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Prediction of inbreeding in commercial females maintained by rotational mating with partially isolated sire lines

BY T. HONDA1, T. NOMURA2, and F. MUKAI3

Corresponding Author: Fumio Mukai
Address: Faculty of Agriculture, Kobe University, Kobe 657-8501, Japan
Phone: +81 (0) 78-803-5802
Fax: +81 (0) 78-803-5801
E mail: fmukai@kobe-u.ac.jp

Key words: inbreeding, rotational mating, commercial females, subdivided population, migration
Summary
The solution of the inbreeding problem for livestock breeds in commercial use is often complicated by hierarchical population structure, in which favorable genes are accumulated in the upper level of hierarchy (breeding population) by artificial selection and the genetic progress achieved is transferred to the lower level through migration of males. When the breeding population is subdivided into several isolated lines, rotational mating with the lines has been shown to be quite an effective system to reduce the short- and long-term inbreeding of commercial females in the lower level. In practice, however, some amount of migration should be allowed among the lines to reduce the rate of inbreeding in each line. In this study, we developed the recurrence equation for the inbreeding coefficient of the commercial females maintained by the rotational mating with partially isolated lines. Numerical computations were carried out to evaluate the effect of the migration on the efficiency of the rotational mating. It was shown that even with a small amount of migration among the lines, the inbreeding of commercial females is substantially inflated. However, when four or five lines are available, the inbreeding coefficient of commercial females can be suppressed to an acceptable level, irrespective of the effective size of line and the migration rate. Application of the mating system to the population of Japanese Black cattle was also examined.
Introduction

Structure of pure breeds of domestic animals frequently shows a hierarchy, in which favourable genes are accumulated in the upper level of the hierarchy by artificial selection and the genetic progress is transferred to the lower level mainly through migration of males (e.g. Barker, 1957; Robertson and Asker, 1951; Vu Tien Khang, 1983). In such a structure, according to the levels of the hierarchy, different strategies will be required for reducing the inbreeding rate and maintaining the genetic diversity.

Farmers in the lower level of the hierarchy usually rear females to produce commercial products and their replacements. Since the traits related to commercial production and reproduction generally show strong inbreeding depression (Falconer and Mackay, 1996; Pirchner, 1985), the suppression of increased inbreeding in the commercial females will be an important issue. Honda et al. (2004a) showed that when the upper level of hierarchy (breeding population) is subdivided into several isolated subpopulations (sire lines), the inbreeding of commercial females can be suppressed to a negligible level by the application of rotational mating with the sire lines. In practice, however, some migration should be allowed among the sire lines, to reduce the rate of inbreeding in each sire line. Since the migration generates genetic relationships among the sire lines, the effectiveness of the rotational mating may be reduced.

In the present study, a theory for predicting the inbreeding coefficient of commercial females maintained by the rotational mating with partially isolated sire lines is formulated, and the effect of migration among sire lines on the efficiency of rotational mating is examined. An application of rotational mating to the population of Japanese Black cattle is also considered. Assuming a situation where five sire lines are constructed from each of the five regional subpopulations in this breed, we have already assessed an optimal management plan of the genetic diversity in the breeding population, in terms of the size of sire lines and the migration rate.
among them (Honda et al., 2005).

**Theory**

(1) **Theory of group coancestry**

To derive the prediction theory, we applied the group coancestry theory (Cockerham, 1967, 1970), which is an extension of the coancestry of individuals (Malécot, 1948). The main variables and notations used for the derivation are listed in Table 1. Under random mating, the group coancestry has the same operational rule as the ordinary coancestry. For example, suppose a group of individuals \( x \), which has the parental group \( p \) and \( q \), and the grand parental group \( a, b, c \) and \( d \), respectively. Let \( \phi_{pq} \) be the group coancestry between the groups \( p \) and \( q \). The expected inbreeding coefficient of individuals in group \( x \) (\( F_x \)) is expressed as

\[
F_x = \phi_{pq} = \frac{1}{4} \left[ \phi_{ac} + \phi_{ad} + \phi_{bc} + \phi_{bd} \right].
\]

The group coancestry of group \( x \) with itself can be considered to be the average pairwise coancestry including reciprocals and self-coancestries (Cabalero and Toro, 2000) as

\[
\phi_{xx} = \frac{1 + F_x}{2N} + \frac{N - 1}{N} \bar{\phi}_x,
\]

where \( N \) is the number of individuals in group \( x \), and \( \bar{\phi}_x \) is the average pairwise coancestry among individuals (excluding self-coancestries).

