Demographic Analysis of Breeding Structure in Japanese Thoroughbred Population

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To investigate the breeding structure in the Japanese Thoroughbred population, we applied a demographic analysis to the populations of foals produced from 1978 to 2005. The migration rate estimated from the proportion of foals produced by imported breeding horses was around 40% over the investigated period. After early 1990s, the migration rate through stallions imported from USA sharply increased. The average generation interval was within range of 10.5–11.5 years. The longer generation interval of Thoroughbred was considered to be a reflection of the fact that Thoroughbred horses begin breeding only after completing their performance in races. After the peak of 729 in 1993, the number of sires of foals progressively declined to 358 in 2005. Although the coefficient of variation of the progeny number of sires was within range of 1.0–1.2 until early 1990s, it gradually increased and reached the value of 1.6–1.7 in recent years. The effective number of sires consistently decreased after the peak of 302.6 in 1992, and reached 120–130 in recent years, which is 25–30% of the actual number of sires. In parallel, the demographic estimate of the effective population size declined after early 1990s. The main cause of the observed change in the breeding structure was inferred to be the intensive use of a limited number of stallions for breeding.

Key words: breeding structure, demographic analysis, effective population size, Thoroughbred

The first stud book for Thoroughbred horses was published in 1791, compiling earlier sources of pedigree information for a small number of horses of either imported or local English origin [2]. The current population expands to more than 300,000 world-wide, and Thoroughbred racing constitutes a huge leisure industry. Because this breed has been effectively closed to other horse breeds since its foundation, there is continuing concern that the reduced genetic diversity may be limiting genetic progress in performance [1, 2, 4, 12]. In fact, Cunningham [1] revealed that winning times in classic Thoroughbred races in England showed no improvements during the recent decades.

We attempted a series of studies to investigate the breeding structure and evaluate genetic diversity in the Japanese Thoroughbred population by demographic and pedigree analysis. In this paper, we report results of demographic analysis of the breeding structure, which provide basic information for the succeeding pedigree analysis. The results are also compared with those for a major beef breed in Japan, the Japanese Black cattle, of which breeding structure has been intensively studied by two of the authors of this report [5, 6, 9, 10]. While reproduction in Thoroughbred is strictly limited to natural service, almost all the progeny of the Japanese Black cattle are produced by artificial insemination with frozen semen. The comparison of
results for the two contrast breeds will characterize the breeding structure of the Thoroughbred population.

Materials and Methods

Data
Registry and pedigree records of foals in Japan from 1978 to 2005, supplied from Equine Research Institute, Japan Racing Association (JRA), were used for the demographic analysis. The numbers of foals by sex in each year are given in Table 1.

Demographic analysis
(1) Migration rate
Migration rate is the proportion of genes flowing into the Japanese Thoroughbred population from foreign populations. Migration rate through male parents (male migration rate: \( m_m \)) was computed by the proportion of foals produced by imported stallions. Analogously, migration through female parents (female migration rate: \( m_f \)) was obtained by the proportion of foals produced by imported mares. Total migration rate (\( m \)) was computed as:

\[
m = \frac{m_m + m_f}{2}.
\]

(2) Generation interval
The generation intervals of four gametic pathways, sire to son (\( L_{sos} \)), sire to daughter (\( L_{sd} \)), dam to son (\( L_{ds} \)), and dam to daughter (\( L_{df} \)), were obtained from records of birth dates of produced foals in each year and the birth dates of their sires and dams. The average generation interval (\( L \)) was computed from:

\[
L = \frac{L_{sos} + L_{sd} + L_{ds} + L_{df}}{4}.
\]

(3) Demographic estimates of effective number of sires and effective population size
Annual effective number of sires (\( N_{m,e} \)) was estimated by the formula given by Nomura [8]:

\[
N_{m,e} = \frac{N_m}{1 + CV^2},
\]

where \( N_m \) is the number of sires of foals produced in a year, and \( CV \) is the coefficient of variation of progeny number of sires. As seen from this formula, \( N_{m,e} \) is equal to the actual (census) number of sires (\( N_m \)) only when all sires equally contribute to their progeny, i.e., \( CV=0 \). When there is a variation in the progeny numbers among sires (\( CV>0 \)), \( N_{m,e} \) is always smaller than \( N_m \).

