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(Citation)
Journal of Animal Breeding and Genetics,121(4):242-252

(Issue Date)
2004-08

(Resource Type)
journal article

(Version)
Accepted Manuscript

(URL)
https://hdl.handle.net/20.500.14094/90000188

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Monitoring of genetic diversity in the Japanese Black cattle population by the use of pedigree information

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Key words: genetic diversity, Japanese Black cattle, effective number of ancestors, pedigee analysis, gene dropping simulation

Summary

The gene pool of the Japanese Black cattle has been completely closed to foreign breeds during the last one hundred years. Genetic diversity of the Japanese Black cattle from 1960 to 2000 was monitored with three estimates of effective number of ancestors. Founder genome equivalent (N_{ge}) accounts for all the causes of reduction of diversity. Effective number of founders (N_{ef}) and non-founders (N_{enf}) explain reduced diversity due to unequal genetic contributions of founders and random genetic drift in non-founders, respectively. Further examination using gene dropping simulation was conducted to obtain information on survival of founder alleles. Unique founder alleles were dropped down along the actual pedigree with Monte Carlo procedure following Mendelian segregation rules, and generated genotypes of all the current live animals (612,959 heads). Pedigree records consisted of 2,075,188 animals was used for these analysis. The estimates of three effective numbers (N_{ef}, N_{ge}, and N_{enf}) decreased from 418.6 to 50.3, 86.6 to 7.3, and 109.2 to 8.5, respectively, during the period from 1960 to 2000. The increasing differences between two kinds of genetic diversity indices derived from N_{ge} and N_{ef} showed that large part of the reduced diversity from 1980 was attributed to genetic drift due to the intensive use of particular limited number of sires. In gene dropping analysis, probabilities of extinction of founder alleles were derived from their distributions of frequency in the current animals. Several founders showed low probabilities of allele extinction, irrespective of their relatively low genetic contributions. This suggests that these founders have lineages through which their alleles are surely transmitted to the

current breed. The use of these founders as a strategy for recovering the genetic diversity was discussed.

Introduction

In parallel to the enhancement of genetic progress, preservation of genetic diversity in the population is an important task in animal breeding, to allow the population to face future economic and environmental changes and to assure a possible long-term response to selection for traits of interest (Barker 2001). Furthermore, the reduction of genetic diversity, i.e., the reduction of the effective population size, associates with various unfavorable phenomena such as inbreeding depression in fitness-related traits and an increased fluctuation in selection response (Falconer and Mackay 1996).

Monitoring of genetic diversity in populations of domestic animals has been traditionally based on the estimated effective population size from the rate of inbreeding (for reviews, see Wright 1977; Pirchner 1983), since this parameter is inversely related to the rate of decay of genetic diversity in the population. In addition to the effective population size, the recent theoretical development in conservation genetics has provided many analytical tools for managing genetic diversity. Although the new tools have been originally proposed for captive breeding of endangered wild species, the application to domestic animal populations is expected to give further insights beyond the effective population size (Rodrigáñez et al. 1998; Toro et al. 2000; Goyache et al. 2003). For example, Lacy (1989) defined the effective number of founders to account for the loss of genetic diversity from unequal founder representations. He also introduced the concept of founder genome equivalents as theoretically expected number of founders that would be required to generate the genetic diversity in the actual population if the founders were equally represented and had lost no alleles (Lacy 1989). Recently, Caballero and Toro (2000) showed the interrelations among these parameters and proposed a new parameter, the effective number of non-founders, which explains the amount of genetic diversity reduced by random genetic drift accumulated in non-founders' generations.

MacCluer et al. (1986) proposed the method of gene dropping simulation, in which different alleles are assigned to founders and the genotypes of all descendants are generated along the actual pedigree. By replicating this process, distributions of frequencies of founders' alleles and probabilities of allele extinction in a population under question can be estimated. Although the mean of the distribution of allele frequency for a founder should coincide with the genetic contribution computed from pedigree analysis, the probability of allele extinction can be obtained only through the gene dropping simulation.

In the present study, we apply these analytical tools to the population of the Japanese Black cattle, and discuss the management plans for the genetic diversity. The recent pedigree analysis of this breed has indicated a drastic reduction of the effective population size during the last two decades (Nomura et al. 2001).

