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Inbreeding and effective population size of Japanese Black cattle

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ABSTRACT: The objective of this research was to estimate the amount of inbreeding and effective population size of the Japanese Black breed using pedigree records from bulls and heifers registered between 1985 and 1997. Inbreeding was quantified by three *F*-statistics: actual inbreeding, inbreeding expected under random mating, and inbreeding due to population subdivision. During the period of 1985 to 1997, the inbreeding expected under random mating increased from 2.3% to 5.0%, whereas the increase of actual inbreeding was more gradual (from 4.7% to 5.4%). The inbreeding due to population subdivision decreased almost linearly and reached 0.5% in 1997, indicating that genetic subdivision of the Japanese Black cattle population has essentially disappeared. The effective size of the breed was estimated from the increasing rate of inbreeding expected under random mating. In the earlier half of this period (1986 to 1990), the breed maintained an effective size of approximately 30. However, after 1991 the effective size sharply decreased and the harmonic mean between 1993 and 1997 was only 17.2. The main cause of this reduction of the effective size was considered to be the intensive use of a few prominent sires. To increase the effective size, an upper limit in the use of AI semen per sire should be imposed.

Key Words: Effective Population Size, Generation Interval, Inbreeding, Japanese Black

Introduction

Among four domestic beef breeds in Japan (i.e., Japanese Black, Japanese Brown, Japanese Shorthorn, and Japanese Poll), the Japanese Black is most common, with a population of 0.53 million reproductive cows (MAFF, 1999). This breed is characterized by prominent intramuscular fat deposition (marbling) and has recently received greater interest from researchers in the United States (Xie et al., 1996a,b; Myers et al., 1999a,b), Canada (Kazala et al., 1999), and Australia (Yang et al., 1998). Mannen et al. (1998) suggested that the Japanese Black is important to our understanding of the origin of native cattle in northeastern Asia.

For a short period before establishing the Japanese Black breed in 1944, native cattle in Japan were cross-bred with various foreign breeds, such as Simmental, Ayrshire, and Brown Swiss (Namikawa, 1992). The breeds used and degree of crossing varied among prefectures. Even after establishment of the Japanese Black breed, most of the breeding programs were carried out within prefectures, though there was limited migration among prefectures, usually of males. Thus, in 1980 the breed was genetically subdivided into several local sub-populations (Nomura and Sasaki, 1988).

Since liberalization of beef import restrictions in 1991, domestic production of high-quality beef has received more emphasis in Japan, and genetic evaluation of meat quality characteristics, with BLUP methodology, was initiated in 1991. The breeding program is now less stratified. However, due to the intensive use of a few sires with high marbling EBV, the decline of genetic diversity is an increasing problem. The objective of this study was to assess the genetic diversity of the Japanese Black cattle population in terms of the amount of inbreeding and effective population size.

Materials and Methods

Pedigree records of Japanese Black cattle are kept by the Wagyu Registry Association. They can be completely traced to an ancestral population of the foundation period (1944 or before). Thus, inbreeding relative to the foundation period may be estimated. Furthermore, this breed was completely closed to foreign germplasm after its establishment. This is suitable for obtaining an accurate estimate of the rate of inbreeding (Woolliams and Mäntysaari, 1995).

Data from all bulls and heifers registered from 1985 to 1997 were used in this study. Numbers of bulls and heifers, registered by year, are given in Table 1. Pedigrees of bulls and heifers were traced back to ancestors

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Table 1. The numbers of bulls and heifers registered from 1985 to 1997

Year	Bulls	Heifers
1985	204	58,199
1986	187	61,744
1987	210	64,163
1988	250	74,608
1989	284	78,405
1990	301	76,627
1991	290	73,967
1992	248	65,403
1993	248	57,952
1994	307	56,276
1995	355	57,518
1996	346	53,939
1997	326	57,560

born in 1945 or before, and a pedigree file was created. The total number of ancestors included in the pedigree file was 1,809,932 animals.

