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Evaluation of genetic diversity in Japanese Brown cattle population by pedigree analysis

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Summary

The Japanese Brown is the second most common domestic beef breed, however, numerical reduction due to pressure from a profitable domestic breed is an increasing problem. This breed is uniformly characterized by its brown coat color, but is comprised of two isolated sub-breeds, Kumamoto and Kouchi, each possessing a different gene pool. Pedigree analyses were carried out for the two sub-breeds using the pedigree records of animals born from 1970 to 2000. The effective population size has been consistently reducing during the last three decades in both sub-breeds. The current effective sizes were estimated to be 25.5 and 6.0 for the Kumamoto and Kouchi sub-breeds. The estimate of the effective number of founders (N_{ef}) in the Kumamoto sub-breed decreased from 152.1 to 74.4; that of non-founders (N_{enf}), from 41.7 to 5.3; and that of founder genome equivalents (N_{ge}),from 32.7 to 4.9. The corresponding changes in the Kouchi sub-breed were from 108.2 to 79.4, 16.2 to 4.1, and 14.1 to 3.9. Increasing differences between the two genetic diversity indices in the sub-breeds indicate that the greater part of the reduction of genetic diversity can be attributed to genetic drift that accumulated in the non-founders' generations. A comparison with published estimates for several cattle breeds suggests the extremely limited genetic diversity of Japanese Brown. In addition to the avoidance of further reduction of genetic diversity, it will be important to counteract the process of breed decline by establishing a production system to efficiently utilize the unique characteristics of this breed and by developing links between the breed and products with market value.

Introduction

A recent census of beef cattle in Japan (MAFF 2004) revealed that 94.9% of the reproductive cows are Japanese Black. Japanese Brown is the second most common domestic beef breed; its share of reproductive cows is only 3.2%. Numerical reduction is an increasing problem in this breed due to pressure from the high-quality beef from Japanese Black.

Japanese Brown was approved as a breed in 1944 on the basis of the uniformity in exterior appearance (characterized by its brown coat color in particular; Nishida 1973); however, this breed is comprised of two completely isolated sub-breeds, each with a different gene pool. One is the Kumamoto sub-breed, which primarily distributes in Kumamoto prefecture on Kyushu Island. This sub-breed originated from anciently imported Korean cattle that adapted to the regional climate of the prefecture. The present population consists of descendants of animals crossbred primarily with Simmental in the early 1900's. The other sub-breed (Kouchi sub-breed) has been bred chiefly in Kouchi prefecture on Shikoku Island. The origin of this sub-breed is animals crossbred between Korean and native cattle in the 1800's. The cattle of this sub-breed exhibit common characteristics of black body parts, such as horns, hoofs, eyelids, and nose.

Current domestic beef production depends largely on Japanese Black. However, Japanese Brown possess several superior abilities in certain production traits, such as growth rate, feed utilization efficiency, and grazing aptitude. Their genes and gene combinations could potentially represent future breeding materials. A pedigree analysis was carried out for this present study to evaluate the genetic diversity in the two Japanese Brown sub-breeds. We previously reported the results of pedigree analyses of the Japanese Black cattle population in a series of studies (Nomura et al. 2001, 2005; Honda et al. 2002, 2004). We then compared the results of this present study with those of the Japanese Black population to clarify the current genetic status of the Japanese Brown population.

Materials and Methods

Data

Separate analyses were carried out for the Kumamoto and Kouchi sub-breeds using the respective pedigree records kept by the Association for Japanese Brown Registration and the Wagyu Registry Association. The registered animals born in each year from 1970 to 2000 were the reference populations of the pedigree analyses, for which various population genetic parameters were estimated. The numbers of bulls and heifers in the reference populations for every five years are given in Table 1. The pedigrees of the animals in the reference populations were traced back as far as possible to obtain the base populations of the Kumamoto and Kouchi sub-breeds, which consist of ancestors born around 1928 and 1940. Boichard et al. (1997) designated the ancestors with unknown parents, i.e. the ancestors in the base population, as founders, and all of their descendants as non-founders. There were 11,192 founders and 97,900 non-founders in the analyzed pedigree files of the Kumamoto sub-breed and 741 and 12,416 in the Kouchi sub-breed files. The number of founders (N_f) traced from the reference populations every five years are listed in Table 2.