Materials and methods

Breed history of the Japanese Black cattle

Among four domestic breeds in Japan (i.e., Japanese Black, Japanese

Brown, Japanese Shorthorn, and Japanese Poll), the Japanese Black is most common, with 0.61 million reproductive cows. The breed has been maintained by pure breeding, after a short period of crossbreeding between native cattle and several foreign breeds such as Simmental, Ayshire, and Brown Swiss (Namikawa 1992) in the early 20th century. In 1944, the Japanese Black was approved as purebred by the government. Although the Japanese Black cattle had been mainly bred for dual purpose (draft and beef) in 1950's, the use had gradually turned into beef production, in response to the mechanization of farming and the rapid increase of demand for beef in 1960's. Accordingly, the progeny testing for carcass traits was initiated in 1968, and 99.9% of calves are produced by year-round artificial insemination by selected sires. In 1980's, the intramuscular fat deposition (marbling) had become the main breeding objective.

A notable feature in the breed history is that most of breeding projects had been carried out within prefectures, though there was limited migration among prefectures, usually of males. For example, in the crossbreeding prior to the breed establishment, the breeds used and the degree of crossing varied among prefectures, and the progeny testing has also been carried out within a station of each prefecture. Thus, the breed was genetically subdivided into several local subpopulations (Nomura and Sasaki 1988). In the subdivided breed structure, subpopulations in the five prefectures in western region of Japan (i.e., Hyogo, Tottori, Okayama, Shimane, and Hiroshima prefectures in Chugoku district) have played important roles as suppliers of breeding stocks to the whole breed. Among the breeders of the Japanese Black, it has been well known that the five subpopulations had their unique characteristics; e.g., the high meat quality in Hyogo and the high growth rate in Tottori and Shimane.

Since liberalization of beef import restriction in 1991, domestic production of high-quality beef has received more emphasis in Japan, and the genetic evaluation with best linear unbiased prediction (BLUP) under animal model using field carcass records was initiated from the same year. However, due to the intensive use of a few sires with high marbling predicted breeding values (PBVs), the decline of genetic diversity is an increasing problem. From the analysis of inbreeding, Nomura et al. (2001) showed that the effective size of the breed decreased sharply after 1991, and the harmonic mean between 1993 and 1997 was only 17.2.

Pedigree depth and effective numbers of ancestors

Pedigrees of the Japanese Black cattle can be traced to an ancestral population of foundation period (1944 or before). All the available pedigree data kept by the Wagyu Registry Association was used in the analysis, which consisted of 2,075,188 animals. According to Boichard et al. (1997), the ancestors with unknown parents are defined as founders, and all of their descendants as non-founders. The analysis was carried out for populations born in every five years from 1960 to 2000. These populations are referred to as reference populations. The number of bulls and cows in each reference population are given in Table1, together with the number of their founders. The database in the Wagyu Registry Association includes pedigree records of all the breeding animals born after 1980. Although the database before 1975 was not complete, it covered 25-45% of the breeding animals born in each year.

The depth of pedigree in each reference population was examined by computing the number of discrete generation equivalents (g_e), which is the expected number of generations from the base population to the reference populations if generation proceeded discretely. This parameter is obtained by

$$g_e = \frac{1}{N} \sum_{j=1}^{N} \sum_{i=1}^{n_j} \frac{1}{2^{g_{ij}}},$$

where n_j is the total number of ancestors of animal j in the reference population, g_{ij} is the number of generations between animal j and its ancestor i, and N is the number of animals in the reference population (Wooliams and Mäntysaari 1995).

To assess the amount of genetic diversity and clarify the causes of the reduction, we estimated three types of effective numbers of animals, i.e. effective number of founders, founder genome equivalents, and effective number of non-founders. The effective number of founders (N_{ef}) is estimated by

$$N_{ef} = \frac{1}{\sum_{i=1}^{N_f} \left(\frac{c_i}{N} \right)^2},$$

where N_f is the number of founders, N is the number of animals in the reference population, and c_i is the sum of direct relationships between founder i and animals in the reference population (Lacy 1989; Rochambeau et al. 1989). In this study, we defined c_i / N as genetic contributions of founder i, so that it can be considered as the expected frequencies of alleles derived from founder i in the reference population. Since N_{ef} explains only the loss of genetic diversity due to unequal contributions of founders to the reference population, and does not account for the effect of genetic drift accumulated in the non-founders, it overestimates genetic variability of the reference population (Caballero and Toro 2000).

