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Conservation of genetic diversity in the Japanese Black cattle population by the construction of partially isolated lines

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Key words: genetic diversity, conservation, subdivided population, migration, Japanese Black cattle

Summary

In the Japanese Black cattle population, five genetically divergent subpopulations have played important roles as suppliers of breeding stocks to the entire breed. We supposed a situation where five lines were constructed from each of the five subpopulations, and applied to this set of lines a management plan to conserve genetic diversity. Assuming that the male migration pattern among the lines followed the island model, we assessed the optimum male migration rate and required male numbers in each line, satisfying the following three conditions simultaneously: (1) the rate of inbreeding in each line was below 0.01 per generation; (2) at least 97% of the initial genetic diversity was preserved after 10 generations; (3) more than 50% of the genes in an initial line were retained in the line after 10 generations. We found that approximately one breeding male should be selected per year and one breeding male should be exchanged among the lines per generation in each line to satisfy these three conditions. Numerical analysis with the migration rates actually observed among the five subpopulations demonstrated that the initial genetic differentiation among the lines was rapidly decayed by an asymmetrical migration pattern. For a successful plan, migration among lines should be strictly managed.

Introduction

A subdivided structure is frequently found in wild and domesticated animal populations. In the maintenance of such populations, a crucial question is how much gene flow should be allowed between the subpopulations. In designing a conservation program for endangered species with fragmented habitats, much effort has been devoted to finding a migration rate to integrate the subpopulations into an effectively single breeding population (e.g. FRANKLIN, 1980; FRANKEL and SOULÉ, 1981; ROUX, 1995).

In livestock breeds with a subdivided population structure, a considerable amount of genetic diversity exists between subpopulations (e.g. HONDA et al., 2002; SÖLKNER et al., 1998). The genetic diversity between subpopulations may allow greater potential for future breeding materials than the same amount of genetic diversity dispersed over the entire population, because it saves time for assembling genes conforming to various commercial demands. A genetically subdivided structure is also useful for the reduction of inbreeding and genetic drift in both breeding and commercial populations. In the breeding population, increased inbreeding in a subpopulation can be easily reduced by crossing animals from other subpopulations. Although genetic drift within a subpopulation leads to a random change of gene frequency in a neutral locus, the change is independent among subpopulations. Thus, the total change of gene frequency due to genetic drift can be reduced in a subdivided population structure (K_{IMURA} and C_{ROW}, 1963). For the reduction of inbreeding in the commercial population, HONDA et al. (2004a) showed that the rotational use of sires supplied from several subpopulations can suppress the inbreeding of commercial females to a trivial level.

Considering these merits of population subdivision, an appropriate amount of migration in a livestock breed with a subdivided structure should be determined so as to maintain genetic diversity both within and between subpopulations. Apparently, this problem involves a trade-off: if the gene

flow among subpopulations is limited to a smaller amount, larger genetic diversity can be maintained among the subpopulations; however, due to a higher rate of inbreeding within the subpopulations, the genetic diversity within them rapidly decays, and vice versa.

In the present study, we suppose a situation where lines are constructed from existing subpopulations, and apply to the set of lines a management plan to conserve genetic diversity within and between the lines. Based on population genetic theories, the optimal migration rate among lines and the required size of lines can be assessed.

Throughout this study, most of the analytical concepts and procedures are illustrated with the breeding population of Japanese Black cattle. In this breed, five regional subpopulations have played important roles as suppliers of breeding stocks to the entire breed (HONDA et al., 2004b). Although the genetic diversity of the breed has been reduced by the intensive use of sires from limited strains during the past decade (NOMURA et al., 2001; HONDA et al., 2004b), the five regional subpopulations still maintain their unique genetic compositions (HONDA et al., 2002). Conservation of genetic diversity among the five subpopulations is an urgent task for the future breeding of Japanese Black cattle (HONDA et al., 2004b).

Materials and methods

Model and assumptions

We suppose a situation where n lines are constructed from each of n subpopulations. Each line has a constant size of N_m males and N_f females over generations. Mating within a line is assumed to be 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 a parent, giving the effective size of the line as

$$N_{e,s} = 4N_m N_f / (N_m + N_f).$$

As a migration pattern among the lines, we first assume the island model (WRIGHT, 1943), in which each line receives a proportion of d_m males and d_f females drawn randomly from the other lines before the mating of each generation. The effects of departure from this simplified model will be discussed later.