Depth of the pedigree and generation interval

The depth of the 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 (Woolliams & Mäntysaari 1995). This parameter was 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 (Woolliams & Mäntysaari 1995).

The generation intervals of four gametic pathways, i.e. sire to son (L_{ss}), sire to daughter (L_{sd}), dam to son (L_{ds}), and dam to daughter (L_{dd}), were estimated from the birth dates of animals in each reference population and those of their sires and dams. The average generation interval (L) was computed from

$$L = \frac{L_{ss} + L_{sd} + L_{ds} + L_{dd}}{4}.$$

F-statistics and effective population size

The F-statistics (F_{IT}, F_{ST}, and F_{IS}; Wright 1951, 1969) were estimated in each reference population to assess the amount of inbreeding and the population structure. The coefficient F_{IT} is the average inbreeding coefficient of the reference population, and F_{ST} is the inbreeding coefficient expected under random mating. The latter coefficient was estimated as the average coancestry between the sires and dams of the reference population. The third coefficient, F_{IS}, was obtained by the formula of Wright (1951, 1969), as

$$F_{IS} = \frac{F_{IT} - F_{ST}}{1 - F_{ST}}.$$

This coefficient measures the deviation of the actual mating from randomness. The actual inbreeding (F_{IT}) exceeds the level expected under random mating (F_{ST}) when $F_{IS} > 0$, implying that mating among more closely related parents than average is predominant, or that the population is partitioned into subpopulations and mating is more or less restricted within each subpopulation. In contrast, avoidance of inbreeding or mating between subpopulations is predominant in populations with $F_{IS} < 0$.

The effective size of the sub-breed was estimated from the increasing rate of F_{ST} per generation (Wright 1977; Caballero & Hill 1992). The annual increasing rate ($\Delta F_{ST,y}$) was first computed by

$$\Delta F_{ST,y} = \frac{F_{ST,t} - F_{ST,t-1}}{1 - F_{ST,t-1}},$$

where $F_{ST,t-1}$ and $F_{ST,t}$ are the coefficients of F_{ST} in two successive years. The annual increasing rates from 1971 to 2000 were averaged over every ten years. The averaged annual increasing rate ($\Delta \bar{F}_{ST,y}$) in each ten-year period was then converted into the expected increasing rate per generation (ΔF_{ST}), using the average annual increment of the generation (Δg_e) estimated from the difference between the discrete generation equivalents in the first and last years in the period, as

$$\Delta F_{ST} = \frac{\Delta \bar{F}_{ST,y}}{\Delta g_e}.$$

Finally, the effective size (N_e) in the period was obtained from

$$N_e = \frac{1}{2\Delta F_{ST}}.$$

Effective number of ancestors and genetic diversity

Three effective numbers of ancestors, i.e. the effective number of founders, founder genome equivalents, and the effective number of non-founders, were estimated to assess the genetic diversity and clarify the causes of changes in genetic diversity. The effective number of founders (N_{ef}) was 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 the direct relationships between founder i and the animals in the reference population (Lacy 1989; Rochambeau et al. 1989). 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 diversity of the reference population (Caballero & Toro 2000).

All causes of the reduction of genetic variability are fully accounted for by the 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 the additive relationship coefficient between individuals i and j. The denominator is the average of the full additive relationship matrix, including reciprocals and diagonal elements (Lacy 1995; Caballero & Toro 2000).

The third 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

$$\frac{1}{N_{ge}} = \frac{1}{N_{ef}} + \frac{1}{N_{enf}} \tag{1}$$

(Caballero & Toro 2000).

