from C_6 to C_{25} was 1.14% per cycle (Table 1). Thus, the rate of inbreeding per generation is estimated to be 10.4% (= 1.14×365×10/400) in H20N if we assume that the generation interval of Japanese Black is ten years (Nomura *et al.* 2001).

An accumulation of inbreeding is unavoidable if the strain has been closed. It is difficult to determine what kind of increase is acceptable since each population has a different genetic status, *e.g.* the effect and frequency of detrimental genes. Goddard & Smith (1990) recommend an effective population size of 40, which is equivalent to 1.25% per generation, as an example that allows high short-term gains while alleviating fears about inbreeding. The rate expected in future Tajima strains is extremely high compared with their recommendation.

Effect of the service period

The highest genetic gain per cycle was achieved with H20N (highly skewed distribution for sire usage, 20 sires used at a time and normal service period) (Table 1). H20S was the only strategy examined that gave almost the same genetic gain and revealed no significant difference from H20N. The average generation interval from sires to progeny was 5.9 cycles in H20S and 6.7 in H20N. H20S resulted in a 7.0% lower rate of inbreeding relative to H20N and also a slight increase in founder genome equivalents at C_{25}. Although the differences were not significant, a small effect of shortening the service period appeared to exist. The effect increased under less-skewed frequencies, as indicated in Table 1. For example, the efficiency (genetic gain / rate of inbreeding) of M20S was 14.9% greater than M20N, while only 8.9% greater efficiency was observed for H20S compared to H20N. A similar tendency was observed between strategies of equal frequency. One method for reducing inbreeding is to slow down the turnover of generations (Sonesson *et al.* 2002). Strategies with a shorter service period would accelerate the turnover and contribute to greater inbreeding. However, they can terminate the use of genetically outstanding sires and, as a consequence, lead to fewer

progeny per sire and reduced variance in the number of progeny. In terms of genetic merit, they force the use of inferior sires. Thus, they are a factor in decreasing genetic gain. However, comparable genetic gain can be obtained from a shorter service period with gain from a normal period if selection is applied properly, since any decreased genetic gain per generation can be compensated by accelerated generation turnover.

Effect of the number of sires

Using 40 sires resulted in 19.3% less inbreeding and a 5.3% reduction in genetic gain at highly skewed frequencies (H20N vs H40N, Table 1 and Fig. 3). A significant effect on inbreeding was observed. The efficiencies of 40-sire strategies were 22.0, 27.6, and 16.9% greater in highly skewed, moderately skewed, and equal frequencies than those of 20 sires. The mechanism to reduce inbreeding by adding more sires seems similar to that by a shorter service period. Both have the effect of increasing the number of males to be parents and contribute to a reduced number of sibs. Optimized strategies do not necessarily use 20 sires at each cycle because sires with negative mating frequencies are removed, whereas other strategies must use specified numbers of sires. A negative frequency can occur when the off-diagonal element in the relationship matrix is greater than the diagonal element (Eding *et al.* 2002). The number of actually used sires for all optimized strategies except $w \approx 0$ tended to increase in the early cycles. The numbers then settled and stayed the same at later cycles (data not shown), most likely due to the lack of available sires as a result of high coancestry with other sires and dams in early cycles. Continuing the strategies considering the relationships among progeny appeared to create new sire lines with lower coancestry with the current population. Optimized strategies with $w = 0.25$, 0.50, 0.75, and 1.00 utilized averages of 2.1, 3.6, 7.4, and 15.1

sires per cycle during the simulation. More sires were used as the need for genetic diversity increased.

Effect of the mating frequency

The mating frequency had significant effects on inbreeding, as indicated in Table 1 and Fig. 3. M20N, E20N, and O20N $w = 1.00$ yielded 12.3, 29.8, and 63.2% less inbreeding compared to H20N. The cumulative inbreeding at C_{25} from the respective strategies was 0.372, 0.343, and 0.274. Reductions in genetic gain were 4.6, 9.2, and 16.0% in M20N, E20N, and O20N $w = 1.00$. The impact on inbreeding was much greater than the loss in genetic gain. Variation of family size is the most important deviation from the breeding system of an idealized population and usually renders an effective number that is lower than the actual amount (Falconer & Mackay 1996). Manipulating the mating frequency directly affects the family size and results in a lower inbreeding rate. The founder genome equivalents at C_{25} were 1.30, 1.40, and 1.76 for M20N, E20N, and O20N $w = 1.00$. Continuing with O20N $w = 1.00$ consumes 0.49 founder genome in 25 cycles, whereas H20N consumes 1.03 genome, which is equivalent to 45.8% of that which initially remained at C_0.