Probabilities of gene identity by descent

To describe the progress of gene identity by descent under the island model, three coefficients, i.e. the inbreeding coefficient within each line ($F_{(t)}$), and coancestries between two individuals within and among lines before migration ($\theta_{(t)}$ and $\alpha_{(t)}$) should be considered (WANG, 1997). When the numbers of male and female offspring follow independent Poisson distributions, distinguishing the coancestry between individuals according to their sexes is not necessary (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 line and different lines after migration, come from the same line before migration. Similarly, q_{vv} and q'_{vv} are defined as the probabilities that two individuals of the same sex v ($=m$ for male or f for female), taken at random and without replacement from the same line and different lines after migration, come from the same line before migration. In the ordinary finite island model (e.g., WANG, 1997), emigrants from a line are allowed to come back to their birth line as migrants. This possibility should be removed from the present model, giving expressions for the four probabilities q_{mf} , q'_{mf} , q_{vv} , and q'_{vv} as

$$q_{mf} = (1 - d_m)(1 - d_f) + \frac{d_m d_f}{n - 1}$$

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

$$q_{vv} = (1 - d_v) \left(1 - \frac{N_v d_v}{N_v - 1} \right) + \frac{d_v (N_v d_v - n + 1)}{(N_v - 1)(n - 1)}$$

$$q'_{vv} = \frac{d_v (2n - n d_v - 2)}{(n - 1)^2}.$$

With these probabilities, the inbreeding and coancestry coefficients are obtained from the recurrence equation of WANG (1997) as follows,

$$\begin{bmatrix} F_{(t)} \\ \theta_{(t)} \\ \alpha_{(t)} \end{bmatrix} = \begin{bmatrix} 0 & q_{mf} & 1 - q_{mf} \\ \frac{1}{2N_{e,s}} & 1 - \frac{Q}{4} - \frac{q_{mm}}{4N_m} - \frac{q_{ff}}{4N_f} & \frac{Q}{4} - \frac{1 - q_{mm}}{4N_m} - \frac{1 - q_{ff}}{4N_f} \\ 0 & 1 - \frac{Q'}{4} & \frac{Q'}{4} \end{bmatrix} \begin{bmatrix} F_{(t-1)} \\ \theta_{(t-1)} \\ \alpha_{(t-1)} \end{bmatrix} + \begin{bmatrix} 0 \\ \frac{1}{2N_{e,s}} \\ 0 \end{bmatrix}$$

where

$$Q = 4 - q_{mm} - 2q_{mf} - q_{ff},$$

and

$$Q' = 4 - q'_{mm} - 2q'_{mf} - q'_{ff}.$$

Genetic diversity

From the theory described by CABALLERO and TORO (2002), the total genetic diversity ($GD_{(t)}$) retained in the set of lines in generation t , relative to that in generation 0, can be obtained as

$$GD_{(t)} = 1 - \frac{1 + F_{(t)} + 2(N - 1)\theta_{(t)} + 2(n - 1)N\alpha_{(t)}}{2nN},$$

where $N = N_m + N_f$. To evaluate a management plan for genetic diversity in the set of lines, both the genetic diversity of the entire set and the genetic diversity between the lines should be assessed (CABALLERO and TORO, 2002). According to CABALLERO and TORO (2002), the genetic diversity between the lines retained in generation t ($GD_{BS,t}$) can be obtained by

$$GD_{BS(t)} = \frac{(n - 1) \{ 1 + F_{(t)} + 2(N - 1)\theta_{(t)} - 2N\alpha_{(t)} \}}{2nN}.$$

Distribution of genes over the set of lines

To assess the maintainability of the initial genetic diversity between the lines, the distribution of genes over the set of lines originated from each line in generation 0 was computed with the migration matrix defined by BODMER and CAVALLI-SFORZA (1968).

Let m_{ij} be the proportion of individuals migrating from line j to line i in each generation. If the migration rates are estimated for separate sexes, $m_{ij} = (d_{m,ij} + d_{f,ij})/2$, where $d_{m,ij}$ and $d_{f,ij}$ are the male and female migration rates. We define the migration matrix as $\mathbf{M} = [m_{ij}]$. The elements in the matrix \mathbf{M}^t in generation t , $m_{ij(t)}$, give the proportion of genes in line i at generation t that have descended from line j in generation 0 (HEDRICK, 1983).