The amount of genetic diversity (GD) in the reference population relative to the base population is estimated as follows when the genetic diversity is expressed with the expected heterozygosity (Nei 1973):

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

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

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

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

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

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

Results

The discrete generation equivalents (g_e) estimated in the two sub-breeds are listed in the last columns of Table 1. The estimates in the two sub-breeds in 1970 were similar and increased at roughly the same rate until 1990. The discrete generation equivalent in the Kumamoto sub-breed then increased continuously after 1990, while the values in the Kouchi sub-breed remained unchanged between 1990 and 1995, indicating that the turnover of generations in the Kouchi sub-breed ceased in this period.

Table 2 presents the average generation intervals during three periods, from 1970 to 1980, 1981 to 1990, and 1991 to 2000. The average generation intervals were prolonged by 1.1 and 1.2 years in the Kumamoto and Kouchi sub-breeds during the first two periods, primarily due to an increase of the intervals from sires (i.e. L_{ss} in Kumamoto and L_{ss} and L_{sd} in Kouchi sub-breeds). The generation intervals in all pathways, particularly those from sires, were prolonged more remarkably in the last period, suggesting an accelerated long-term use of sires. In fact, the prolongation of the generation interval in the last decade in the Kouchi sub-breed is chiefly due to the use of two full-sib sires born in 1972 and 1981. The delay of generation turnover (c.f. Table 1) was also caused by the use of these two sires.

Pirchner (1983) suggested that L_{ss}=6.5-9, L_{sd}=4.5-6.5, L_{ds}=5-6.5, and L_{dd}=5-6.5 are the standard generation intervals in the four pathways of beef breeds, based on the estimates of generation intervals for several cattle breeds. These values indicate that the generation intervals of the two sub-breeds of Japanese Brown from 1981 to 1990 were approximately within the range of the standard values. However, the current generation intervals in all pathways exceed the standard in both sub-breeds.

Figures 1 (A) and (B) depict the changes in the F-statistics for the Kumamoto and Kouchi sub-breeds. The average inbreeding coefficient (F_{IT}) of Kumamoto and Kouchi sub-breeds in 2000 reached 7.1% and 8.8%, which were slightly higher than the recent estimate (6.0%) in the Japanese Black cattle population (Nomura et al. 2005). The behavior of the F-statistics in the Kumamoto sub-breed clearly reflects a change in the breeding structure: Semen from sires was collected until 1994 at three distant AI facilities, i.e. Kumamoto Prefectural Agricultural Research Center (KPARC) and two local agricultural cooperatives, from which semen had been distributed to farmers in the adjacent areas. Due to this method of dispersed semen management, local differentiation had been retained among the sires used in the areas, so that the population had been genetically subdivided ($F_{IT} > F_{ST}$, $F_{IS} > 0$). However, because the semen has been intensively managed at KPARC since 1994 (Association for Japanese Brown Registration 2002), the local differentiation among sires has rapidly reduced, and the genetically subdivided structure has essentially disappeared since 1996 ($F_{IT} < F_{ST}$, $F_{IS} < 0$). Similar F-statistics behavior was observed in the Kouchi sub-breed; F_{IT} in this sub-breed has exhibited a lower value than F_{ST} for most years since 1980, implying that the genetically subdivided structure has disappeared during the last two decades.

The temporal reductions of F_{ST} observed over several years in the Kouchi sub-breed are not due to migration from outside the population. F_{ST} should monotonically increase over generations in a closed population with discrete generations. However, this is not necessarily true for annual estimates of F_{ST} in a population with overlapping generations; the estimates may indicate a decrease through a temporal reduction of relationships between the sires and dams used during the year.

Estimates of the effective sizes of the sub-breeds are provided in Table 2. The effective size consistently reduced during the last three decades in both sub-breeds. A serious reduction was observed during the last decade in the Kouchi sub-breed in particular. A two-stage testing schemes for bulls, i.e. a performance test for growth ability and feed utilization and a progeny test for carcass traits, was initiated in the Kumamoto sub-breed in the late 1960s in response to a shift in the primary purpose of beef production. This resulted in the selection of closely related sires and an increase of relationships among breeding animals in the next generation. The effect of the scheme is evident in the acceleration of the increasing rate of F_{ST} (Fig. 1 (A)) and the consequent reduction of effective size after 1980. This also explains the reduction of the effective size of the Kouchi sub-breed from 1981 to 1990. In addition, the sharp decline of the effective size in the last decade can be largely attributed to the prolongation of the generation interval (Table 2).

