Development of an Integrated General Model (IGM) System for Comparison of Genetic Gains from Different Bull Selection Strategies for Korean Brown Cattle (Hanwoo)

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ABSTRACT : To advance the effectiveness of the current Hanwoo improvement system, we developed a general simulation that compared a series of breeding schemes under realistic user circumstances. We call this system the Integrated General Model (IGM) and it allows users to control the breeding schemes and selection methods by manipulating the input parameters. The Current Hanwoo Performance and Progeny Test (CHPPT) scheme was simulated with a Modified Hanwoo Performance and Progeny Test (MHPPT) scheme using a Hanwoo Breeding Farm cow population of the Livestock Improvement Main Center (LOMC) of the National Agricultural Cooperatives Federation (NACF). To compare the two schemes, a new method, the Simple Hanwoo Performance Test (SHPT), which uses ultrasound technology for measuring the carcass traits of live animals, was developed. These three models, including the CHPPT, incorporated three types of selection criteria: phenotype (PH), true breeding value (TBV), and estimated breeding value (EBV). The simulation was scheduled to mimic an actual Hanwoo breeding program; thus, the simulation was run to include the years 1983-2020 for each breeding method and was replicated 10 times. The parameters for simulation were derived from the literature. Approximately 642,000 animals were simulated per replication for the CHPPT scheme; 129,000 animals were simulated for the MHPPT scheme and 112,000 animals for the SHPT scheme. Throughout the 38-year simulation, all estimated parameters of each simulated population, regardless of population size, showed results similar to the input parameters. The deviations between input and output values for the parameters in the large populations were statistically acceptable. In this study, we integrated three simulated models, including the CHPPT, in an attempt to achieve the greatest genetic gains within major economic traits including body weight at 12 months of age (BW12), body weight at 24 months of age (BW24), average daily gain from 6 to 12 months (ADG), carcass weight (CWT), carcass longissimus muscle area (CLMA), carcass marbling score (CMS), ultrasound scanned longissimus muscle area (ULMA), and ultrasound scanned marbling score (UMS). (**Key Words :** Breeding Scheme, Hanwoo, Integrated General Simulation Model, Simulation)

INTRODUCTION

The main issues that need to be addressed with the current Hanwoo breeding system include improvements to performance testing records for selecting cows as well as expenses, the length of time to select a sire, and population size. Thus, a more general system for breeding and selecting cattle is needed.

Few studies have been carried out to improve the current Hanwoo breeding scheme. Sul and Chung (1971)

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studied the early selection of Hanwoo. They recommended that selecting animals based on body weight or body measurements between 12 and 15 months of age would be useful. Ju (2001), as well as Ju and Kim (2002), developed a simulation program to examine the current Hanwoo breeding scheme. This comprised a simple linear model with a fixed effect and additive genetic effect, and MTDFREML was used to estimate breeding values. Ju (2001) simulated two different breeding schemes. Model I was a performance test scheme and Model II imitated the current Hanwoo breeding scheme, whereby 10 sires were mated with 1,000 dams. These studies suggested that the weights and carcass records of cows as well as the ultrasound measurements of young bulls should be used to improve the efficiency of the current Hanwoo breeding scheme. The ultrasound measurements of young bulls

would reduce the need for the progeny test (Won et al., 2000; Lee, 2003). However, under the current Hanwoo registration system operated by the Korea Animal Improvement Association (KAIA), some phenotypic variations of the animal, such as small black spots on the nose, would disqualify it for registry, thus depriving it a chance to be selected as a proven bull. The black spot problem can be detected only via the progeny test at present. Moreover, utilizing the carcass data of cows in the slaughterhouse would be difficult because the cows would exhibit different parity, age, and nutritive conditions at slaughter, thus requiring several years to collect such data for analyses.

Therefore, further analysis is needed to find a more feasible and faster way to improve the current cattle breeding scheme. To do this, we focused on the development of a more effective and general Hanwoo improvement system using *in silico* simulation. Specifically, a simulation program for two types of a modified Hanwoo Performance and Progeny Test (HPPT) scheme as well as the current one were developed and compared.