The main variables relevant to the structure and genetic parameters of sire lines are listed in Table 1.

Numerical analysis

We suppose that five lines ($n = 5$) are constructed from each of the five regional subpopulations (Hyogo, Tottori, Shimane, Okayama and Hiroshima) in the Japanese Black cattle population. Table 2 lists the annual census numbers of breeding animals, generation intervals (L), annual effective population sizes ($N_{e(y)}$), and annual effective numbers of males ($N_{m(y)} = N_{e(y)}/4$) in the five subpopulations. The effective population size was estimated with the formula given by NOMURA (2002), which accounts for the census number of breeding males and the variation of progeny numbers among the males.

In the numerical analysis, the maximum number of males in each line was chosen as 10. Since the generation interval averaged over the five subpopulations is around 10 (Table 2), $N_m = 10$ implies that one male (in

the effective number) is selected per year in each line. The estimated annual effective numbers of males in the five subpopulations (Table 2) suggest that a realizable maximum would not largely differ from $N_{m(y)}=1$ in each line. The number of females (N_f) was fixed at 200, because preliminary analysis suggested that the number of females has a minor effect on results. Various rates of male migration ($d_m=0\sim 0.5$) were examined by fixing the female migration rate at zero ($d_f = 0$).

Results and discussion

Figures 1 (A), (B), and (C) exemplify the changes of the inbreeding coefficient within a line ($F_{(t)}$), total genetic diversity of the set of lines ($GD_{(t)}$), and genetic diversity between lines ($GD_{BS(t)}$) over 20 generations for the cases of $N_m = 5$ and various male migration rates (d_m). Although an increase of d_m reduces the increasing rate of $F_{(t)}$, the effect rapidly diminishes as d_m becomes larger (Fig. 1 (A)). As seen from Figure 1 (B), the total genetic diversity retained in the set of lines, $GD_{(t)}$, is less affected by d_m . In contrast, even within range of a small amount of male migration (say $d_m \leq 0.2$), an increase of d_m effectively suppresses the accumulation of genetic diversity between lines (Fig. 1 (C)). Insensitivity of $GD_{(t)}$ to d_m , as observed in Figure 1 (B), is a reflection of the fact that the two opposing effects of migration on the genetic diversity (i.e., the enhanced maintainability of genetic diversity within a line, and the suppressed accumulation of genetic diversity among lines) are largely canceled for any amount of male migration.

Figure 2 illustrates the effects of N_m and d_m on the increasing rate of inbreeding coefficient within a line (ΔF) averaged over the initial 10 generations. Based on knowledge from animal breeding, conservation geneticists have recommended that the rate of inbreeding in animal populations should remain below 0.01 per generation (e.g. FRANKLIN, 1980; SOULÉ, 1980). From Figure 2, it is found that a relation $N_m d_m \geq 1$ gives

an approximated critical condition to satisfy the criterion $\Delta F \leq 0.01$. This implies that irrespective of the number of males within a line (N_m), each line should receive more than one male migrant per generation.

Another criterion for the evaluation of conservation plans is the genetic diversity retained in a conserved population. As a criterion, SOULÉ et al. (1986) proposed that the goal of conservation management should be to preserve at least 90% of the genetic diversity that existed in the initial population over 200 years. This criterion has been applied to the conservation of endangered wild animal species with various modifications (FRANKHAM et al., 2002). For example, in the conservation of the golden lion tamarin, *Leontopithecus rosalia*, the objective is defined as the maintenance of 98% of genetic diversity for 100 years (FRANKHAM et al., 2002). Similar criteria have been quoted in the context of conservation of rare livestock breeds (MACE, 1990; GILL and HARLAND, 1992).

Figure 3 depicts the effects of N_m and d_m on the total genetic diversity after 10 generations ($GD_{(10)}$). In the population of Japanese Black cattle, 10 generations are approximately equal to 100 years (c.f. Table 2). As Figure 1 (B) reveals, $GD_{(10)}$ is less affected by d_m for a given N_m . If our objective is defined as the conservation of at least 97% of total genetic diversity over 10 generations ($GD_{(10)} \geq 0.97$), $N_m \geq 8$ will be required.