Estimates of the three effective numbers of ancestors are presented in Table 4. The most comprehensive effective number, the founder genome equivalents (N_{ge}), decreased from 32.7 to 4.9 and from 14.1 to 3.9 in the Kumamoto and Kouchi sub-breeds during the analyzed period. According to the definition by Lacy (1989), the amount of genetic diversity in each of the recent sub-breeds can be generated by only about four or five non-related founders. The effective number of founders (N_{ef}) in the Kouchi sub-breed was kept at around 80 and 90 after the initial reduction from 1970 to 1975. In contrast, N_{ef} in the Kumamoto breed was approximately halved from 1970 to 1985, indicating that selection enhancing unequal contributions of founders, such as selection of breeding animals descended from limited founders, had been practiced during this period. N_{ef} was much greater than the effective number of non-founders (N_{enf}) in both sub-breeds, and the latter effective number showed a value close to N_{ge} throughout the investigated period.

Figures 2 (A) and (B) illustrate the changes of the two indices of genetic diversity, GD and GD*. The GD index (the index that takes all the causes of reduction of genetic diversity into account) in both sub-breeds sharply declined after 1990, while the changes in GD* (the index accounting for only the decline of genetic diversity due to unequal contributions of founders) were relatively small. Consequently, the difference between GD and GD* sharply increased in the two sub-breeds, indicating that the decay of genetic diversity in the two sub-breeds after 1990 is largely due to genetic drift accumulated over the non-founders' generations.

Discussion

Livestock breeds are important components of world biodiversity because of their unique genes and the gene combinations they carry as a consequence of adaptation to different environments. Numerous authors have stressed the importance of breed conservation (reviewed by Hall & Bradley 1995).

Several factors can result in the numerical reduction of a breed; most are associated with economic pressures, including changes in the production system (Toro et al. 2000). Intensive use of a limited number of highly productive breeds is a worldwide trend in animal production, which accelerates the numerical decline of minor breeds and genetic erosion by crossing with improved breeds. Consequently, a substantial number of livestock breeds have become extinct in the last five decades, and 30% of the existing breeds are presently at risk of extinction (Barker 2001).

Japanese Brown is an example of a breed drastically declining in population size due to pressure from a profitable breed. Domestic production of superior quality beef has been emphasized in Japan since the liberalization of beef import restrictions in 1991. This led to an increased dependence of beef production on Japanese Black, while the Japanese Brown population rapidly declined due to its relatively inferior meat quality (c.f. Table 1).

We have indicated in a series of studies on the population structure of Japanese Black (Nomura et al. 2001; Honda et al. 2002, 2004) that serious reduction of genetic diversity can be observed even in a profitable breed as a result of heavy utilization of a few prominent breeding animals. We compare here the present results with those reported for Japanese Black and other cattle breeds; a contrast that reveals the current genetic status of the Japanese Brown population.

Table 5 summarizes the estimated population genetic parameters in the Japanese Black population (Nomura et al. 2005), three Austrian cattle breeds (Baumung & Sölkner 2002), and three Danish dairy breeds (Sørensen et al. 2005). According to Baumung and Sölkner (2002), the three Austrian breeds are endangered with small population sizes. Danish Holstein is a major dairy breed in Denmark (Sørensen et al. 2005). Danish Jersey and Danish Red are smaller breeds than Danish Holstein, but with a substantial number of live animals (2.9 to 3.8×10^5 calves in 1999 to 2003; Sørensen et al. 2005). Several authors (e.g. Pirchner 1983; Nomura et al. 2001, 2005) have indicated that the effective size (N_e) of a livestock breed is largely independent of the census population size. This is also evident in Table 5; the estimates of N_e drop to within a relatively small range (23.6 to 76). The estimated N_e values for the two sub-breeds of Japanese Brown before 1990 are within the range of the published estimates (Table 3). The estimate (25.5) of the Kumamoto sub-breed from 1991 to 2000 remains within the range, however, the effective size of the Kouchi sub-breed drastically reduced after 1991 and the corresponding estimate (6.0) is far below the range.