A rapid increase in genetic gain was observed in early cycles of O20N $w \approx 0.00$ and $w = 0.50$, but it slowed in later cycles (Fig. 3). Although strategies with smaller w were intended to achieve increased genetic response, O20N $w = 0.75$ yielded the greatest gain among the optimized strategies. The genetic gain from O20N $w \approx 0.00$ in particular was the lowest with the largest standard error (Table 1). This extreme strategy uses only one sire with the highest PBV, and all progeny born in a cycle are half-sibs. It rapidly reduces available number of families and genetic variance. Moreover the accuracies of

PBV for sires do not improve significantly because most of the sires have no chance to leave progeny. Lower accuracy of genetic evaluation is an additional factor for the less gain. The largest standard error also clarifies the risk of using this strategy.

The rates of inbreeding from optimized strategies corresponded to the magnitude of w. O20N $w \leq 0.50$ exhibited the higher rates and lower efficiencies than H20N. The choice of w is not straightforward since the objective function, V, is the sum of two different components. The value of w should change depending on the status of the genetic level and the diversity of the target population. Moreover, the status changes as selection proceeds. Thus, deriving a method that can determine the weights for long term optimization remains an unresolved problem.

Genetic diversity inevitably decreases in a closed population. The diversity of the strain can easily be extended by introducing breeding stock from outside of the Tajima strain. However, Tajima has symbolic significance for Wagyu breeds and thus genetic migration should be the last option, considering the history and importance of the strain. A strategy to reduce a rapid decline in genetic diversity is required so that the effect of detrimental genes would appear gradually.

The mating frequency exhibited the greatest effect among the three factors investigated in this study. Of course, a combination of factors can enhance their effect on the inbreeding rate. The lowest inbreeding strategy, O20N $w = 1.00$, produced the greatest founder genome equivalents at C_{25} (1.76) and the least inbreeding (0.42% / cycle). This could be achieved at the cost of a 16.0% reduction in genetic gain compared with H20N. However, the inbreeding for O20N $w = 1.00$ was equivalent to 3.8% / generation, still greater than the level suggested by Goddard & Smith (1990). Although putting a

commercial beef herd in such a strategy may raise objections because of the low expected genetic gain, we may have to adopt such a strategy in the near future if the breeders want to keep the Tajima strain closed.

This study assumed that the selection for heifers was random. Cow-calf operators selecting replacements tend to keep heifers with superior genetic merit. Therefore, our assumption may be a factor in underestimating both genetic gain and inbreeding in all strategies. Furthermore, we did not include any inbreeding depression for the selected traits and fitness, *i.e.* survival and reproductive traits. We could expect smaller differences in genetic gain among the strategies if we could assume depression for such traits. It could be possible for strategies with less inbreeding to overtake the others, depending on the amount of depression assumed.

Sires for breeding were selected by PBV alone in the simulation. As we also demonstrated, consideration at the mating stage can improve the genetic structure of the population for the next round of selection (Sonesson & Meuwissen 2002), but additional reduction in inbreeding may occur if consideration is done at the selection stage. Moreover, it is important to examine the number of progeny that each parent produced during previous cycles since the impact of inbreeding occurs on a per-generation basis (Grundy *et al.* 2000). Although this study has unresolved issues, it seems likely that somewhat simple manipulations of the sire mating patterns may be useful for preventing the immediate loss of genetic diversity. The strategies examined here can be immediately applied by local governments, which usually manage all Wagyu sires, if they choose to do so.

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Table 1. Average genetic gain (genetic s.d. unit) and increase in inbreeding per cycle during cycle 6-25 (± s.e.), founder genome equivalents at cycle 25 (C_{25}), and efficiency (genetic gain per unit increase in inbreeding) of various strategies.

Strategy[1]	Genetic gain (σ / cycle)	Increase in inbreeding, ΔF (% / cycle)	Founder genome equivalents at C_{25}	Efficiency (σ / %)
H20N	0.131 ± 0.016	1.14 ± 0.32	1.22	0.123
H20S	0.130 ± 0.015	1.06 ± 0.35	1.25	0.134
H40N	0.124 ± 0.012*	0.92 ± 0.30**	1.34	0.150
M20N	0.125 ± 0.012*	1.00 ± 0.27*	1.30	0.134
M20S	0.125 ± 0.013*	0.88 ± 0.28**	1.36	0.154
M40N	0.123 ± 0.011**	0.80 ± 0.24**	1.44	0.171
E20N	0.119 ± 0.011**	0.80 ± 0.23**	1.40	0.160
E20S	0.120 ± 0.010**	0.72 ± 0.21**	1.46	0.185
E40N	0.109 ± 0.009**	0.63 ± 0.18**	1.56	0.187
O20N $w \approx 0.00$	0.098 ± 0.027**	1.67 ± 0.48**	0.91	0.061
O20N $w = 0.25$	0.108 ± 0.017**	1.53 ± 0.47**	0.98	0.077
O20N $w = 0.50$	0.121 ± 0.018**	1.44 ± 0.45**	1.04	0.094
O20N $w = 0.75$	0.124 ± 0.014*	0.96 ± 0.39**	1.28	0.146
O20N $w = 1.00$	0.110 ± 0.013**	0.42 ± 0.07**	1.76	0.268

[1] Strategies are H: highly skewed frequency, M: moderately skewed frequency, E: equal frequency (Fig. 2), O: optimized frequency with weight *w* on genetic diversity, 20: top 20 sires used per cycle, 40: top 40 sires used per cycle, N: normal service period, and S: short service period.