The genetic diversity generated between lines (Fig. 1 (C)) could be future breeding materials. However, for our objective, it will be more important to maintain the initial genetic differentiation among lines. The maintainability can be approximately evaluated by the proportion of genes in a line in generation t that have descended from the line in generation 0. This proportion is obtained by a diagonal element $m_{ii(t)}$ of the matrix \mathbf{M}^t (note that in the island model, $m_{ii(t)}$ is equal for all the diagonal elements). When the five lines ($n = 5$) are completely mixed, $m_{ii(t)} = 1/n = 0.2$. Figure 4 illustrates the proportion in generation 10. If we choose

$m_{ii(10)} \geq 0.5$ as a criterion, the male migration rate should be restricted to $d_m \leq 0.15$. The criterion $m_{ii(10)} \geq 0.5$ is apparently arbitrary, but in a line satisfying this criterion, genes originated from the line in generation 0 can be effectively assembled by selection within the line.

The shaded zone in Figure 5 indicates optimum values of N_m and d_m simultaneously satisfying the three criteria ($\Delta F \leq 0.01$, $GD_{(10)} \geq 0.97$, and $m_{ii(10)} \geq 0.5$). From this figure, $N_m \cong 10$ and $d_m \cong 0.1$ are recommended as an optimum design for the assumed situation, implying that in each line approximately one breeding male should be selected per year, and one breeding male should be received as a migrant per generation.

Throughout the above computations, we have assumed the island model as a migration pattern among lines. For the migration pattern in actual livestock populations, however, this model is apparently an oversimplification. For example, Table 3 gives the estimated male migration rates among the five subpopulations in the Japanese Black cattle population. The male migration rate averaged over all the possible pathways (20 pathways) is 0.05. The migration, however, shows quite an asymmetrical pattern. For example, Hyogo is completely closed, but supplies males to all the other subpopulations. In contrast, Okayama and Hiroshima receive migrants without supplying emigrants.

To examine the effect of the asymmetrical pattern of migration, we computed the distribution of genes in a line in generation 0 over the set of the lines in generation t , by substituting the male migration rates given in Table 3 into the migration matrix \mathbf{M} . Table 4 shows the results for $t=3$ and 10. After three generations of migration ($t=3$), the two lines constructed from Okayama and Hiroshima reduce their original genes to 51% and 61%. These proportions further decrease to 11% and 20% after ten generations ($t=10$). Note that genes originating from the two subpopulations exist only in the lines constructed from themselves. These results emphasize that for a successful management of the set of partially

isolated lines, migration among lines should be managed so as to avoid an extreme asymmetrical pattern of migration.

The success of the proposed plan will also depend critically on how base animals in the initial line are sampled from the subpopulation. Using the gene dropping simulation (MACCLUER et al., 1986), we have shown that several important founders in the five subpopulations have lineages through which their alleles are surely transmitted to the current subpopulations (HONDA et al., 2004b). We have also suggested that gene dropping simulation can be a powerful tool to detect a genetically important group of animals definitely having target alleles for preservation (HONDA et al., 2004b). Construction of the lines should be based on such information.

HONDA et al. (2004a) theoretically showed that if five isolated lines are maintained in the breeding population, the increasing rate of inbreeding in commercial females can be suppressed to a negligible level, by the rotational mating with sires supplied from the lines. Since migration generates genetic relationships among the lines, the effectiveness of the rotational mating may be more or less reduced. The effect of migration among lines on the efficiency of rotational mating will be examined in our processing report.

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Table 1. List of main variables used in computations.

| Variables | Definition |
|---|---|
| <i>Structure of sire lines.</i> | |
| n | The number of sire lines. |
| N_v | The number of animals of sex v ($=m$ for male or f for female) in each line. |
| $N_{e,s}$ | Effective size of each line, i.e., $N_{e,s} = 4N_m N_f / (N_m + N_f)$. |
| d_v | Migration rate of animals of sex v . |
| <i>Probabilities of gene identity by descent.</i> | |
| $F_{(t)}$ | Inbreeding coefficient within each line before migration in generation t . |
| $\theta_{(t)}$ | Coancestries between two individuals within line before migration in generation t . |
| $\alpha_{(t)}$ | Coancestries between two individuals among lines before migration in generation t . |
| <i>Measurements of genetic diversity.</i> | |
| $GD_{(t)}$ | Total genetic diversity of the set of lines in generation t . |
| $GD_{BS(t)}$ | Genetic diversity among the lines in generation t . |
| <i>Migration matrix.</i> | |
| $d_{v,ij}$ | Migration rate through animals of sex v from line j to line i in each generation. |
| m_{ij} | Proportion of animals migrating from line j to line i in each generation, i.e., $m_{ij} = (d_{m,ij} + d_{f,ij})/2$. |
| \mathbf{M} | Migration matrix composed of m_{ij} in the element (i, j) . |
| $m_{ij(t)}$ | Proportion of genes in line i at generation t that have descended from line j in generation 0. This is obtained as the element (i, j) of \mathbf{M}^t . |