(2) **Breeding population**

**Population structure**

We suppose that the breeding population is subdivided into \( n \) partially isolated subpopulations (referred to as ‘sire lines’ hereafter), each with \( N_m \) males and \( N_f \) females each generation. Males in the sire lines are not only the breeding animals for the lines but also the sires used in the commercial population. Mating within each sire line is assumed to be at
random and the numbers of male and female offspring (which become parents in the next generation) per parent follow independent Poisson distributions within the sex of parent, giving the effective size of a sire line as

\[ N_{es} = \frac{4N_m N_f}{N_m + N_f}. \]

Prior to mating, breeding animals are exchanged among the sire lines. As a migration pattern, we assumed the island model (WRIGHT, 1943), in which each sire line receives a proportion of \( d_m \) males and \( d_f \) females drawn at random from the other sire lines. The groups of male and female animals in sire line \( i \) \( (=1,2,\cdots,n) \) before and after migration are denoted by \( m(i) \) and \( f(i) \), and \( M(i) \) and \( F(i) \), respectively.

**Probability of gene identity by descent in the breeding population**

To describe the progress of the gene identity by descent in the breeding population, three coefficients in generation \( t \), i.e. the inbreeding coefficient within each sire line (\( F^*_t \)), and coancestries between two individuals within and among sire lines before migration (\( \theta_t \) and \( \alpha_t \), respectively) should be considered (WANG, 1997). Note that when the numbers of male and female offspring follow independent Poisson distributions, there is no need to distinguish the coancestry between individuals according to their sexes, i.e.,

\[ \bar{\phi}_{m(i),t} = \bar{\phi}_{f(i),t} = \phi_{m(i),f(i),t} = \theta_t \] (3a)

and

\[ \phi_{m(i)=m(j),t} = \phi_{f(i)=f(j),t} = \phi_{m(i)=f(j),t} = \alpha_t \] (3b)

for \( i \neq j \) (see WANG (1997) for more detail).

Let \( q_{mf} \) and \( q'_{mf} \) be the probabilities that two individuals of different sexes, taken at random from the same sire line and the different sire lines after migration, come from the same sire line before migration, respectively. Similarly, \( q_{vv} \) and \( q'_{vv} \) are defined as the probabilities that two individuals of the same sex \( v \) \( (=m \text{ for male and } f \text{ for female}) \), taken at
random and without replacement from the same sire line and the different sire lines after migration, come from the same sire line before migration, respectively. HONDA et al. (2005) obtained the expressions for these probabilities as

\[ q_{mf} = (1 - d_m)(1 - d_f) + \frac{d_md_f}{n-1} \]

\[ q'_{mf} = \frac{(d_m + d_f)(n-1) - nd_md_f}{(n-1)^2} \]

\[ q_{sv} = (1 - d_v)\left(1 - \frac{N_v d_v}{N_v - 1}\right) + d_v\frac{(N_v d_v - n + 1)}{(N_v - 1)(n-1)} \]

\[ q'_{sv} = \frac{d_v(2n - nd_v - 2)}{(n-1)^2}. \]

Putting \( P_t^* = 1 - F_t^* \), \( h_{w,t} = 1 - \theta_t \) and \( h_{b,t} = 1 - \alpha_t \), and defining a column vector \( s_t = [P_t^*, h_{w,t}, h_{b,t}] \), we can express the recurrence relation obtained by WANG (1997) as

\[ s_t = Ts_{t-1}, \]  

where

\[
T = \begin{pmatrix}
0 & q_{mf} & 1 - q_{mf} \\
\frac{1 - Q}{4N_v} & 1 - \frac{q_{mm}}{4N_m} - \frac{q_{ff}}{4N_f} & \frac{Q}{4} & \frac{1 - q_{mm}}{4N_m} & \frac{1 - q_{ff}}{4N_f} \\
0 & 1 - \frac{1}{4}Q' & \frac{1}{4}Q'
\end{pmatrix},
\]

and

\[ Q = 4 - q_{mm} - 2q_{mf} - q_{ff} \]

\[ Q' = 4 - q'_{mm} - 2q'_{mf} - q'_{ff}. \]

(3) Population of commercial females

Rotational mating system

Commercial population of females is assumed to be maintained by random mating with sires rotationally supplied from the \( n \) sire lines before migration.
Generations are discrete and proceed with the same interval as in all the sire lines. The population of commercial females is denoted by $c$.