Following Nomura [8], a demographic estimate of the annual effective population size (\( N_{e,a} \)) was obtained with \( N_{m,e} \) as:

\[
N_{e,a} = 4N_{m,e}.
\]

Results and Discussion
Figure 1 shows the change in migration rates over the investigated period. After the progressive decline
during the period from 1978 to 1990, the male migration retained the rate of 50–70%. The female migration rate was consistently lower than the male migration rate, but with a gradual increase after 1990. Total migration rate was around 40% throughout the investigated period, meaning that the amount of annual gene flow from foreign countries into Japan was about 40%.

For a more detailed information of migration trend, the migration rates were computed by birth country of migrants. Figures 2 and 3 present the results for male and female migrations, respectively. For male migration, the migration from USA sharply increased during the period from 1990 to 1997. The increase of migration from USA after 1990 was also observed in the female migration. In response to the horse racing boom and the prosperity in 1990s, Japanese horse breeders paid much money for importing foreign breeding stocks with high performance. Several imported horses made great successes as breeding stock in Japan. In particular, progeny of the stallion “Sunday Silence” imported from USA in 1991 won many graded races in Japan. This success would accelerate the migration from USA.

Change of the generation interval is shown in Fig. 4. Although the generation intervals from dams ($L_{dm}$ and $L_{df}$) tended to increase and those from sires ($L_{sm}$ and $L_{sf}$) showed no consistent trends, the changes in the generation intervals of the four gametic pathways were rather small over the investigated period. The average
The generation interval was within range of 10.5–11.5 years. Gaffney and Cunningham [3] estimated the average generation interval of Thoroughbred in England as 11 years. Comparable estimates (10.6 and 10.7 years) have been reported in French Thoroughbred [7] and in Brazilian Thoroughbred [11]. Our estimate well agrees with these published estimates. It could be generally concluded that Thoroughbred has a long generation interval from 10 to 12 years compared with other domesticated mammals whose values are half of those or less. As pointed out by Moureaux et al. [7] and Thiruvenkadan et al. [12], the longer generation interval might be due to the fact that Thoroughbred horses begin breeding only after completing their performance in races.

Table 2 shows the number of sires of foals produced in each year ($N_m$), the coefficient of variation of the progeny numbers of sires (CV), the effective number of sires ($N_{me}$), and the ratio $N_{me}/N_m$. After the number of sires ($N_m$) had been retained the value around 450 until the middle of 1980s, it tended to increase in the next decade. The increase in $N_m$ in this period would be a reflection of the progressively increased importation of stallions particularly from USA (Fig. 2). After the peak of 729 in 1993, $N_m$ progressively decreased to 358 in 2005. Although the coefficient of variation of the progeny numbers of sires (CV) was within range of 1.0–1.2 until early 1990s, it tended to gradually increase and reached the value of 1.6–1.7 in recent years. This increase of CV indicates that the difference of the progeny numbers among sires were enhanced after early 1990s. Both the decreased $N_m$ and increased after CV early 1990s lead to a decrease of the effective number of sires ($N_{me}$). As shown in the fourth column in Table 2, $N_{me}$ consistently decreased after the peak of 302.6 in 1992, and reached 120–130 in recent years, which is 25–30% of the actual number of sires ($N_m$).