The generation interval of four gametic pathways, sire to son (L_{mm}), sire to daughter (L_{mf}), dam to son (L_{fm}), and dam to daughter (L_{ff}), were obtained from records of birth dates of registered animals in each year and the birth dates of their sires and dams. The average generation interval (L) was computed from

$$L = \frac{L_{mm} + L_{mf} + L_{fm} + L_{ff}}{4}.$$

To assess the amount of inbreeding and the population structure, the F-statistics (Wright, 1951, 1969) were estimated for each year. The average inbreeding coefficient of registered animals was denoted F_{IT}, and the inbreeding coefficient expected under random mating was denoted F_{ST}. Following Wright (1951, 1977), F_{ST} was computed from a hypothetical population produced by matching sires and dams of the registered animals in each year at random. In the preliminary analysis with the animals registered in 1990 and 1995, 20 hypothetical populations were generated for each year, and F_{ST} was computed for each population to obtain an empirical sampling error. Because the sampling errors were quite small (CV = 0.40% for both years), F_{ST} was computed for a single hypothetical population generated for each year of the examined period. The third statistic, F_{IS}, is given by the formula of Wright (1951, 1969):

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

This coefficient expresses the departure from randomness in the actual mating. When $F_{IS} > 0$, the actual inbreeding (F_{IT}) exceeds the level expected under random mating (F_{ST}), implying that mating among more closely related parents than the average is predominant, or the population is partitioned into subpopulations and mating is more or less restricted within each subpopula-

tion. In contrast, in the population with $F_{IS} < 0$, avoidance of inbreeding or mating between subpopulations is carried out predominantly.

The effective size of the breed was estimated from the increasing rate of F_{ST} per generation (Wright, 1977; Caballero and Hill, 1992). The annual increasing rate ($\Delta F_{ST,y}$) of F_{ST} 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. Then, with the generation interval (L) in year t, the effective population size (N_e) was estimated as:

$$N_e = \frac{1}{2\Delta F_{ST,y}L}$$

(Hill, 1972; Nomura, 1996).

Results and Discussion

Table 2 shows the number of sires of the registered animals, together with the average and variance of their progeny number. The number of sires was essentially constant over the period of 1985 to 1990 but showed a gradual decline after 1991. The most notable feature of Table 2 is the sharp increase in the variance of progeny number among sires. The variance in number of progeny per sire in 1995 to 1997 was 2.5 to 3 times larger than in 1985. This increase of the variance was mainly due to the intensive use of a few popular sires. The acceleration of the intensive use of a few sires can be clearly seen from Figure 1, in which the percentage of registered animals sired by the five bulls most intensively used in each year is plotted. After 1991, the percentage increased rapidly, and more than 30% of all the registered animals in 1997 were the progeny of only five sires.

Table 2. The number of sires of registered animals and the average and variance of their progeny numbers

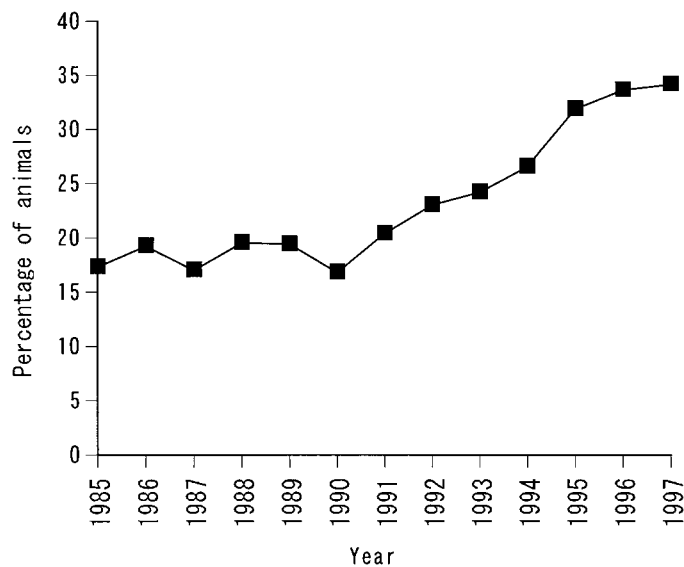| Year	No. of sires	No. of progeny/sire	
		Average	Variance
1985	1,004	58.2	41,414.5
1986	1,009	61.4	54,168.1
1987	1,018	63.2	50,597.2
1988	1,067	70.2	73,514.5
1989	1,045	75.3	84,012.6
1990	1,063	72.4	73,646.5
1991	981	75.7	89,053.4
1992	965	68.0	84,272.8
1993	884	65.8	81,186.5
1994	859	65.9	91,057.4
1995	834	69.4	126,962.7
1996	779	69.7	131,043.2
1997	821	70.5	132,356.9