Table 2. Annual census numbers of breeding males and females, the generation interval (L), the annual effective size ($N_{e(y)}$), and the annual effective number of males ($N_{m(y)}$) in the five subpopulations of the Japanese Black cattle.

| Subpopulation | Annual number | | L | $N_{e(y)}$ | $N_{m(y)}$ |
|---------------|---------------|--------|------|------------|------------|
| | Male | Female | | | |
| Hyogo | 9.2 | 1260.3 | 10.2 | 2.06 | 0.52 |
| Tottori | 8.7 | 418.8 | 9.8 | 3.92 | 0.98 |
| Shimane | 18.3 | 1106.0 | 10.2 | 2.85 | 0.71 |
| Okayama | 20.0 | 506.7 | 8.9 | 6.34 | 1.59 |
| Hiroshima | 10.7 | 558.2 | 8.2 | 3.91 | 0.98 |
| Average | 13.4 | 770.0 | 9.5 | 3.82 | 0.96 |

All the values are the averages over 1996-2001.

Table 3. Male migration rates among the five subpopulations in the Japanese Black cattle.

| Recipient | Source | | | | |
|-----------|--------|---------|---------|---------|-----------|
| | Hyogo | Tottori | Shimane | Okayama | Hiroshima |
| Hyogo | 1.0 | 0 | 0 | 0 | 0 |
| Tottori | 0.11 | 0.81 | 0.08 | 0 | 0 |
| Shimane | 0.07 | 0.03 | 0.90 | 0 | 0 |
| Okayama | 0.18 | 0.07 | 0.16 | 0.59 | 0 |
| Hiroshima | 0.14 | 0.07 | 0.09 | 0 | 0.70 |

All the rates are the averages over 1996-2001.
 Figures on the diagonal are the proportions of genes from own bred sires.

Table 4. Proportions of genes in lines in generation t ($=3$ and 10), that have descended from lines in generation 0. The computation is based on the migration rates in Table 2.

| t | Subpopulation | Originated from: | | | | |
|-----|---------------|------------------|---------|---------|---------|-----------|
| | | Hyogo | Tottori | Shimane | Okayama | Hiroshima |
| 3 | Hyogo | 1.0 | 0 | 0 | 0 | 0 |
| | Tottori | 0.17 | 0.73 | 0.10 | 0 | 0 |
| | Shimane | 0.12 | 0.03 | 0.86 | 0 | 0 |
| | Okayama | 0.23 | 0.09 | 0.19 | 0.51 | 0 |
| | Hiroshima | 0.19 | 0.09 | 0.10 | 0 | 0.61 |
| 10 | Hyogo | 1.0 | 0 | 0 | 0 | 0 |
| | Tottori | 0.44 | 0.36 | 0.20 | 0 | 0 |
| | Shimane | 0.34 | 0.05 | 0.61 | 0 | 0 |
| | Okayama | 0.53 | 0.11 | 0.29 | 0.11 | 0 |
| | Hiroshima | 0.48 | 0.13 | 0.19 | 0 | 0.20 |

Figure legends

Figure 1. Inbreeding coefficient within line, F , (A), total genetic diversity of the set of lines, GD , (B), and genetic diversity between lines, GD_{BS} , (C), in the set of five lines ($n=5$) each with $N_m=5$ males and $N_f=200$ females.