All the causes of the reduction of genetic variability are fully accounted for by founder genome equivalents (N_{ge}). This parameter is estimated by

$$N_{ge} = \frac{1}{\sum_{i=1}^{N}\sum_{j=1}^{N} a_{ij} \Big/ N^2},$$

where a_{ij} is additive relationship coefficient between individual i and j. The denominator is the average of full additive relationship matrix A (including reciprocals and diagonal elements) (Lacy 1995; Caballero and Toro 2000).

The third type of effective number of animals, the effective number of non-founders (N_{enf}), accounts only for the effects of genetic drift in non-founder generations. This effective number is obtained from the relation

$$\frac{1}{N_{ge}} = \frac{1}{N_{ef}} + \frac{1}{N_{enf}} \qquad (1)$$

(Caballero and Toro 2000).

When genetic diversity is expressed with the expected heterozygosity, that is a common measure of genetic diversity (Nei 1973), the amount of genetic diversity (GD) in the reference population relative to the base population is estimated by

$$GD = 1 - \frac{1}{2N_{ge}},$$

(Lacy 1989, 1995). Analogously, the genetic diversity estimated by

$$GD^{*}=1-\frac{1}{2N_{ef}}$$

accounts only for the decay due to unequal contributions of founders (Caballero and Toro 2000). From equation (1), the difference of these two indices of genetic diversity is

$$GD^{*}-GD=\frac{1}{2N_{enf}}.$$

This difference represents the amount of the genetic diversity reduced by the genetic drift accumulated over non-founders' generations (Caballero and Toro 2000).

Gene dropping simulation

Gene dropping simulation proposed by MacCluer et al. (1986) was applied to the population of all the reproductive cows alive in August 2001 (612,959 heads). In the simulation, unique alleles were assigned to founders, and the genotypes of all descendants along the actual pedigree were generated through Monte Carlo simulation following Mendelian segregation rules. By replicating 20,000 times of this process, the distribution of frequencies of alleles from each founder was estimated. Theoretically, the expected value of the distribution of allele frequencies for a founder should agree with the genetic contribution of the founder (Lacy 1989; Rochambeau et al. 1989; Caballero and Toro 2000). From the estimated distribution, the probability of extinction of alleles originated from a given founder (Pr(lost)) was calculated as the proportion of replicates in which both alleles from the founder had not existed in the reference population.

All the computations for the pedigree analysis and gene dropping simulation were conducted with our original Fortran programs.

Results and discussion

The depth of pedigree in each reference population is shown in the last column of Table 1. From 1960 to 2000, discrete generation equivalents (g_e) increased from 5.1 to 10.2. Dividing the period by the increment of g_e gives an estimate of average generation interval in the last four decades as 7.8 years. The increase of g_e along years was essentially linear, implying that the change of generation interval was not large during the analyzed period.

The estimates of the three effective numbers of ancestors are given in Table 2. The most comprehensive effective number, founder genome equivalents (N_{ge}), decreased from 86.6 to 7.3 during the period analyzed. According to the definition by Lacy (1989), the amount of genetic diversity in the recent population could be generated by only 7 or 8 non-related founders. The sharp decline of the effective number of founders (N_{ef}) in the earlier period (1960-80) suggests that selection enhancing unequal contributions of founders, such as selection among strains, had been practiced, and genes in minor strains would be mostly lost during this period. Nevertheless, throughout the investigated period, N_{ef} was much larger than the effective number of non-founders (N_{enf}), and the latter effective number showed close value to N_{ge}, suggesting that for the cause of reduction of genetic diversity, random genetic drift accumulated in the non-founder generations is more serious than the unequal contributions of founders.

Assuming a closed population with a constant selection scheme, Wray and Thompson (1990) predicted that although variation among contributions of founders is inflated by selection, the variation approaches an asymptotic value within several generations. From this prediction, it is expected that the effective number of founders (N_{ef}) attains a steady value within several generations (Caballero and Toro 2000). Although the breeding objectives in the Japanese Black have been altered during the past four decades, the rapid decrease of N_{ef} in the earlier period and the much smaller decrease of N_{ef} after 1980 are roughly in agreement with the theoretical expectation.