The published estimates of the effective number of founders (N_{ef}) are also within a relatively small range (21.0 to 70.0), except for the two Danish dairy breeds, Danish Jersey and Danish Red. The larger N_{ef} for these two breeds is presumably a result of the recent import of breeding animals from the USA (c.f. Sørensen et al. 2005). The estimates for the two sub-breeds of Japanese Brown are close to the upper range of the published estimates. However, this parameter has limited usefulness for monitoring and evaluating genetic diversity since N_{ef} remains constant over generations once the contributions of the founders have converged (Caballero & Toro 2000). Genetic contributions are expected to converge after several generations in an ideal situation of discrete generations and a constant breeding system (Wray & Thompson 1990; Bijma & Woolliams 1999). In fact, the changes in N_{ef} in the two sub-breeds of Japanese Brown progressively diminished after 1985, at which time the discrete generation equivalent reached around 8 (see Tables 1 and 4).

The estimates of the founder genome equivalents (N_{ge}) in the two sub-breeds (4.9 and 3.9, provided in Table 4) are below the lower range of the published estimates (Table 5), which suggests extremely limited genetic diversity in the current Japanese Brown population. The critical genetic diversity situation can be illustrated by plotting the position of the breed on the relation between N_{ge} and genetic diversity (c.f. equation (1)). Figure 3 depicts the curve of the relation, on which the positions of the two Japanese Brown sub-breeds are plotted, together with the breeds listed in Table 5. It is clearly evident that the current Japanese Brown sub-breeds are in critical positions, at which a small reduction of N_{ge} results in a drastic reduction of genetic diversity.

Preventing further reduction of genetic diversity is essential to genetic management of the Japanese Brown population. Many methods have been proposed in recent years to minimize the loss of genetic diversity in small populations (see Fernández & Caballero 2001, for a review). Most methods are based on the fundamental rule that a group of breeding individuals must be chosen to minimize the average coancestry among them (e.g. Ballou & Lacy 1995; Toro et al. 1999; Fernández & Toro 1999). Minimization of the average coancestry has been theoretically proven to be the most efficient method to preserve genetic diversity (Caballero & Toro 2000, 2002) and allow flexible application to various practical situations (Fernández et al. 2003). This rule was originally developed for populations with discrete generations, but it has recently been extended to populations with overlapping generations (Nomura 2005).

In addition to such genetic management, it is important to counteract numerical reduction before sub-breeds become too small. Efforts must be made to establish a production system for efficient use of unique characteristics, such as a high growth rate and feed utilization efficiency, and to develop links between the breed and products with market value, which will improve the breed's profitability.

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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 estimated discrete generation equivalents (g_e).

Kumamoto						Kouchi					
Year	Bulls	Cows	Total	N_f	g_e	Year	Bulls	Cows	Total	N_f	g_e
1970	28	1,245	1,273	1,951	5.1	1970	8	148	156	377	5.0
1975	26	1,834	1,860	2,535	6.2	1975	9	218	227	464	6.0
1980	35	3,970	4,005	4,063	7.1	1980	13	436	449	563	7.1
1985	20	4,541	4,561	3,994	8.3	1985	10	492	502	549	7.8
1990	27	3,113	3,140	3,076	8.8	1990	9	389	398	490	8.4
1995	13	1,957	1,970	2,206	9.4	1995	5	243	248	407	8.4
2000	6	983	989	1,569	10.2	2000	4	152	156	353	8.9

Table 2. Generation intervals of four gametic pathways and the average generation interval.