MATERIALS AND METHODS

Development of the simulation program

The simulation program was written in C language (Kernighan and Ritchie, 1988) and compiled by gcc (GNU compiler). The program consisted of five modules: building the base population with the given parameters, genetic evaluation using BLUPF90IOD (Tsuruta et al., 2001), phenotypic evaluation of steers to evaluate their sires (young bulls), selection of proper animals with the given parameters, and mating selected animals in a random manner with the given parameters.

The simulation program needed to maintain a certain number of female cows and calves for stable simulation. The age distribution in the herd was calculated using the SAS/IML package according to the procedure proposed by Azzam et al. (1990). For calculating the inbreeding coefficient for each animal, the algorithm reported by Meuwseen and Luo (1992) was implemented. Selection was made based on the true breeding value (relative weights for each trait should be entered into the program via a parameter file), phenotypic value (relative weight needed), and estimated breeding value (relative weight needed).

When relative weights were given, all observations were standardized and multiplied with the given weights to calculate a selection index before selection. A rank was given per animal according to its selection index and these were sorted in descending order. Therefore, giving negative weight to the traits sorted in ascending order was necessary. A random mating algorithm was implemented in this simulation program. Sires were selected in a random manner and, as a result, all dams should be mated with a random sire. In some specific cases, sires did not have a chance to mate. In addition, a user can restrict the number of sires by entering fewer sires than the total number of proven bulls, and the young bulls for progeny test enables them an equal chance to breed.

For cows, two culling methods were incorporated in the program. The first encompassed natural selection based on the given survival rate of animals at each age. To mimic natural selection, a random number drawn from a uniform distribution was compared with the survival rate. If the random value was greater than that, then the animal was culled. This was done according to animal's age and the survival rate (1.0 = culling rate), which should be given by the user. The second culling method incorporated artificial selection. We conducted selection in some schemes for yearling animals. Only certain numbers of animals with high index scores could survive. Given that the number of animals in each year may vary, selection was made by providing the number of animals to select rather than by using a selection ratio. Therefore, the selection ratio can be slightly different from year to year, but will be similar in the long run. When artificial selection is used, the survival ratio should be changed for the relevant age to maintain the age distribution of a population. If this were not done, the population size would diminish with time.

For bulls, culling was done based on the animal's age, taking into account three different groups: proven bulls, steers (progeny of young bulls selected for the progeny test), and ordinary bulls. Animals belonging to each group were culled according to the given age of the group.

Test of the simulation program

The simulated traits included body weight at 12 months of age (BW12), body weight at 24 months of age (BW24), average daily gain from 6 to 12 months (ADG), carcass weight (CWT), carcass longissimus muscle area (CLMA), carcass marbling score (CMS), ultrasound scanned longissimus muscle area (ULMA), and ultrasound scanned marbling score (UMS). The parameters used in the simulation were derived from the literature.

In total, 100,000 animals were simulated with the given parameters to verify whether the developed program generated breeding values, error values, and phenotypic values within an acceptable range compared to the parameters shown in the Supplementary General Assumption and T1-T4. A sex ratio of 0.50 and means for different traits were given by sex. The trait means predetermined for males were 300, 435, 530, 300, 77, 2.3, 77, and 2.3 for BW12, BW24, ADG, CWT, CLMA, CMS, ULMA, and UMS, respectively, and trait means given for females were 215, 334, 530, 300, 77, 2.3, 77, and 2.3 for BW12, BW24, ADG, CWT, CLMA, CMS, ULMA, and

UMS, respectively. Therefore, only the means of BW12 and BW24 differed by sex. Verification was carried out with the SAS package (SAS institute, 1990) and means, medians, variances, and skewedness of each trait, as well as sex ratio, phenotypic and genetic correlations, were validated. The realized phenotypic correlations between traits were calculated for male and female populations separately because of different means by sex.

Simulation of Hanwoo breeding schemes

For the automatic regulation of population size, especially for female populations, a Leslie's transition matrix A was used. The fertility was set at 70% and the raising rate (i.e., the percentage of animals of age 1 year that can successfully reach 2 years) was assumed to be 0.70. For the convenience of the simulation, the survival rate was assumed to be 0.90 for ages 2-6 years. The maximum animal age in the population was assumed to be 6 years because the average parity of Hanwoo is known to be approximately 3 years. The age distribution of the population at equilibrium is shown in Supplementary Table 4. Only the female population was managed at equilibrium and male calves were assumed to be sold at an age of 2 years from the 5th year of base population simulation. During the first 4 years of simulation, bull calves were used as a source for proven bulls. The average age in a herd was 3.07 years, while the average age of culled cows was 3.87 years and the population size growth rate was 1.0009 per year.