The line supplying sires to the commercial females in a given generation is referred to as the supplier at that generation. We give sequential numbers 1, 2, ..., $n$ to the suppliers in generations 0, 1, ..., $n-1$, respectively. Letting $S_{t-i}$ be the sequential number of the supplier in generation $t-i$, $S_{t-i}$ could be determined by
$$S_{t-i} = \text{MOD}(t-i, n) + 1,$$
where $\text{MOD}(x, n)$ is the remainder of integer $x$ divided by $n$. Note that, because of the nature of rotational mating, $S_{t-i} = S_{t-i-kn}$ for a given integer number $k$. An arbitrary line that is not the supplier at generation $t-i$ is referred to as non-supplier, and is denoted as $N_{S_{t-i}}$.

**Probability of gene identity by descent in the commercial female population**

To obtain the recurrence equation for probability of gene identity by descent in the commercial female population, we need to specify the three coefficients in generation $t$, i.e., the inbreeding coefficient of commercial females ($F_t$), the group coancestry between males (before migration in generation $t$) in the supplier in generation $t-1$ and commercial females in generation $t$ ($\phi_{m(S_{t-1})c,t}$), and the group coancestry between males (before migration in generation $t$) in a non-supplier in generation $t-1$ and commercial females in generation $t$ ($\phi_{m(N_{S_{t-1}})c,t}$). By the operational rule of coancestry (eqn (1)), $F_t$ is simply expressed as
$$F_t = \phi_{m(S_{t-1})c,t-1} \cdot (6)$$

Figure 1 (A) shows the diagram for deriving the expression of $\phi_{m(S_{t-1})c,t}$. Applying the operational rule of group coancestry (eqn (1)) to the diagram, we can obtain the expression
$$\phi_{m(S_{t-1})c,t} = \frac{1}{4} \left[ \phi_{M(S_{t-1})M(S_{t-1})} + \phi_{M(S_{t-1})c} + \phi_{F(S_{t-1})m(S_{t-1})} + \phi_{F(S_{t-1})c} \right]_{t-1}. \quad (7)$$
Note that in the parental groups of each sex in the supplier after migration \((M(S_{t,1})\) and \(F(S_{t,1})\)), non-immigrants and immigrants from an arbitrary sire lines are contained with the proportions of \(1-d_v\) and \(d_f/(n-1)\), respectively. Furthermore, applying the operational rule (eqn (2)) and noting that the relations (3) hold in our model and for the same reason, \(\phi_{m(i)c,t-1} = \phi_{f(i)c,t-1}\), we can express the four group coancestries on the right hand of eqn (7) as

\[
\phi_{M(S_{t,1})m(S_{t,1})c,t-1} = (1-d_m)\left[1 + \frac{F^*}{2N_m} + \frac{N_m - 1}{N_m} \theta_{t-1}\right] + d_m \alpha_{t-1}
\]

\[
\phi_{M(S_{t,1})c,t-1} = (1-d_m)\phi_{m(S_{t,1})c,t-1} + \frac{d_m}{n-1} \sum_{i \in S_{t,1}} \phi_{m(i)c,t-1}
\]

\[
\phi_{F(S_{t,1})m(S_{t,1})c,t-1} = (1-d_f)\theta_{t-1} + d_f \alpha_{t-1}
\]

\[
\phi_{F(S_{t,1})c,t-1} = (1-d_f)\phi_{m(S_{t,1})c,t-1} + \frac{d_f}{n-1} \sum_{i \in S_{t,1}} \phi_{m(i)c,t-1}
\]

Substituting these expressions into (7) gives

\[
\phi_{m(S_{t,1})c,t} = \left[ r\phi_{m(S_{t,1})c} + s \sum_{i \in S_{t,1}} \phi_{m(i)c} + xF^* + y\theta + z\alpha \right]_{t-1} + x, \quad \text{(8)}
\]

where \( r = \frac{2-d_m-d_f}{4} \), \( s = \frac{d_m+d_f}{4(n-1)} \), \( x = \frac{1-d_m}{8N_m} \),

\[
y = \frac{(1-d_f)N_m + (1-d_m)(N_m-1)}{4N'_m}, \quad \text{and} \quad z = \frac{d_m+d_f}{4}.
\]