Sub-breed	Period	L_{ss}	L_{sd}	L_{ds}	L_{dd}	Average
Kumamoto	1970-1980	5.8	5.8	6.2	6.2	6.0
	1981-1990	8.4	6.6	6.8	6.5	7.1
	1991-2000	11.4	9.8	8.8	7.5	9.4
Kouchi	1970-1980	5.4	5.0	6.4	5.2	5.5
	1981-1990	7.5	6.3	7.3	5.7	6.7
	1991-2000	14.2	10.7	9.9	7.0	10.4

L_{ss} : sire to son, L_{sd} : sire to daughter, L_{ds} : dam to son, L_{dd} : dam to daughter

Table 3. Effective sizes of the sub-breeds in the Japanese Brown, estimated from the average inbreeding rate during the three period.

Period	Kumamoto	Kouchi
1971-1980	68.8	42.3
1981-1990	31.6	38.6
1991-2000	25.5	6.0

Table 4. Founder genome equivalents (N_{ge}), effective number of founders (N_{ef}), and effective number of non-founders (N_{enf}) in each reference population.

Kumamoto				Kouchi			
Year	N_{ge}	N_{ef}	N_{enf}	Year	N_{ge}	N_{ef}	N_{enf}
1970	32.7	152.1	41.7	1970	14.1	108.2	16.2
1975	23.7	116.7	29.7	1975	10.8	79.6	12.4
1980	16.0	107.4	18.8	1980	8.8	86.9	9.8
1985	10.9	85.7	12.5	1985	7.6	91.9	8.3
1990	9.2	82.8	10.4	1990	6.9	87.8	7.5
1995	5.6	75.4	6.1	1995	4.9	79.7	5.2
2000	4.9	74.4	5.3	2000	3.9	79.4	4.1

Table 5. Estimates of population genetic parameters of several cattle breeds, published in the recent works.

		Austria[b)]			Denmark[c)]		
	Japanese[a)] Black	Original Pinzgau	Tux-Zillertal	Carinthian Blond	Danish Holstein	Danish Jersey	Danish Red
N_e	23.6	76	43	76	49	53	47
N_{ef}	50.2	65.4	21.0	29.9	70.0	115.7	207.2
N_{ge}	7.3	19.5	9.7	22.6	11.9	11.4	21.7

N_e : Effective population size, N_{ef} : Effective number of founders, N_{ge} : Founder genome equivalents

a) Data from Nomura et al. (2005)
b) Data from Baumung and Sölkner (2002)
c) Data from Sørensen et al. (2005)

Figure legends

Figure 1. Changes of *F*-statistics in (A) Kumamoto and (B) Kouchi sub-breeds from 1970 to 2000.

Figure 2. Changes of two indices of genetic diversity, GD and GD*, in (A) Kumamoto and (B) Kouchi sub-breeds from 1970 to 2000.

Figure 3. Relation between genetic diversity (GD) and founder genome equivalent (N_{ge}). The current positions of the two sub-breeds of Japanese Brown and the breeds listed in Table 5 are indicated by different symbols according to their country (closed circle: Japan, open square: Austria, open triangle: Denmark).
JKM: Japanese Brown (Kumamoto), JKCH: Japanese Brown (Kouchi),
JB: Japanese Black,
AOP: Original Pinzgau, ATZ: Tux-Zillertal, ACB: Carinthian Blond,
DH: Danish Holstein, DJ: Danish Jersey, DR: Danish Red