The flowchart of the integrated general model (IGM) is shown in Figure 1. Selection and mating processes share the same parameter file, while generation of the base population and genetic evaluation processes used their own parameter files. The user should calculate the age distribution of the population at equilibrium before generating a base population. The overall assumptions used in this simulation study are summarized in Table 1.

MODEL 1: Current HPPT scheme (CHPPT) (Supplementary Figure 1)

This model was running the performance and progeny test for a given population size. For computational simplicity, the number of animals was maintained to be the same as the initial state. For the first four years of simulations young bulls and proven bulls were selected from the population based on phenotypes rather than breeding values.

MODEL 2: Modified HPPT scheme (MHPPT) (Supplementary Figure 2)

The Modified Hanwoo Performance and Progeny Test scheme was prepared by the Ministry of Agriculture and Forestry (MAF) and will be implemented in the near future. The MHPPT scheme has undergone major changes from the CHPPT scheme; e.g., cows were recorded and selected based on performance, the cows mated for progeny tests were also selected from Hanwoo Breeding Farms (HBFs), and the offspring of young bulls can be selected as young bulls again.

MODEL 3: Simple Hanwoo performance test scheme (SHPT) (Supplementary Figure 3)

A simple Hanwoo performance test scheme (SHPT) was compared with two other schemes. SHPT utilized ultrasound technology for carcass trait evaluation so that the time needed for progeny testing could be reduced. The female calf selection was conducted within farms. During the first 3 years of simulation, proven bulls were selected from the base population based on phenotypes. Thereafter, it was selected based on phenotypes, estimated breeding values, and/or true breeding values. Heifers were also
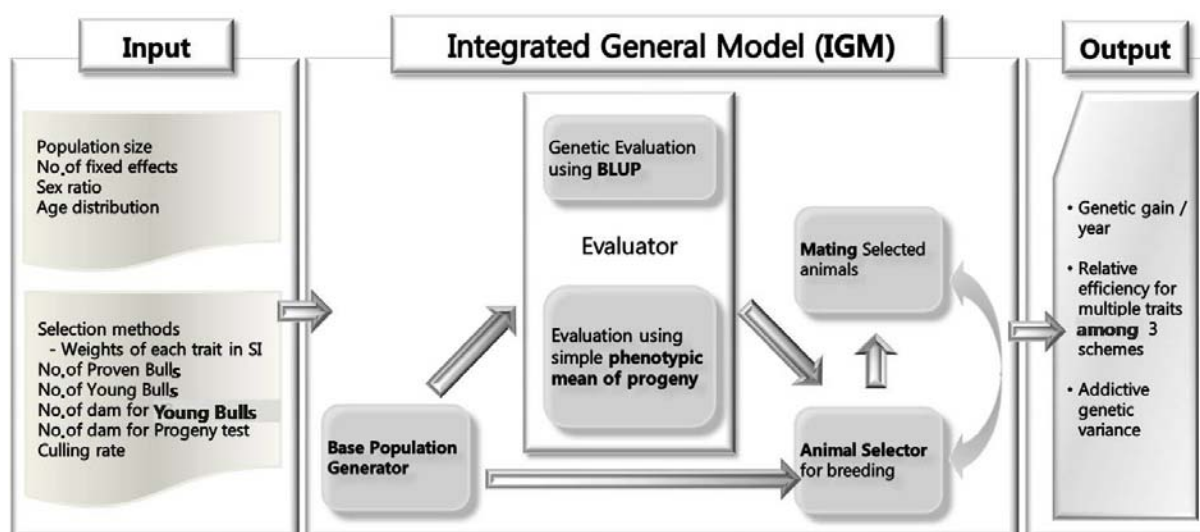

Figure 1. Integrated General Model (IGM) System Process.