In the recent work of Boichard et al. (1997), N_{ef} for three cattle breed in France (i.e., Abondance, Normande, and Limousine) were estimated to be 69, 132, and 790, respectively. The corresponding estimates of N_{ge} were 17, 22, and 206, respectively. Sölkner et al. (1998) reported that N_{ef} and N_{ge} for four main cattle breeds in Austria (i.e., Simmental, Braunvieh, Pinzgauer and Grauvieh) varied from 66.2 to 220.8 and from 20.8 to 94.3, respectively. In addition, those values for three endangered breeds in the same country (i.e., Original Pinzgau, Tux-Zillertal, and Carinthian Blond) ranged from 21.0 to 65.4 and from 9.7 to 22.6, respectively (Baumung and Sölkner 2002). Estimate of N_{ef} for UK Holstein-Friesian population by Roughsedge et al. (1999) was 93. Comparison with these published estimates characterizes the extremely limited genetic diversity in the current Japanese Black population.

Figure 1 shows the change of the two genetic diversity indices, GD and GD^*, relative to the foundation period of the breed. As the effective number of founders essentially remained unchanged after 1980, there were little changes in the index GD^* (the index accounting only for the decline of genetic diversity due to unequal contributions of founders) during the later period. In contrast, the index GD (the index taking all the causes of reduction of genetic diversity into account) declined continuously throughout the period analyzed. The index enhanced its decreasing rate after 1975, and the decrease was further accelerated after 1990.

In a population with a constant effective size (N_e), Caballero and Toro (2000) showed that GD reduces linearly with the advance of generation as

$$GD = 1 - \frac{t}{2N_e},$$

where t is the generation numbers from the founders' generation. Since the change of generation interval in the Japanese Black population was not large during the investigated period (Fig. 1), i.e., generation number has increased in parallel with succeeding year, the acceleration of decrease of GD observed in Figure 1 will be mainly a reflection of the reduced effective size. From the rate of inbreeding, Nomura (1988) estimated the effective sizes of the Japanese Black population in 1960 and 1980 to be 1724 and 125, respectively. The estimate in 1960 was exceptionally larger than the published estimates for breeds of domestic animals ($N_e \approx 100$; see Wright (1977) and Pirchner (1983)), presumably because of the breed subdivision into divergent strains. Due to the large effective size, the population in 1960 maintained 99.4% of the genetic diversity in the foundation period (GD=0.994 in 1960). The selection among strains, suggested from the behavior of N_{ef} in Table 2, reduced the effective size and enhanced the decreasing rate of *GD* after 1975. Nevertheless, the population in 1980 still maintained the effective size (N_e=125) comparable to the published estimates. However, the reduction of the effective size had continued and the harmonic mean of the effective size between 1993 and 1997 declined to 17.2 (Nomura et al. 2001). The serious reduction of the effective size is reflected in the acceleration of reduction of the genetic diversity after 1990. Nomura et al. (2001) showed that the main cause for the recent reduction of the effective size of the Japanese Black population is the intensive use of a limited number of sires after 1990. Although about half the new-born animals in the current breed were progeny of only five sires (Nomura et al., 2001), the intensive use of a few sires did not cause a large reduction of the effective number of founders (N_{ef}) and the corresponding diversity index (*GD**). As seen from *GD**-*GD* in Figure 1, the major part of the reduction of genetic diversity after 1980 was reflection of the enhanced random genetic drift over the non-founders' generations.

In considering the preservation or the recovery of genetic diversity in the Japanese Black population, the genetic contributions of subpopulations (populations of prefectures) existed in the foundation period will provide useful information. In Figure 2, the genetic contributions of founders, summed up by their birth prefecture, are presented. As expected from the breed history, the genetic contributions of the five traditional breeding units (i.e., Hyogo, Tottori, Okayama, Shimane and Hiroshima prefectures) have predominated since the early time. Due to the current emphasis on the meat quality in beef production in Japan, the genetic contribution of Hyogo prefecture increased after 1980 and the contribution to the breed in 2000 was beyond 40%. The results in Figure 2 indicate that genes originated from the subpopulations less represented in the current breed (i.e., Okayama, Shimane and Hiroshima prefectures) are of special importance for the recovery of genetic diversity.