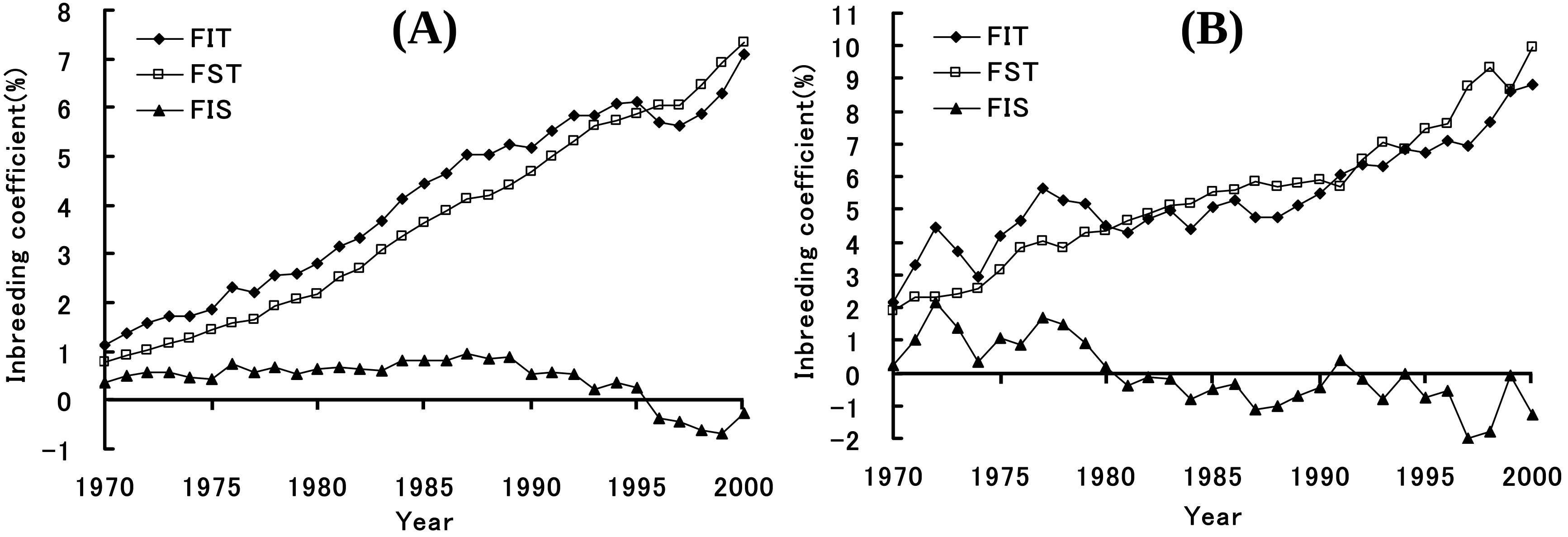

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Figure 1

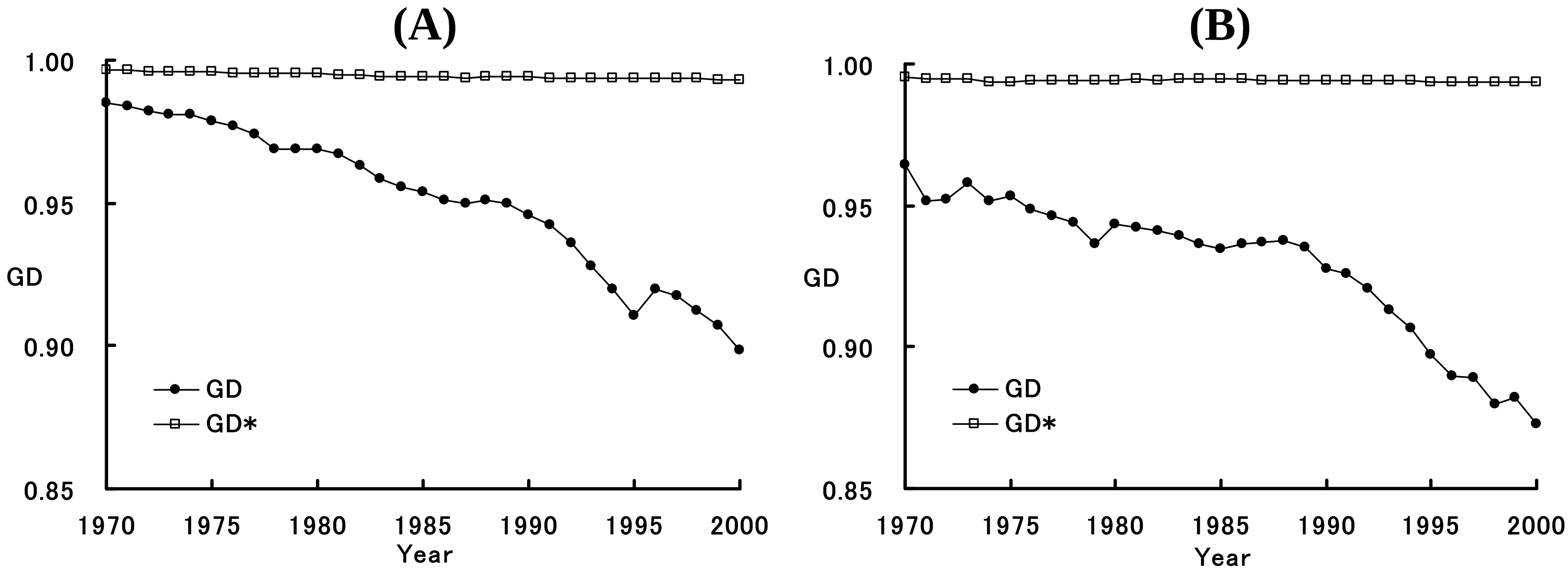