Table 1. Technical assumptions used for simulation

Source[1]	CHPPT	MHPPT	SHPT
Parameters given	Supplementary Table 1-4	Supplementary Table 1-4	Supplementary Table 1-4
Traits simulated	8	8	8
Simulation time[5]	38 years (1983-2020)	38 years (1983-2020)	38 years (1983-2020)
Time schedule	Figure 3	Figure 3	Figure 6
SI_{YB}[1]	$S_{BW12}^{3}+S_{ADG}^{3}$	$S_{BW12}+S_{ADG}$	Not available
SI_{PB}[1]	$0.75\,S_{CWT}^{3}+0.75\,S_{CLMA}^{3}$ $+1.5\,S_{CMS}^{3}$	$0.75\,S_{CWT}^{3}+0.75\,S_{CLMA}^{3}$ $+1.5\,S_{CMS}^{3}$	$0.75\,S_{BW12}^{3}+0.75\,S_{ULMA}^{3}$ $+1.5\,S_{UMS}^{3}$
SI_{HF}[1]	Not available	$S_{BW12}^{3}+S_{ADG}^{3}$	$S_{BW12}^{3}+S_{ADG}^{3}$
Use cow record (Traits utilized)[2]	No	Yes (BW12, ADG)	Yes (BW12, ULMA, UMS)
No. of proven bulls selected	20 of 40	20 of 40	20 of 400
No. of young bulls selected	40 of 400	40 of 400	400 of about 840
No. of steers in the progeny test	400	400	Not available
Selection method at the initial state (1983-1987)	Phenotype	Phenotype	Phenotype
Selection method since GEV starts (1988-)	PH, EBV, TBV	PH, EBV, TBV	PH, EBV, TBV
No. of replications	10	10	10
Selection for heifers	No	Yes (within farm)	Yes (within farm)
Fertility	0.7	0.7	0.7
Survival rate at age 1 year	0.7	1.0 (0.7)[4]	1.0 (0.7)[4]
Survival rate at age ≥2 years	0.9	0.9	0.9
Maximum cow age, years	6	6	6
Maximum proven bull age, years	6	6	6

[1] SI_{YB} = Selection index for young bulls, SI_{PB} = Selection index for proven bulls, SI_{HF} = Selection index for heifers.

[2] BW12 = Body weight at age 12 months, ADG = Average daily gain (6-12 months), ULMA = Longissimus muscle area taken from the ultrasound, UMS = Marbling score taken from the ultrasound.

[3] S_{BW12}, S_{ADG}, S_{CWT}, S_{CLMA}, S_{CMS}, S_{ULMA}, S_{UMS}: standardized values of corresponding traits, BW12, ADG, CWT, CLMA, ultrasound measured LMA, and ultrasound measured MS. SIPB: standardized index that is mimicked in the current Hanwoo breeding scheme.

[4] Survival rate 1.0 was given to a program to incorporate the selection of heifers. However, the approximate survival rate was expected to be approximately 0.70.

[5] The breeding program was started in 1983 to mimic the real Hanwoo breeding program and to monitor the real current state indirectly. Additionally, this program was run up to 2020 to generate predictions up to approximately 10 years in the future.

selected based on their phenotypes during the first 3 years and later changed according to each selection method. With the selection of heifers, the culling rate at age 1 year was changed from 0.1 to 0.0 to maintain the same population size from year to year. It was important to maintain an equal population size by year for keeping the selection intensity at the same level and maintaining stability of the breeding scheme. Throughout the simulation, the number of live cows was managed as the same as that at the beginning of simulation.

Three different breeding schemes, three different selection methods, and 10 replications were performed for each year. The proven bull used prior to applying a selection method in 1988 was selected based on its phenotypic value using the same weight for the selection index throughout the simulation in the CHPPT and MHPPT schemes. The proven bull used prior to application of the selection method in 1986 was selected based on its

phenotypic value using the same weight for the selection index throughout the simulation in the SHPT scheme. Therefore, proven bulls used from 1983 to 1987 in the CHPPT and MHPPT, as well as those during 1983 to 1885 in the SHPT, were chosen based on phenotypic values.