Figure 1. Percentage of animals sired by the five bulls most intensively used in each year.
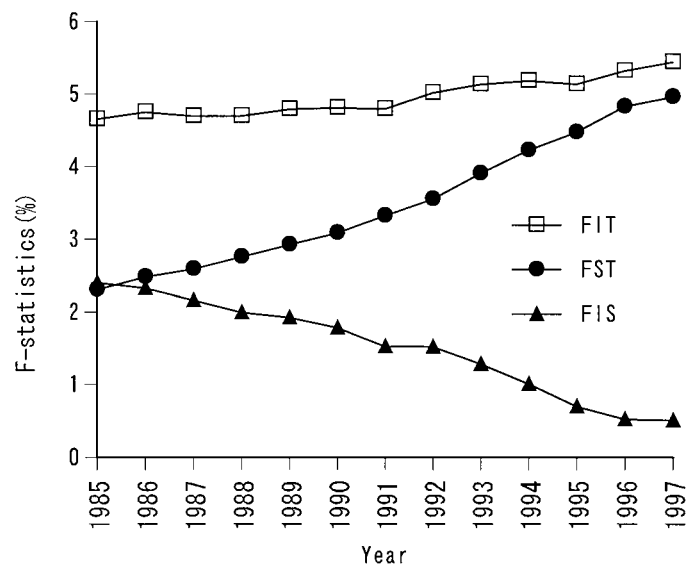

Figure 2. Change of *F*-statistics in the population of Japanese Black from 1985 to 1997.

Table 3 shows the estimates of generation interval in each year. The average generation interval remained essentially constant during the period of 1985 to 1990. However, in the following 7 yr, the generation interval tended to increase, mainly due to increased generation intervals of the two paths from sires (L_{mm} and L_{mf}). Most notably, the generation interval from sire to son was approximately 2 yr longer than that from 1985 to 1990. Since the liberalization of beef import restrictions in 1991, domestic production of high-quality beef has received increased emphasis in Japan. Accordingly, genetic evaluation with BLUP under animal models was initiated in that year. Because the genetic evaluation is based on records collected from carcass markets, there is a lag of about 2 yr between the completion of progeny testing at stations (onset of service of sires) and the time when their EBV become available. The increased generation intervals in the two pathways from sires after 1991 are largely attributed to the selective use of proven sires.

The change of *F*-statistics from 1985 to 1997 is presented in Figure 2. The drastic change of population structure in this period is characterized by the behavior of F_{ST}. The value of F_{ST}, which has a direct relation to the effective population size, showed a sharp increase, whereas the increase of F_{IT} was more gradual. Thus, F_{IS} decreased almost linearly and reached 0.5% in 1997, indicating that genetic subdivision among prefectures has essentially disappeared. As shown in Table 4, the linear regression coefficients of *F*-statistics on years were significantly different between the periods before and after the initiation of the BLUP evaluation.

Table 3. Generation intervals of four genetic pathways and the average generation interval (yr)

Year	Pathway[a]				
	S-S	S-D	D-S	D-D	Average
1985	10.35	9.61	7.14	6.19	8.32
1986	11.11	10.22	7.20	6.36	8.72
1987	10.89	10.04	7.31	6.47	8.68
1988	11.69	9.92	7.70	6.57	8.97
1989	11.55	10.07	7.77	6.62	9.00
1990	11.57	10.20	7.35	6.62	8.94
1991	12.04	10.49	7.72	6.55	9.20
1992	12.47	11.11	7.48	6.55	9.40
1993	13.09	11.48	7.67	6.60	9.71
1994	13.54	11.62	7.55	6.60	9.83
1995	13.89	11.73	8.05	6.65	10.08
1996	13.64	11.78	7.92	6.75	10.02
1997	13.39	11.50	8.30	6.83	10.00

[a]S-S: sire to son, S-D: sire to daughter, D-S: dam to son, D-D: dam to daughter.

Table 4. Regression coefficients of F-statistics on years

Item	1985–1990	1991–1997	D[a]
F_{IT}	0.023	0.091	**
F_{ST}	0.164	0.289	**
F_{IS}	−0.141	−0.202	*

[a]Significance of the difference of regression coefficients between the two periods.
*$P < 0.05$.
**$P < 0.01$.

Table 5 gives the estimates of effective population size. In the earlier half of the period (1986 to 1990), the breed maintained an effective size of approximately 30. However, after 1991 the effective size sharply decreased. A surprising result is the small effective size of the recent population. Although the effective size fluctuated, the harmonic mean between 1993 and 1997 was only 17.2. An increase of the effective size was observed in 1997, but this was temporary. An additional analysis with the most updated data, which covered more than 60% of the registered animals in 1998, showed that the effective size again dropped to 17.4. Furthermore, 42.9% of the registered animals in 1998 were the progeny of only five sires, indicating that the intensive use of a small number of sires became more prominent.