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Figure 2

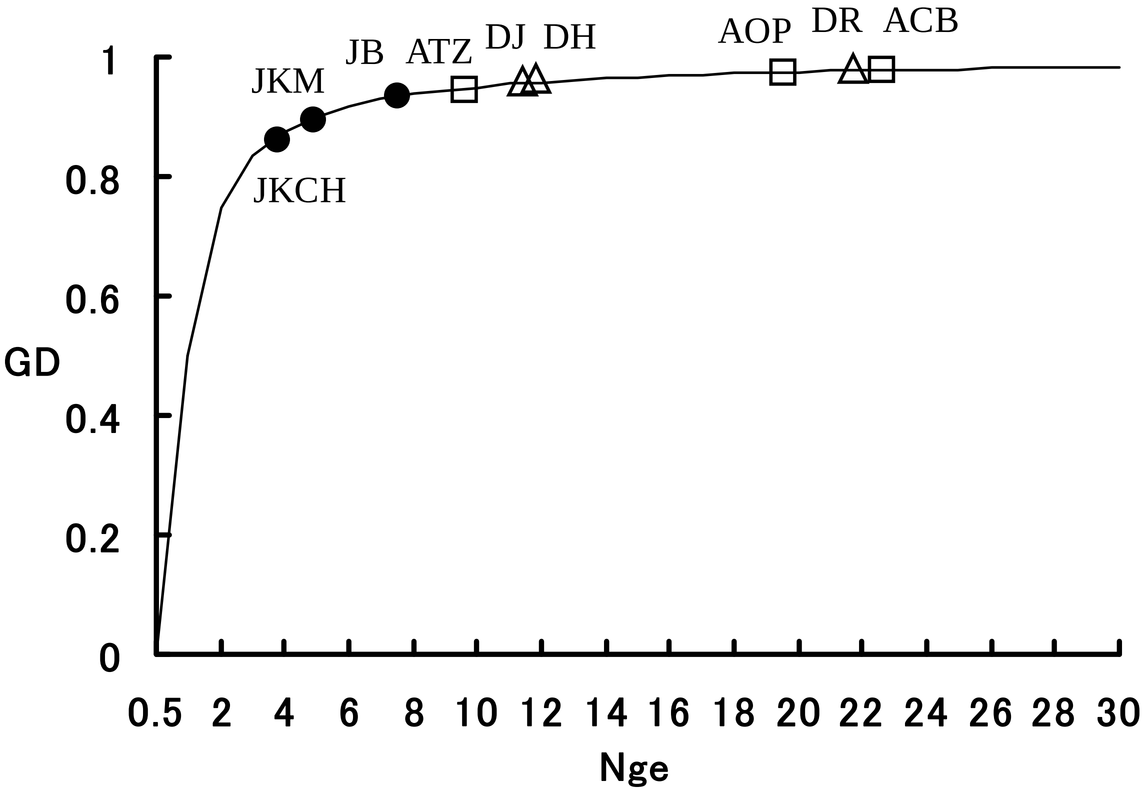

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Figure 3