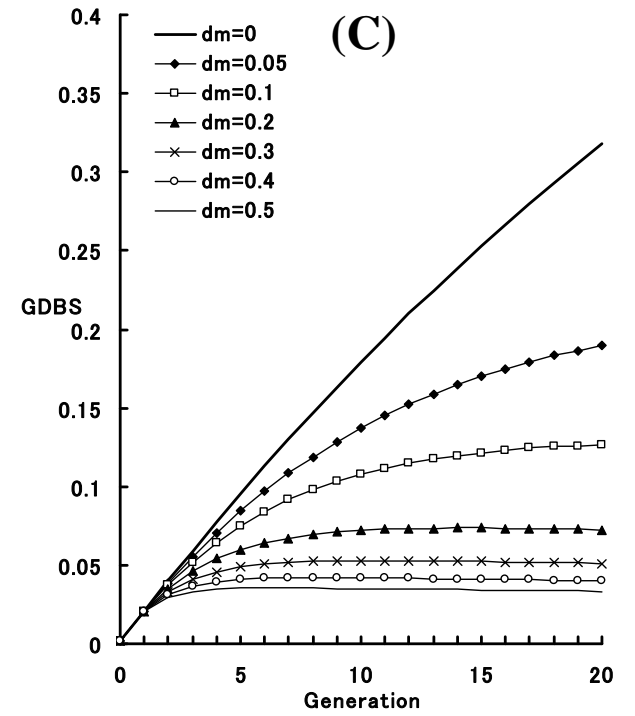
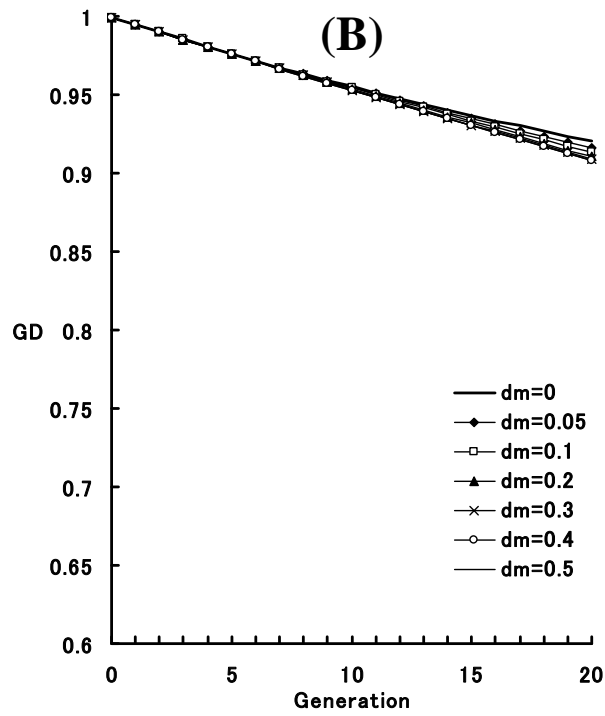
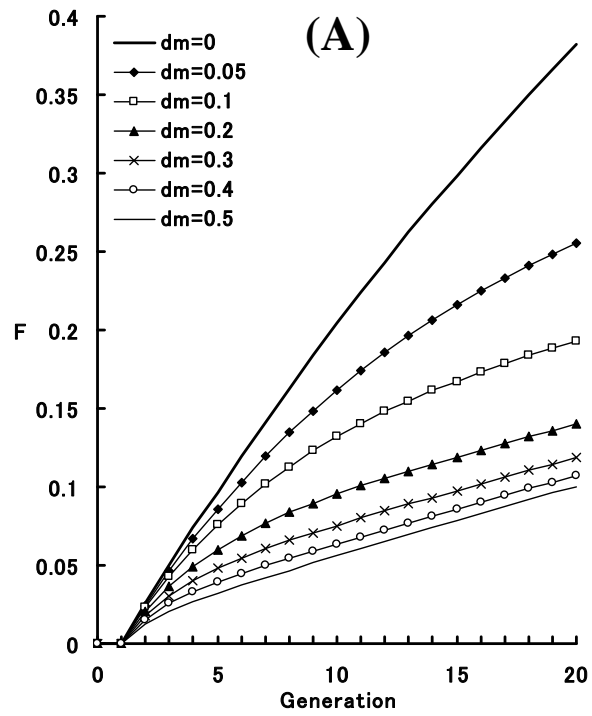
d_m = male migration rate

Figure 2. Effect of the number (N_m) and the migration rate (d_m) of males on the rate of inbreeding (ΔF) within line averaged over the initial 10 generations.