Figure 5 presents the average number of foals of sires ($k_m$) and the foal number of the most intensively used sire ($k_{m,max}$) in the Japanese Thoroughbred population from 1978 to 2005.
Japan, with a population of 0.61 million reproductive Japanese Black cattle is the most common beef breed in the Japanese Black cattle population from 1978 to 2004.

| Year | Ne | CV  | Ne,e | Ne,e/Ne |
|------|----|-----|------|---------|
| 1978 | 1,031 | 2.459 | 146.3 | 0.142 |
| 1979 | 1,055 | 2.530 | 142.3 | 0.135 |
| 1980 | 1,064 | 2.534 | 141.5 | 0.133 |
| 1981 | 1,135 | 2.598 | 146.4 | 0.129 |
| 1982 | 1,132 | 2.585 | 147.3 | 0.130 |
| 1983 | 1,048 | 2.666 | 129.3 | 0.123 |
| 1984 | 1,048 | 2.071 | 100.5 | 0.096 |
| 1985 | 1,004 | 3.312 | 83.9 | 0.084 |
| 1986 | 1,009 | 3.640 | 70.8 | 0.070 |
| 1987 | 1,019 | 3.408 | 80.8 | 0.079 |
| 1988 | 1,067 | 3.761 | 70.4 | 0.066 |
| 1989 | 1,045 | 3.758 | 69.1 | 0.066 |
| 1990 | 1,064 | 3.653 | 74.2 | 0.070 |
| 1991 | 981 | 3.841 | 62.3 | 0.063 |
| 1992 | 966 | 4.146 | 53.1 | 0.055 |
| 1993 | 884 | 4.180 | 47.9 | 0.054 |
| 1994 | 860 | 4.434 | 41.6 | 0.048 |
| 1995 | 834 | 5.007 | 32.0 | 0.038 |
| 1996 | 779 | 5.051 | 29.4 | 0.038 |
| 1997 | 822 | 5.155 | 29.8 | 0.036 |
| 1998 | 787 | 6.032 | 21.1 | 0.027 |
| 1999 | 747 | 6.502 | 17.3 | 0.023 |
| 2000 | 732 | 7.933 | 11.4 | 0.016 |
| 2001 | 719 | 7.237 | 13.5 | 0.019 |
| 2002 | 727 | 6.950 | 14.7 | 0.020 |
| 2003 | 756 | 7.301 | 13.9 | 0.018 |
| 2004 | 752 | 6.917 | 15.4 | 0.020 |

In comparison with the results for Thoroughbred population (Table 2), the most notable feature is the difference of CV between the two populations. As already shown, CV in the Thoroughbred population increased after early 1990s, but the value was still around 1.7 even after 2000, which is less than 25% of the corresponding value in the Japanese Black cattle population. This will be a reflection of difference in reproductive methods applied in the two breeds. In the Japanese Black cattle, almost all the progeny are produced by artificial insemination with frozen semen, which enables to reproduce about 60,000 progeny per year from a limited number of sires. In particular, the most intensively used sire produces more than 10,000 progeny in a year. In Thoroughbred, even for the stallion with the maximum number of progeny after 1995, the number of foals in a year was below 200. This is because natural service limits a heavy use of one popular stallion. This difference of reproductive method between the two breeds is also reflected in the effective number of sires. While the actual number of sires (Ne) in the Japanese Black cattle population after 2000 is more than 2 times of that in the Thoroughbred population, the effective number (Ne,e) is below 10% of Ne,e in the Thoroughbred population.

Table 3. The number of sires (Ne), the coefficient of variation of their progeny number (CV), effective number of sires (Ne,e) and the ratio Ne,e/Ne in the Japanese Black cattle population from 1978 to 2004.

In conclusion, our demographic analysis clearly showed that the breeding structure of the Japanese Thoroughbred population has been largely changed after early 1990s. This change could be considered as a reflection of the horse racing boom and the prosperity at that time. Breeders imported many horses from USA as breeding stock. In accordance, limited stallions with
high performance have been intensively used for breeding, leading to the declines of the effective number of sires and the effective population size. However, the magnitude of the change was much smaller than the similar change in the Japanese Black cattle population. The smaller change in the Thoroughbred population will ascribe to the fact that the reproduction is strictly limited to natural service, which prevents breeders from using a few prominent stallions heavily. In succeeding reports, we assess the impact of the change in breeding structure on the genetic constitution of population and evaluate the genetic diversity by population genetic analysis with pedigree information.

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