Evaluation of three different breeding schemes

The inbreeding coefficient of an individual was calculated using the algorithm reported by Meuwseen and Luo (1992) and averaged based on the individual's birth year. The annual rates of inbreeding caused by different breeding schemes and different selection methods were compared. The expected rate of inbreeding per generation was calculated using an approximation equation (Falconer, 1996). The annual rate of inbreeding was derived by dividing the rate of inbreeding by the generation interval calculated from the average parental age at the birth of an animal.

Annual genetic gains for each scheme were estimated by simple linear regression and relative efficiencies, and were compared to those calculated using the CHPPT. Given that the proven bull selection method is in the early stages of simulation (i.e., all proven bulls were selected based on phenotypic values from 1983 to 1987 in the CHPPT and MHPPT schemes, as well as from 1983 to 1985 in the SHPT scheme), genetic gains after 1988 were used for comparison.

The additive genetic variances were checked for each breeding scheme by calculating the variance from the true breeding values of animals by birth year. The additive genetic variances were compared based on the selection method within the same breeding scheme. A Pearson's correlation between the true breeding value and estimated breeding value was computed to check the accuracy of the BLUP estimation. The SAS package (SAS Institute, 1990) was used for several statistical calculations needed for this study.

RESULTS AND DISCUSSION

Verification of the IGM

In total, 100,000 simulated animals were generated with the parameters listed in Supplementary Table 1, 2, 3, 4 and 5 to test whether the simulation program generated proper values. The sex ratios and frequencies of age groups were checked. The simulated sex ratio (male per female) was 1.0096 with given parameter 1.0 (Supplementary Table 6). The simulated proportions of each age group were 25.83%, 18.19%, 16.40%, 14.64%, 13.10%, and 11.85%, while the given proportions were 25.90%, 18.10%, 16.30%, 14.70%, 13.20%, and 11.90% for age groups 1 through 6, respectively. No significant differences existed between the simulated and given values.

The simulated genetic and phenotypic correlations were checked with the given parameters. The simulated genetic correlations were almost the same given the genetic correlations and the differences did not exceed 0.01 magnitude (Supplementary Table 7). The simulated

Table 2. Descriptive statistics of base populations for testing programs

Source		Simulated data[1]				Given parameter (p)		Difference (a-p)	
Type	Trait	Mean(a)	Median	Var	Skew	Mean	Var	Mean	Var
True BV	BW12	0.1082	0.081	251.2	0.00	0.000	250.00	-0.1082	1.20
	BW24	0.1266	0.109	621.3	0.01	0.000	620.00	-0.1266	1.30
	ADG	0.0004	0.000	0.0	0.00	0.000	0.0032	-0.0004	-0.003
	CWT	0.0368	0.036	254.9	0.00	0.000	255.00	-0.0368	-0.10
	CLMA	0.0112	0.005	21.9	0.02	0.000	22.00	-0.0112	-0.10
	CMS	-0.0040	-0.005	0.8	0.01	0.000	0.77	0.0040	0.03
	ULMA	0.0009	-0.014	21.9	0.01	0.000	22.00	-0.0009	-0.10
	UMS	-0.0047	-0.007	0.8	0.01	0.000	0.77	0.0047	0.03
True error value	BW12	-0.0714	-0.107	978.2	0.00	0.000	970.00	0.0714	8.20
	BW24	0.0066	-0.091	2154.5	0.00	0.000	2140.00	-0.0066	14.50
	ADG	-0.0003	0.000	0.0	-0.01	0.000	0.01	0.0003	-0.014
	CWT	0.0386	0.056	724.2	0.00	0.000	720.00	-0.0386	4.20
	CLMA	0.0054	-0.003	42.2	0.00	0.000	42.00	-0.0054	0.20
	CMS	-0.0017	0.003	0.9	-0.01	0.000	0.92	0.0017	-0.02
	ULMA	0.0182	0.002	42.0	0.01	0.000	42.00	-0.0182	0.00
	UMS	0.0015	-0.002	0.9	0.01	0.000	0.92	-0.0015	-0.02
Phenotypic value		Male	Female	Male	Female	Pooled	Pooled	Male	Female
	Obs	50,239	49,761	50,239	49,761	50,239	49,761	Mean	Female
								Mean	Mean
	BW12	315.2	209.9	315.2	210.0	4,001.7	0.00	315.0	210.0	0.20	-0.10
	BW24	580.2	330.0	580.2	330.0	1,8431.2	-0.01	580.0	330.0	0.20	0.00
	ADG	1.0	0.4	1.0	0.5	0.1	-0.01	1.0	0.5	0.00	-0.05
	CWT	300.1	300.1	300.0	300.1	981.3	0.00	300.0	300.0	0.10	0.10
	CLMA	77.0	77.0	77.1	77.0	63.9	-0.01	77.0	77.0	0.00	0.00
	CMS	2.4	2.4	2.4	2.4	1.7	0.00	2.4	2.4	0.00	0.00
	ULMA	77.0	77.0	77.0	77.0	63.7	0.01	77.0	77.0	0.00	0.00
	UMS	2.3	2.3	2.3	2.3	1.7	0.00	2.3	2.3	0.00	0.00