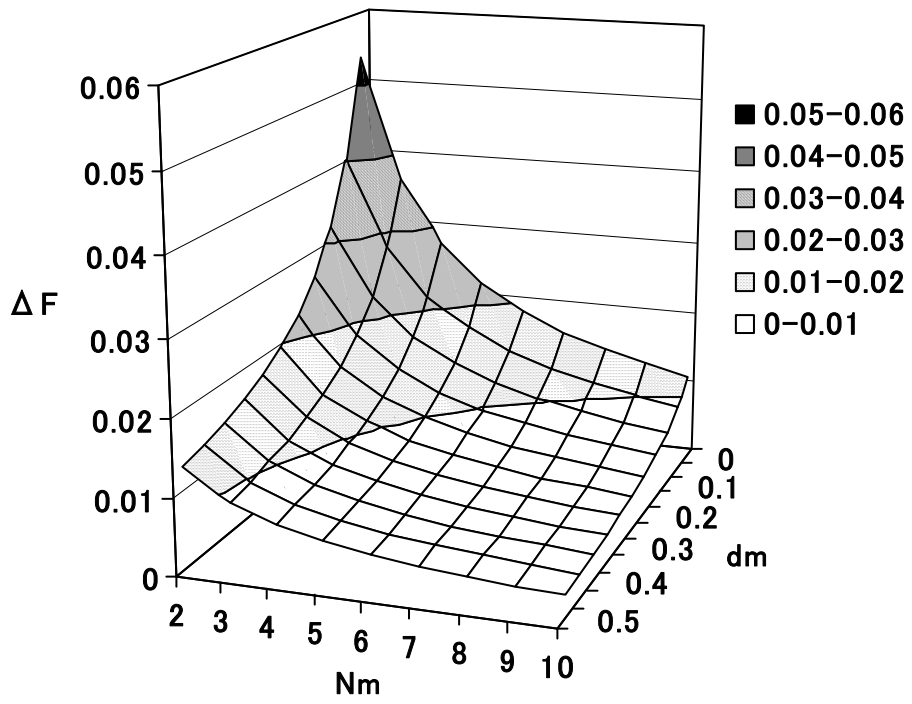
Figure 3. Effect of the number (N_m) and the migration rate of males (d_m) on the total genetic diversity after 10 generations ($GD_{(10)}$).

Figure 4. Proportion ($m_{ii(10)}$) of genes in a line in generation 10 that have descended from the line in the initial generation. The dashed line indicates the proportion of $m_{ii(10)} = 0.5$.

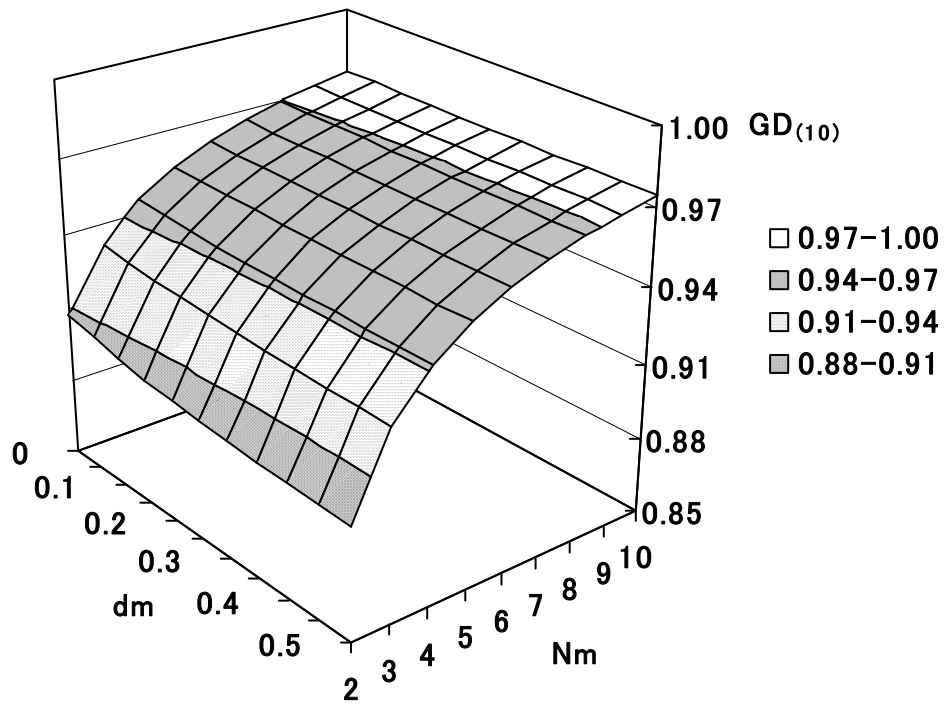
Figure 5. Graphical solution for the optimum number of males (N_m) and male migration rate (d_m), which satisfy the three criteria ($\Delta F \leq 0.01$, $GD_{(10)} \geq 0.97$ and $m_{ii(10)} \geq 0.5$) simultaneously.