Applying the similar argument to Figure 1(B), we can obtain the expression of \(\phi_{m(N_{S_{t,1}})c,t}\) as

\[
\phi_{m(N_{S_{t,1}})c,t} = \left[ r\phi_{m(N_{S_{t,1}})c} + s \sum_{i \in N_{S_{t,1}}} \phi_{m(i)c} + uF^* + v\theta + w\alpha \right]_{t-1} + u, \quad \text{(9)}
\]

where \( u = \frac{d_m}{8(n-1)N_m} \), \( v = \frac{d_m(N_m-1)+d_fN_m}{4(n-1)N_m} \), \( w = \frac{2(n-1)-(d_m+d_f)}{4(n-1)} \).
Recurrence equations in vector-matrix form

Putting \( P_t = 1 - F_t \) and \( h_{m(i)} = 1 - \phi_{m(i)} \), and defining a column vector \( \mathbf{h}_t \) and a matrix \( \mathbf{G} \) with order \((n+4) \times (n+4)\) as

\[
\mathbf{h}'_t = \begin{bmatrix}
P_t & h_{m(S_1)} & h_{m(S_2)} & \cdots & h_{m(S_{n+3})} & P_{t-1}^r & h_{w_1} & h_{w_2}
\end{bmatrix}
\]

\[
\mathbf{G} = \begin{bmatrix}
0 & 0 & 1 & 0 & \cdots & 0 \\
0 & \vdots & \ddots & \vdots & \cdots & \vdots \\
0 & \ddots & \ddots & \ddots & \cdots & \ddots \\
0 & \ddots & \ddots & \ddots & \ddots & \ddots \\
0 & \ddots & \ddots & \ddots & \ddots & \ddots \\
0 & \ddots & \ddots & \ddots & \ddots & \ddots \\
0 & \ddots & \ddots & \ddots & \ddots & \ddots \\
0 & \ddots & \ddots & \ddots & \ddots & \ddots \\
\end{bmatrix}
\]

we can combine equations (4) and (6), (8), and (9) as

\[
\mathbf{h}_t = \mathbf{Gh}_{t-1},
\]

where \( \mathbf{T} \) is the matrix defined by eqn (5), \( \mathbf{O} \) is the null matrix with order \( 3 \times n \),

\[
\mathbf{U} = \begin{bmatrix}
s & r & s & \cdots & s \\
s & s & r & \ddots & \vdots \\
\vdots & \ddots & s & \ddots & s \\
s & \ddots & \ddots & \ddots & r \\
r & s & \cdots & s & s
\end{bmatrix}_{n \times n}
\]

\[
\text{and} \quad \mathbf{V} = \begin{bmatrix}
x & y & z \\
u & v & w \\
\vdots & \vdots & \vdots \\
\vdots & \vdots & \vdots \\
u & v & w
\end{bmatrix}_{n \times 3}
\]

Note that \( \mathbf{U} \) is a circular matrix describing the periodic nature of rotational mating such as \( S_{t-1} = S_{t+n-1} \).

Rotational mating with a partial set of sire lines

Rotational mating will have practical merit in its application to the commercial female population, because it does not require systematic controls of mating over the population (HONDA et al., 2004a). For example, if five sire lines (say A, B, C, D and E) are available, some farmers could rotationally use the four lines A, B, C and D, while other could adopt the mating with the four lines B, C, D and E.

We suppose a situation where \( n \) sire lines are available and a group of commercial females are maintained by the rotational mating with...
n′(<n) sire lines. The inbreeding coefficient of the commercial females can be predicted by replacing the submatrix $U$ in eqn (10) by $W$ defined as

\[
W = \begin{bmatrix}
U_{n'\times n'} & s & \cdots & s & s \\
s & r & s & \cdots & s \\
\vdots & s & r & \ddots & \vdots \\
s & \vdots & \ddots & \ddots & s \\
s & s & \cdots & s & r_{n'\times n'}
\end{bmatrix}.
\]

Asymptotic rate of inbreeding of commercial females

Honda et al. (2004a) proved that when each sire line is completely closed ($d_m = d_f = 0$), the inbreeding coefficient of commercial females asymptotically approaches an intermediate value ($0 \leq F_w \leq 1$). However, when migration is allowed among the sire lines, the inbreeding coefficient of commercial females asymptotically approaches unity. The asymptotic rate of inbreeding ($\Delta F = \lim_{t \to \infty} (F_t - F_{t-1})/(1 - F_{t-1})$) is obtained from the largest eigenvalue ($\lambda$) of $G$ as $\Delta F = 1 - \lambda$.