[1] In total, 100,000 animals were generated.
BW12 and BW24 = Body weight at age of 12 and 24 months, respectively; ADG = Average daily gain tested from 6 to 12 months; CWT = Carcass weight at finish (24 months); CLMA = Carcass LMA; CMS = Carcass marbling score; ULMA = Ultrasound measure of the longissimus muscle area; UMS = Ultrasound measure of the marbling score.

Table 3. Average age of sires and dams and the generation interval

Birth year	CHPPT			MHPPT			SHPT		
	Sire	Dam	Mean	Sire	Dam	Mean	Sire	Dam	Mean
Mean[1]	5.0	3.8	4.4	4.5	3.8	4.2	3.8	3.8	3.8
Generation interval[2]		4.4			4.2			3.8	

[1] Only data between 1988 and 2020 were used to calculate means.

[2] The generation interval was calculated from the averaged age of the sire and dam at the animals' birth according to Falconer (1996).

phenotypic correlations were calculated for males and females separately because the mean values of sex in traits BW12 and BW24 were different. Only female phenotypic correlations are listed (Supplementary Table 7) because those of the males showed almost the same correlations.

The means, medians, variances, and skewedness of simulated traits were checked and listed in Table 2. The means of simulated traits as true breeding values or error values ranged from -0.0714 to 0.1266; no values of exactly zero were observed, and no evidence indicated that means were not zero (i.e., all were significant in the *t*-test under the null hypothesis, $\mu = 0$; p>0.5). To verify the degree of asymmetry of a distribution, skewedness was checked for each trait. The skewedness of the true breeding values ranged from -0.01 to 0.02, which suggested that the tail at the low end of the distribution and the right tail at the high end of the distribution were almost equal and the distributions were all symmetric. Variances of the true breeding values and error values of each trait were calculated. The given variances of true breeding values for BW12, BW24, ADG, CWT, CLMA, CMS, ULMA, and UMS were 250, 620, 0.0032, 255, 22, 0.77, 22, and 0.77, respectively. The realized variances from the simulation for BW12, BW24, ADG, CWT, CLMA, CMS, ULMA, and UMS were 251.2, 621.3, 0.0, 254.9, 21.9, 0.8, 21.9, and 0.8, respectively. Slight but negligible differences between the given variances and simulated variances were noted. The given variance of the error values for BW12, BW24, ADG, CWT, CLMA, CMS, ULMA, and UMS were 970, 2,140, 0.014, 720, 42, 0.92, 42, and 0.92, respectively. Moreover, calculated variances from simulation for BW12, BW24, ADG, CWT, CLMA, CMS, ULMA, and UMS were 978.2,

2154.5, 0.0, 724.2, 42.0, 0.9, 42.0, and 0.9, respectively. Small differences between the given and simulated variances were found. The phenotypic means of each trait were calculated for BW12 and BW24, and the means were calculated separately by sex. The differences of means for each trait and sex were very small.