Information additional to the genetic contributions will be obtained from gene dropping simulation. The results of simulation are summarized in Table 3, in which the probabilities of allele extinction (Pr(lost)) are given for the five highest contributors (founders) in each of the five traditional subpopulations. Under the assumption that all the founders (39,966 heads) equally contribute to the current live animals, genetic contributions of each founders would be equivalent to 2.5×10^{-5}. The female founder 'Fukue' in Hyogo showed an exceptionally high genetic contribution, since her famous son 'Tajiri' had played an important role in the production of breeding stocks with high genetic merits of marbling. Although 'Tajiri' is not a founder, his genetic contribution to the current breed is 0.168.

In considering the management of genetic diversity, Pr(lost) gives a useful information. For example, two founders, 'Moku' and 'Hana' in Hyogo contribute to the current breed with a similar proportion, but Pr(lost) of 'Moku' is much higher than 'Hana'. A detail survey of pedigree revealed that 'Moku' showed a low genetic contribution in the early period of the breed history. Thus, the alleles had passed a strong bottleneck in the early period, leading to the allele extinction with a high probability. In contrast, the low probability of allele extinction of the founder 'Hana' imply that she has lineage through which her alleles can be surely transmitted to the current breed. Although the genetic contributions of the founders in Shimane, Okayama and Hiroshima prefectures were relatively low, several founders showed low probabilities of allele extinction. This result suggests that a part of the current population is connected with these founders without severe bottleneck of lineages.

Although the current genetic evaluation of the Japanese Black has been limited to carcass traits, evaluations of other economically important traits such as reproductive performance, growth rate, and maternal ability are planed. To produce breeding animals with a high aggregated performance, formation of several strains with different genetic characteristics and crossing among them will be an efficient strategy. Maintaining several strains will also contribute to the preservation of genetic diversity within the breed. Although we have used the gene dropping simulation to examine allele survival in the breed, this technique could be applied to each live animal or local group of animals, to detect genetically important animals or a local group surely having target founder alleles for preservation. Breeding scheme based on the information could effectively contribute to the recovery of genetic diversity in the Japanese Black population.

As suggested by several researchers (Chesser et al. 1980; Lacy 1987, 1994), subdivided population structure is favorable for the maintenance of genetic diversity in the whole population. Sölkner et al. (1998) showed that the high genetic diversity in the Austrian Simmental is largely owing to the population structure subdivided into partially isolated subpopulations. We have also reported the average additive relationships within and between prefectures in the current population of the Japanese Black cattle, showing that genetic differentiation is still maintained among several prefectures (Honda et al. 2002). However, the management plan with a subdivided population should be carefully designed. Simulation and theoretical studies (Lacy 1987; Wang 1997 a, b) have shown that three matters are critically important for a successful management plan; the number and the size of subpopulations, and the migration rate among subpopulations. For a population with a given size, the genetic diversity ultimately maintained in the whole population is maximized when the population is divided into numerous isolated subpopulations (Kimura and Crow 1963; Yonezawa et al. 1996). However, this strategy could not be implemented in livestock populations, because of the high rate of inbreeding within subpopulations. It would be practically important to find a best compromise among the three matters. Recently, Caballero and Toro (2002) gave a basic theory to conserve genetic diversity in a subdivided population, based on the genetic diversities within and between subpopulations. In the light of the theory, theoretical studies to find an optimum population structure of the Japanese Black will be considered in our future reports.

Acknowledgements

This work was partially funded by a Grant-in-Aid for Scientific Research from the Ministry of education, culture, sports, science and technology.

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Table 1. Numbers of reproductive bulls and cows born in each year, and the actual number of founders (N_f) and the number of discrete generation equivalents (g_e).