(4) Numerical computations and an application

To evaluate the efficiency of the proposed mating system, numerical computations with eqn (11) were carried out for various combinations of the number of sire lines ($n = 2 - 5$), number of males in each sire line ($N_m = 2 - 10$) and male migration rate ($d_m = 0 - 0.5$). In all the computations, the female migration rate was set to zero ($d_f = 0$). Since preliminary analysis showed that the number of females in each sire line has a minor effect on results, $N_f$ was fixed to 200. In addition, for a fixed total size of breeding population, the effects of the number of sire lines on the inbreeding coefficients of the breeding and commercial populations were examined.
As a working example, we considered an application of rotational mating to the population of Japanese Black cattle. The breeding population was assumed to consist of five sire lines \( (n=5) \) constructed from each of the five regional subpopulations (for more details on these subpopulations, see HONDA et al. (2004a,b)). Commercial females were assumed to be maintained by rotational mating with \( n' = 3, 4 \) and \( 5 \) sire lines chosen from the five available lines. Computations with \( N_m = 10 \) and \( d_m = 0, 0.1 \) and \( 0.2 \) were carried out over 10 generations (approximately 100 years in this breed). In addition to the inbreeding coefficient, the total genetic diversity, relative to generation 0, retained in the set of the five sire lines in generation 10 and the proportion of genes in a line in generation 10 that have descended from the line in generation 0 \( (GD_{10} \) and \( m_{10} \), respectively) were also computed (for the computational procedures of these parameters, see HONDA et al. (2005)). The former measures expected heterozygosity in the set of the five sire lines, and the latter is an indicator of maintainability of the initial genetic differentiation among the sire lines. From viewpoints of animal breeding and conservation genetics, HONDA et al. (2005) set three conditions of \( \Delta F^* \leq 0.01, GD_{10} \geq 0.97 \) and \( m_{10} \geq 0.5 \) for the maintenance of set of the five sire lines, and suggested that the management with \( N_m = 10 \) and \( d_m = 0.1 \) is an optimum plan, which satisfies the conditions simultaneously.

**Results and discussion**

Our previous report (HONDA et al., 2004a) showed that with completely closed sire lines \( (d_m = d_f = 0) \), the inbreeding coefficient of commercial females asymptotically approaches an intermediate value \( F_{\infty} = 1/(2^n - 1) \).

However, when migration is allowed among sire lines, the asymptotic inbreeding coefficient reaches unity \( (F_{\infty} = 1) \) irrespective of the number of sire lines \( (n) \). In Figure 2, the evolution of inbreeding in the commercial
females over initial 20 generations is exemplified, for the cases of \( n = 3 \), \( N_m = 2 \) and various rates of male migration among the sire lines \( (d_m = 0 - 0.5) \). The migration among the sire lines substantially increases the initial inbreeding in the commercial females, and for all the computed cases the inbreeding coefficient in generation 20 is already beyond the asymptotic value \( (F_\infty = 14.3\%) \) expected under \( d_m = 0 \). Under \( d_m = 0.1, 0.2, 0.3, 0.4 \) and 0.5, the asymptotic rate of inbreeding are predicted as 1.51, 1.71, 1.78, 1.82 and 1.84\%, respectively.

Figures 3 (A)-(D) show the effect of the number of males \( (N_m) \) in each sire line and male migration rate \( (d_m) \) on the inbreeding coefficient of commercial females in generation 20 \( (F_{20}) \), for the cases of \( n = 2, 3, 4, \) and 5, respectively. For given \( n \) and \( N_m \), a small amount of male migration (say \( d_m < 0.1 \)) substantially inflates the inbreeding coefficient of commercial females, but the rate of inflation is diminished as \( d_m \) becomes larger. With the same total size of males \( (nN_m) \), \( n \) is more significant factor than \( N_m \) for the restriction of inbreeding in commercial females, especially when \( d_m \) is small. For example, when \( n=2 \) and \( N_m = 10 \), \( F_{20} \) are 7.1\% and 11.3\% for \( d_m = 0 \) and 0.5, respectively (Fig. 3 (A)). On the other hand, when \( n=5 \) and \( N_m = 4 \), corresponding values are 1.3\% and 9.8\%, respectively (Fig. 3 (D)). When four or five sire lines are available, \( F_{20} \) remains below 20\% (or approximately the rate of inbreeding is kept below 1\%) under most of the investigated combinations of \( N_m \) and \( d_m \).