*, **: Averages are significantly different with H20N at 5% or 1% level, respectively.

Legends of figures

Figure 1
Proportion of breeding cows by number of calving in lifetime

Figure 2
Mating frequency of sires used in simulation

Figure 3
Change of average breeding value (genetic s.d. unit) against cumulative inbreeding during cycle 0 to 25. See Table 1 for details of strategies.

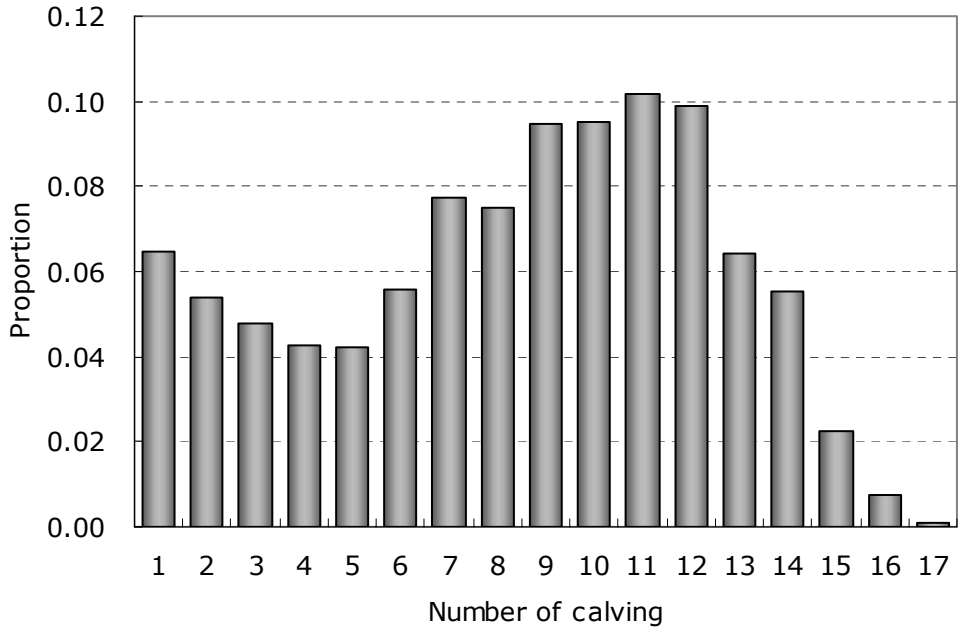

0.12
0.10
0.08
0.06
0.04
0.02
0.00
Proportion
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Number of calving