Year	Bulls	Cow	Total	N_f	g_e
1960	447	11,972	12,419	16,739	5.1
1965	256	13,658	13,914	17,455	6.0
1970	224	22,795	23,019	23,909	6.7
1975	232	36,138	36,370	29,227	7.6
1980	250	72,885	73,135	36,750	8.2
1985	204	58,199	58,403	29,651	8.7
1990	301	76,624	76,925	29,642	9.2
1995	355	57,512	57,867	24,579	9.8
2000	289	63,410	63,699	23,168	10.2

Table 2. Founder genome equivalents (N_{ge}), effective number of founders (N_{ef}), and effective number of non-founders (N_{enf}) in each reference population.

Year	N_{ef}	N_{ge}	N_{enf}
1960	418.6	86.6	109.2
1965	272.2	55.3	69.4
1970	286.9	45.1	53.4
1975	221.8	35.0	41.6
1980	96.2	21.7	28.0
1985	74.1	14.9	18.7
1990	69.3	12.6	15.5
1995	52.4	9.4	11.4
2000	50.3	7.3	8.5

Table 3. Genetic contributions (*gc*) and probabilities of allele extinction (Pr(lost)) of five founders with the highest genetic contributions in each of five traditional breeding prefectures.

Prefecture	Founders' name	Sex [a]	*gc*	Pr(lost)
Hyogo	Fukue	F	0.1134	0.000
	Moku	F	0.0211	0.575
	Hana	F	0.0192	0.028
	Ume	F	0.0143	0.018
	Kumanami	M	0.0134	0.530
Tottori	Nishikawa	F	0.0144	0.184
	5th Shige	F	0.0121	0.288
	Akahori	F	0.0080	0.097
	Kiku 3	F	0.0072	0.464
	Kotani 2	F	0.0063	0.002
Shimane	4th Ryuun	M	0.0086	0.000
	1st Kamezu	F	0.0035	0.011
	Nitowakazuki	F	0.0035	0.000
	2nd Hidaka	F	0.0025	0.136
	Moriwaki	F	0.0021	0.023
Okayama	13th Hanayama	M	0.0093	0.000
	Senka 4	F	0.0048	0.556
	Nitta	F	0.0042	0.000
	Nakamura	F	0.0038	0.002
	Hanahide	M	0.0026	0.016
Hiroshima	4th Kakefuda	M	0.0046	0.000
	3rd Yasuda	F	0.0020	0.109
	20th Okuda	F	0.0013	0.143
	10th Hayashi	F	0.0011	0.078
	2nd Hiwa	M	0.0010	0.279

[a] M: male, F: female

Figure legends

Figure 1. Changes of genetic diversity (*GD* ; ◆, *GD** ; □) in each reference population. *GD* accounts for both the effects of the unequal genetic contributions of founders and the genetic drift, while *GD** taking only the former effect into account.

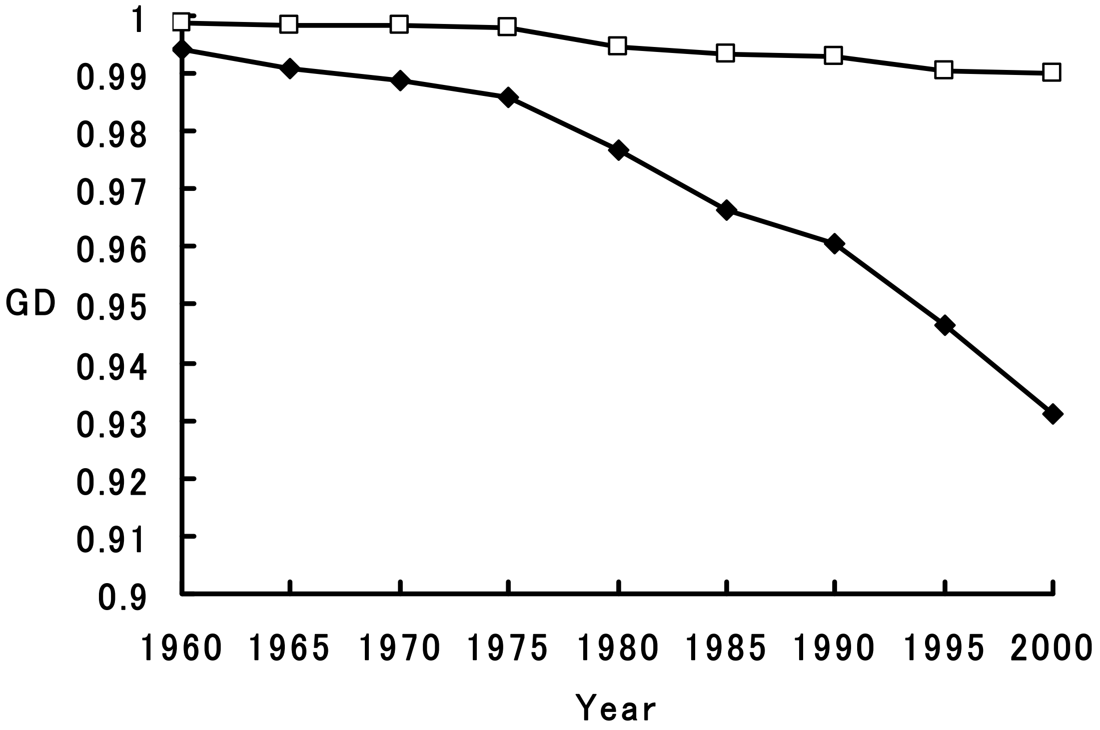
Figure 2. Classification of genetic contributions by the birth place of founders.