When the breeding population has an undivided structure at the initiation of rotational mating, it will raise a question of how many sire lines should be established. To illustrate this problem, we supposed a situation where the breeding population has a fixed size of 60 males and 480 females \( (T_m = 60 \) and \( T_f = 480 \)\), and \( n \) sire lines each with \( N_m = T_m / n \) and \( N_f = T_f / n \) are constructed. Figures 4 (A) and (B) show the inbreeding coefficients in the breeding and commercial populations in generation 20, respectively. The inbreeding in the breeding population is inflated by an
increase in $n$, since it is accompanied by an decrease in the size of each sire line (Fig. 4 (A)). A small amount of migration among the sire lines effectively reduces the increase of inbreeding, but the effect is rapidly diminished as the migration rate becomes larger. With a high rate of migration (say $d_m > 0.4$), the inbreeding coefficient tends to converge to a single value regardless of the number of sire lines, since the breeding populations essentially behave as a single population. In contrast, the increase in $n$ and $d_m$ have reversal effects on the inbreeding coefficient of commercial females (Fig. 4 (B)). As illustrated by this example, the optimum structure of breeding population should be empirically found so as to balance the conflicting effects on the inbreeding in the breeding and commercial populations.

As a working example, we consider an application of rotational mating to the population of Japanese Black cattle. The results of the application are summarized in Table 2. When the sire lines are completely closed ($d_m = 0$), the inbreeding coefficient of commercial females is minimized, but the criterion for the rate of inbreeding in each sire line ($\Delta F^* \leq 1\%$) is violated. Under the optimum rate of male migration ($d_m = 0.1$) defined by HONDA et al. (2005), the inbreeding of commercial females is inflated compared to the case of $d_m = 0$, but the inbreeding coefficient of commercial females in generation 10 is suppressed to a negligible level, irrespective of the number of sire lines ($n'$) used in the commercial population. An excess of migration ($d_m = 0.2$) leads to a rapid decay of the genetic variability among the sire lines, as seen from the lower value of $m_{10}$. These results suggest that the optimum management plan of the set of sire lines defined by HONDA et al. (2005) could also give a successful rotational mating for the maintenance of commercial females.

Throughout the present study, we have assumed the island model as a migration pattern. The migration pattern in actual livestock populations will more or less depart from this idealized model. For example, the male
migration among the five regional subpopulations in the population of Japanese Black cattle shows an asymmetrical pattern (Honda et al., 2005). With the migration matrix defined by Hedrick (1983), Honda et al. (2005) predicted that when this asymmetrical pattern is persisted over generations, the genetic variability among the subpopulations will be seriously decayed within a few generations. The decay will largely reduce the merit of rotational mating with the sire lines constructed from the different subpopulations. For a successful rotational mating, the management of migration to avoid an extreme asymmetrical pattern has an essential importance.

The hierarchical population structure as assumed in the present study has been found in many livestock breeds (for a review, see Vu Tien Khang (1983)). The subdivision of the upper level of hierarchy (breeding population) has been also reported in many breeds (e.g. Honda et al., 2002; Solkner et al., 1998). For these breeds, the mating system proposed in this study could be a guideline to the conservation of genetic diversity in the breeding population and the suppression of inbreeding in the commercial population.

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References


Authors’ address: Graduate School of Science and Technology, Kobe University, Kobe 657-8501, Japan, Faculty of Engineering, Kyoto Sangyo University, Kyoto 603-8555, Japan, and Faculty of Agriculture, Kobe University, Kobe 657-8501, Japan (correspondence; Phone: +81-78-803-5802; Fax +81-78-803-5802; E-mail: fmukai@kobe-u.ac.jp)
Table 1. List of main variables and notations used in this study.