Figure 1

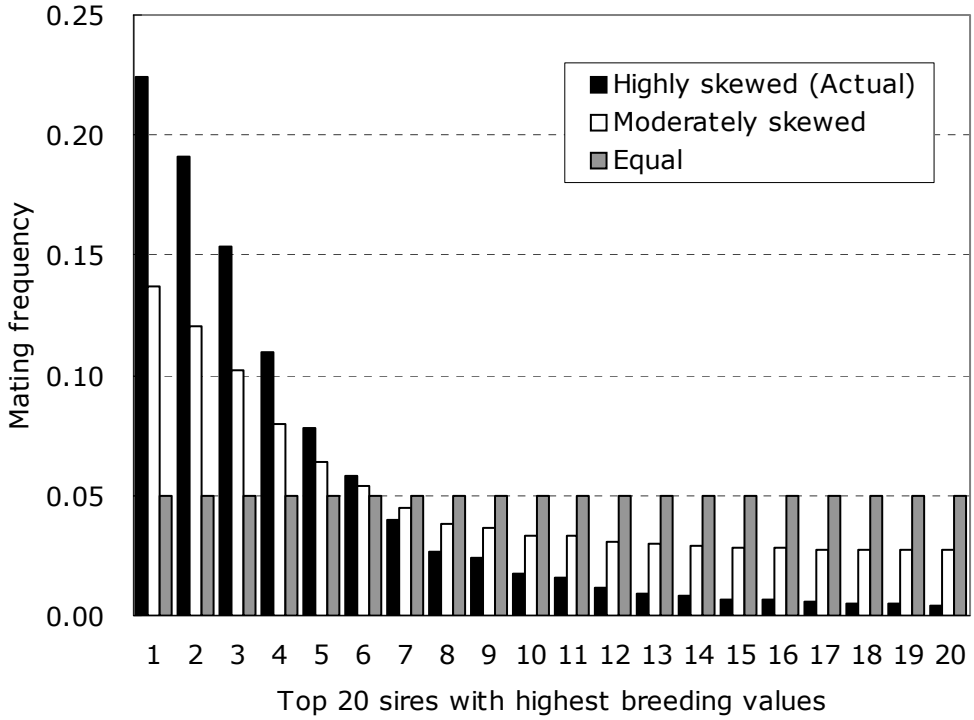

0.25
0.20
0.15
0.10
0.05
0.00
Mating frequency
Highly skewed (Actual)
Moderately skewed
Equal
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Top 20 sires with highest breeding values

Figure 2

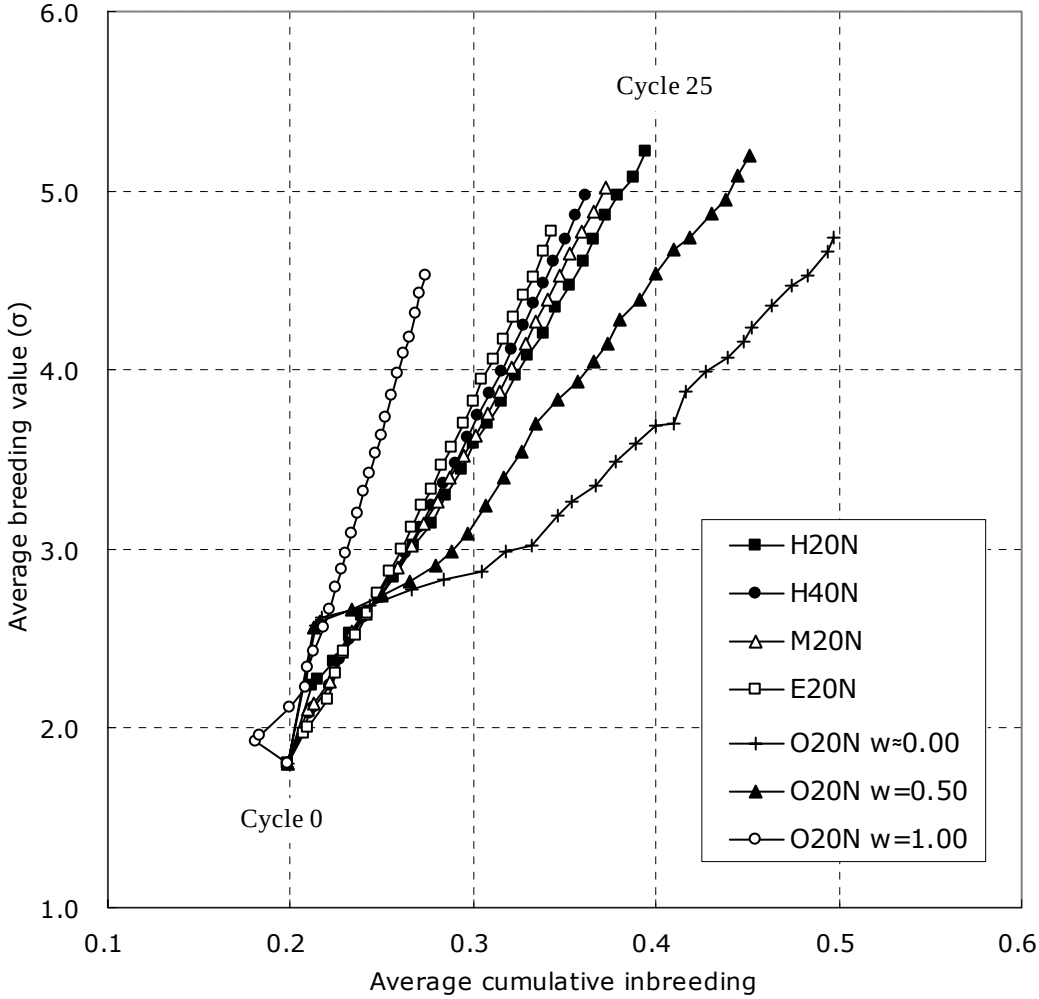

6.0
5.0
4.0
3.0
2.0
1.0
0.1
0.2
0.3
0.4
0.5
0.6
Average breeding value (σ)
Average cumulative inbreeding
Cycle 25
Cycle 0
H20N
H40N
M20N
E20N
O20N w≈0.00
O20N w=0.50
O20N w=1.00

Figure 3