Figure legends

Figure 1. Changes of genetic diversity (GD ; ◆, GD^* ; □) in each reference population. GD accounts for both the effects of the unequal genetic contributions of founders and the genetic drift, while GD^* taking only the former effect into account.

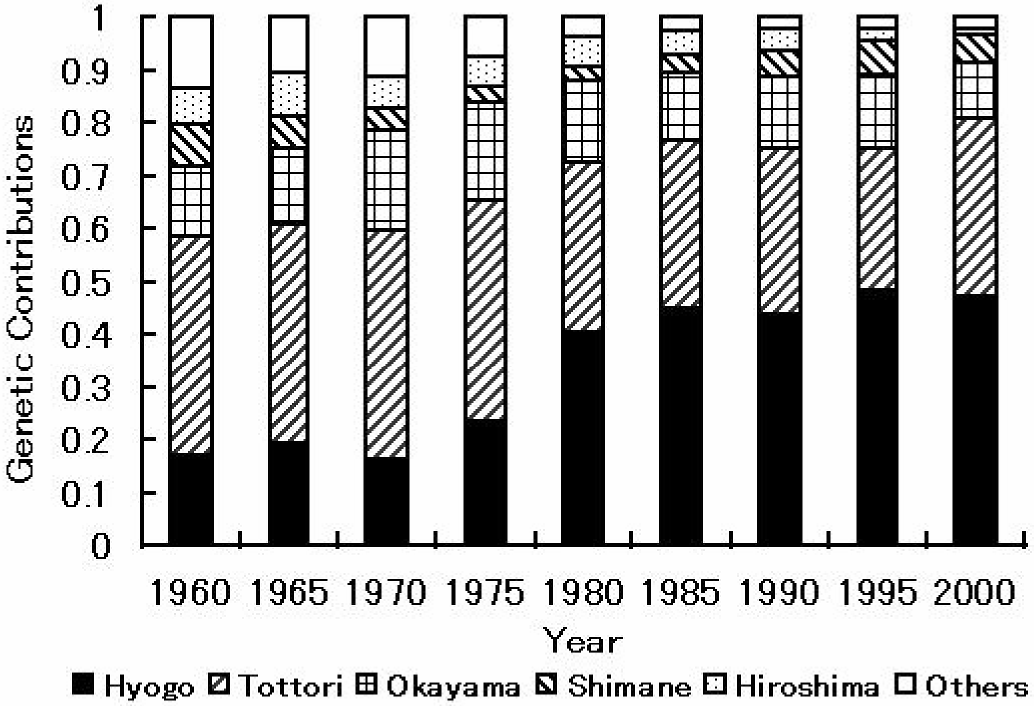
Figure 2. Classification of genetic contributions by the birth place of founders.

Figure 1



GD
1
0.99
0.98
0.97
0.96
0.95
0.94
0.93
0.92
0.91
0.9
1960
1965
1970
1975
1980
1985
1990
1995
2000
Year

Figure 2



Genetic Contributions
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1960
1965
1970
1975
1980
1985
1990
1995
2000
Year
Hyogo
Tottori
Okayama
Shimane
Hiroshima
Others