<table>
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<tr>
<th>Variables and Notations</th>
<th>Definition</th>
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<tr>
<td><strong>Structure of sire lines.</strong></td>
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<tr>
<td>$n$</td>
<td>Number of sire lines.</td>
</tr>
<tr>
<td>$N_v$</td>
<td>Number of breeding animals of sex $v$ (=m for male or f for female) in each line.</td>
</tr>
<tr>
<td>$d_v$</td>
<td>Migration rate of sex $v$.</td>
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<tr>
<td><strong>Groups of animals.</strong></td>
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<tr>
<td>$S_{t,i}$</td>
<td>Sire line supplying sires to the commercial females in generation $t-i$, which is referred to as supplier at the generation.</td>
</tr>
<tr>
<td>$NS_{t,i}$</td>
<td>Sire line that is not the supplier at generation $t-i$, which is referred to as non-supplier at the generation.</td>
</tr>
<tr>
<td>$v(i)$</td>
<td>Group of animals of sex $v$ in sire line $i$ before migration.</td>
</tr>
<tr>
<td>$V(i)$</td>
<td>Group of animals of sex $V$ (=M for male or F for female) in sire line $i$ after migration.</td>
</tr>
<tr>
<td>$c$</td>
<td>Commercial females.</td>
</tr>
<tr>
<td><strong>Probabilities of gene identity by descent.</strong></td>
<td></td>
</tr>
<tr>
<td>$\phi_{x,y,t}$</td>
<td>Group coancestry between groups $x$ and $y$ in generation $t$.</td>
</tr>
<tr>
<td>$F_t$</td>
<td>Inbreeding coefficient of commercial females in generation $t$.</td>
</tr>
<tr>
<td>$F_t^*$</td>
<td>Inbreeding coefficient within each line before migration in generation $t$.</td>
</tr>
<tr>
<td>$\theta_t$</td>
<td>Coancestries between two individuals within line before migration in generation $t$.</td>
</tr>
<tr>
<td>$\alpha_t$</td>
<td>Coancestries between two individuals among lines before migration in generation $t$.</td>
</tr>
</tbody>
</table>
Table 2. Application of rotational mating to the population of Japanese Black cattle. Five sire lines (n=5) each with the size of $N_m=10$ males and $N_f=200$ females are assumed to be available for rotational mating.

<table>
<thead>
<tr>
<th>$d_m$ b)</th>
<th>$\Delta F^*(%)$ c)</th>
<th>$F^*_10(%)$</th>
<th>$GD^*_{10}$ d)</th>
<th>$m_{10}$ e)</th>
<th>Commercial females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$n' = 3$ a)</td>
</tr>
<tr>
<td>0</td>
<td>1.17</td>
<td>11.1</td>
<td>0.975</td>
<td>1.00</td>
<td>0.47</td>
</tr>
<tr>
<td>0.1</td>
<td>0.74</td>
<td>7.1</td>
<td>0.975</td>
<td>0.62</td>
<td>0.54</td>
</tr>
<tr>
<td>0.2</td>
<td>0.52</td>
<td>5.1</td>
<td>0.975</td>
<td>0.41</td>
<td>0.60</td>
</tr>
</tbody>
</table>

a) $n'$: Number of sire lines used in the rotational mating.
b) $d_m$: Male migration rate
c) $\Delta F^*$: Rate of inbreeding averaged over the initial 10 generations.
d) $GD^*_{10}$: Total genetic diversity, relative to generation 0, retained in the set of the five sire lines in generation 10.
e) $m_{10}$: Proportion of genes in a line in generation 10 that have descended from the line in generation 0.
Figure legends

Figure 1. Pedigree diagrams to derive the group coancestry ($\phi_{m(S_{i+1})e,t}$) between the commercial females ($c$) and the males of the supplier in generation $t-1$ (A), and the group coancestry ($\phi_{m(NS_{i+1})e,t}$) between the commercial females and the males of an arbitrary non-supplier in generation $t-1$ (B). $m(i)$ represents the group of male in sire line $i$ before migration, and $M(i)$ and $F(i)$ represent the groups of male and female in sire line $i$ after migration, respectively. The group coancestries relevant to $\phi_{m(S_{i+1})e,t}$ and $\phi_{m(NS_{i+1})e,t}$ are shown by dashed curves with arrows of both direction.

Figure 2. Inbreeding coefficient of the commercial females under rotational mating using $n=3$ sire lines each with $N_m=2$ males and $N_f=200$ females.

$d_m$=migration rate of males

Figure 3. Effects of the number of males ($N_m$) in each sire line and male migration rate ($d_m$) on the inbreeding coefficient of commercial females in generation 20 ($F_{20}$), for the cases of (A) $n=2$, (B) $n=3$, (C) $n=4$, and (D) $n=5$.

Figure 4. Inbreeding coefficients in the sire lines (A) and the commercial females (B) in generation 20, for the cases of $n$ (=2,3,4 and 5) sire lines each with $60/n$ males and $480/n$ females.
Figure 1
Figure 2
Figure 3
Figure 4