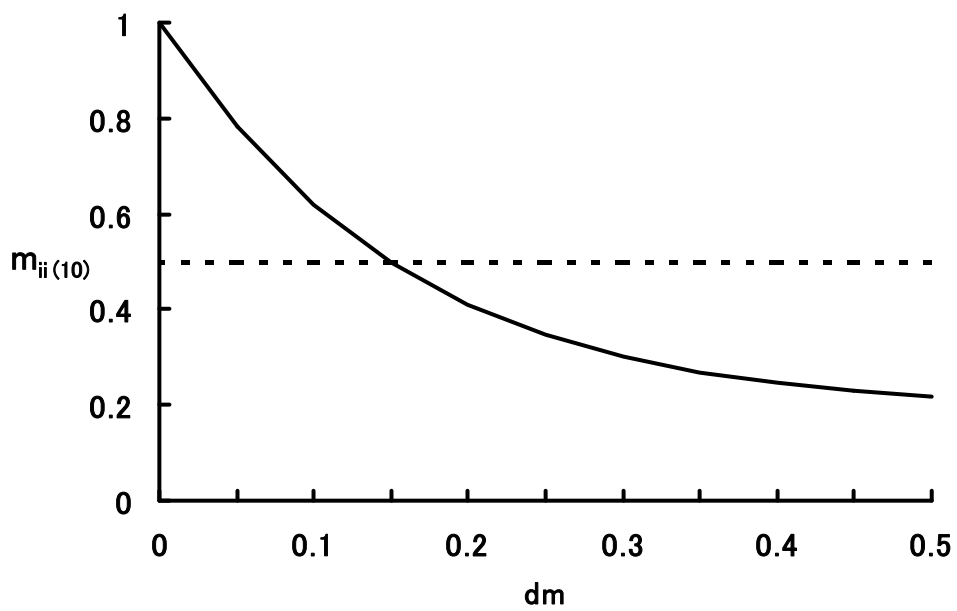
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Figure 1



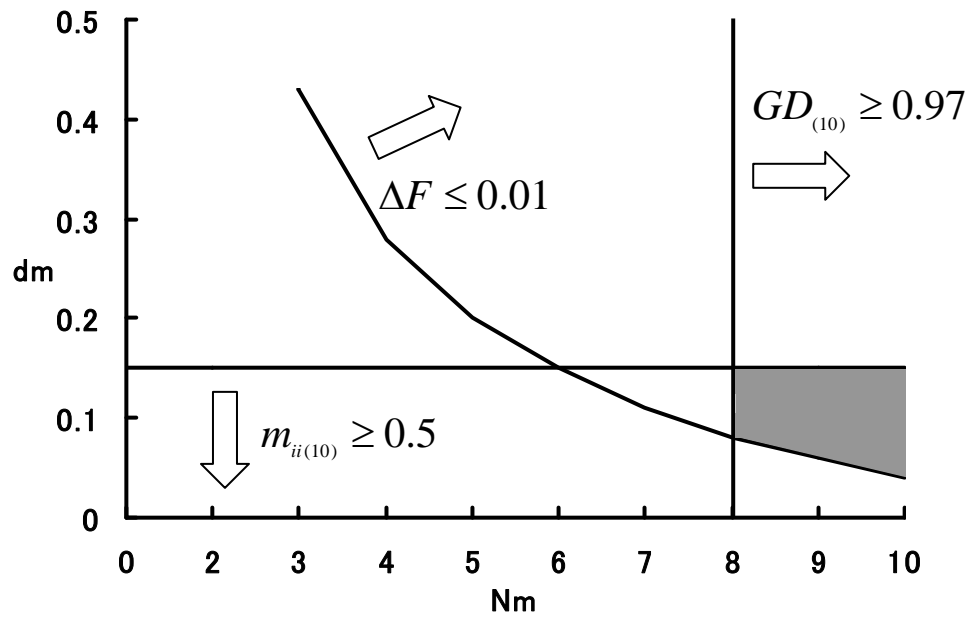
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Figure 2



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 Conservation of genetic diversity in the Japanese Black
 Figure 3



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Conservation of genetic diversity in the Japanese Black
Figure 4



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Conservation of genetic diversity in the Japanese Black
Figure 5