Wright (1977) and Pirchner (1983) summarized the estimates of effective size of various livestock breeds. Although the estimates for cattle breeds vary from 32 (Shorthorn in foundation period) to 330 (U.S. Holstein in 1881 to 1931), it is striking that most of the estimates are around 100 and, as pointed out by Pirchner (1983), they are essentially independent of the actual (census) size of the breed population. In the recent work of Woolliams and Mäntysaari (1995), the rate of inbreeding per generation in Finnish Ayshire population was estimated to be 0.0147, leading to the estimated effective size of 34. Boichard et al. (1997) reported effective sizes of 47 and 106 for two local dairy breeds in France. The effective size of the current population of Japanese Black is below the lower range of the published estimates.

Table 5. Estimated effective population size per generation

Year	Effective population size
1986	32.1
1987	52.1
1988	32.5
1989	32.5
1990	33.7
1991	22.2
1992	22.4
1993	14.0
1994	15.3
1995	19.1
1996	13.4
1997	36.3

The reduction of the effective size observed in the present study is partially due to the decreased number of sires between 1991 and 1997 (Table 1). However, a more important cause is the intensive use of a few sires, which resulted in a drastic increase of the variance of progeny number per sire. The relative importance of the two causes for the reduced effective size may be seen from the basic formula of effective population size:

$$N_e = \frac{4N}{V_k + 2}$$

(Wright, 1938), where N is the number of breeding animals and V_k is the variance of family size. Although the number of sires decreased during the period of 1991 to 1997, over 70% of the number in 1985 was still maintained in 1997. Thus, the reduction in number of breeding animals may not be largely responsible for the decrease in the effective size. In contrast, the variance of progeny number per sire increased 2.5 to 3 times during this period, and this increase of the variance led to the sharp decrease of the effective size. Similar reasoning by Mukai et al. (1989) explained the reduction of effective size of core strains in Japanese Black. The intensive use of a few sires is also a major reason for the disappearance of genetic subdivision seen in Figure 2.

Several researchers have addressed the question of appropriate minimum effective size of livestock populations. From a consideration of the net genetic response in economic merit in dairy cattle breeding, Goddard and Smith (1990) suggested 40 as a minimum effective size. Another approach toward defining minimum effective size was considered by Meuwissen and Woolliams (1994), which balanced inbreeding depression and gain in fitness through natural selection. This resulted in recommendations of the order of 30 to 250. Using a similar approach, a minimum viable effective size for conservation of endangered species has been estimated to be 50 (Franklin, 1980; Lande and Barrowclough, 1987). When the variation of selection response due to random genetic drift is used as a criterion, a much larger effective size (on the order of several hundreds) is required for reducing the variation to an acceptable level (Nicholas, 1989). The current effective size of Japanese Black is much smaller than these critical values.

After the pioneering work of Robertson (1961), theories of the effective size in breeding populations have been developed (Woolliams et al., 1993; Santiago and Caballero, 1995; Nomura, 1999). In accordance with this development, various methods for maximizing genetic gain while keeping the effective size at an acceptable level have been proposed (e.g., Toro and Perez-Enciso, 1990; Caballero et al., 1996; Meuwissen, 1997). In the breeding of Japanese Black, optimizing mate allocation through genetic algorithm techniques (Oyama and Mukai, 1998) is now being implemented in several prefectures. However, these methods target small nucleus populations, in which selection and mating can be inten-

sively managed, and may not contribute much to the increase of the effective size of the whole breed.

Current genetic evaluation of Japanese Black has been limited to carcass traits, but evaluations of other economically important traits such as reproductive performance, growth rate, and maternal ability are planned. This is expected to reduce the use of a few sires with prominent EBV for meat quality. In parallel, an upper limit for the use of AI semen per sire will be required to increase the effective size of Japanese Black. This upper limit should be optimized to balance the genetic gain obtained by the intensive use of genetically prominent sires and the negative effects of the reduced effective size, such as the reduction of genetic gain due to the decreased genetic variability, and inbreeding depression of economic and fitness-related traits. The information required for this strategy should be collected in future studies.

Implications

From 1986 to 1997, the effective population size of Japanese Black cattle decreased sharply, and the current breed has an effective size of only 17.2. The small effective size may cause the reduction of future genetic gain due to decreased genetic variability, and the inbreeding depression of economic and fitness-related traits. Because the major reason for this reduction of the effective size was the intensive use of a few prominent sires, an upper limit in the use of AI semen per sire should be imposed to increase the effective size.

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