Average generation interval and expected rate of inbreeding

The average generation interval was calculated by averaging the ages of sires and dams when the calves were born (Falconer, 1996). The calculated generation interval is presented in Table 3. To calculate the generation interval, data prior to 1988 were discarded to eliminate unstable stages of the simulation in which proven bulls were selected based on phenotypic values from a male population of 500 with a similar age distribution to that of the female population. The generation interval was 4.3 for the CHPPT scheme, 4.2 for MHPPT, and 3.8 for SHPT. For the CHPPT and MHPPT schemes, proven bulls were supposed to be selected at age 5, but younger bulls (age 2 years) were also included in the progeny test. Coupled with the average age of cows in the population and the young bulls, the generation interval falls between 4.3 and 4.2. Given that no progeny test was used in SHPT scheme, the generation interval was shorter than that of the CHPPT or MHPPT (Table 3). The expected annual rate of inbreeding for the CHPPT scheme was calculated from the generation interval and is listed in Table 3. In Table 4, the expected annual rates of inbreeding were compared to those of the CHPPT, MHPPT, and SHPT schemes. The expected rate of inbreeding for SHPT fell within the range of the realized

Table 4. Expected and realized rate of inbreeding

Scheme	No. of females	No. of cows[4]	No. of proven bulls	Generation interval	dF/Gen[1]	dF/year[2]	dF (realized)[3]
CHPPT	31,500	23,310	40	4.4	0.0031	0.00071	0.00031-0.00052
MHPPT	7,100	5,254	40	4.2	0.0031	0.00075	0.00038-0.00062
SHPT	5,600	4,144	40	3.8	0.0032	0.00083	0.00077-0.00092

[1] Rate of inbreeding (dF) was calculated as $\Delta F = \dfrac{1}{8N_m} + \dfrac{1}{8N_f}$ (Falconer, 1996).

[2] Annual rate was calculated by dividing the rate of inbreeding (dF) with the generation interval.

[3] Realized rate of inbreeding by simulation (Supplementary Tables 8-10).

[4] Number of calf-bearing aged cows (i.e., aged 2-6 years): calculated as (No. of females×(1-0.26)) according to the age distribution in Supplementary Table 4.

one, whereas the expected rates of inbreeding for CHPPT and MHPPT were slightly higher than that realized. For proven bulls, the rates of inbreeding were much higher than expected, but ranged less than 5%. At this rate of inbreeding, the proven bulls of the current Hanwoo breeding scheme pose no concern.

Comparison of the selection response of TBV, EBV, and PH for each trait among three different schemes (Supplementary Tables 8, 9 and 10)

We compared the selection responses of the TBV, EBV, and PH schemes of the Hanwoo breeding program (CHPPT, MHPPT, and SHPT). Genetic trends for each trait with three different selection methods for each scheme are presented (see Supplementary Tables 8, 9 and 10). Selection for TBV, EBV, and on PH started in 1988. For all three selection methods, proven bulls were selected based on their phenotypic value of BW24 from 1983 to 1987. Therefore, apparent fluctuations occurred around 1988, after which the selection method stabilized and the BW12 steadily increased for all three methods. In cases of overlapping generations, the animals selected for breeding in the next generation would be the progeny of parents from different age groups and that exhibited different average genetic merit values. The candidate animals exhibited two or more different distributions with different means (Bichard et al., 1973). Thus, using Falconer's (1996) equation for predicting the selection response ($\Delta G = h^2 S$) from a single generation was difficult. For this reason, the genetic gain was calculated from the averaged true breeding values of animals by their birth year.

For BW12, as shown Table 5, the annual genetic gains of TBV, EBV, and PH selection as predicted by the MHPPT scheme were 2.046 kg, 1.462 kg, and 1.147 kg, respectively. As expected, the selection efficiency of EBV was highly improved compared to that of the CHPPT scheme. Since the MHPPT scheme utilized female performance data for genetic evaluation, the accuracy of the EBV improved, while only male performance data were used for genetic

evaluation in the CHPPT. Although BW12 in the SHPT scheme was incorporated in the selection index, the relative efficiency of EBV selection was not higher than that of the CHPPT or MHPPT schemes. The relatively low efficiency of EBV selection appeared to have been caused by attributes of traits comprising the selection index used in the SHPT scheme. The SHPT had no progeny test and the proven bulls were selected directly on their performances, which caused the performance of TBV selection to be far higher than that of other selection methods.

The genetic trend of ADG in a real Hanwoo population was 0.001 kg per year, as reported by Park et al. (1998), which was a startling discovery at the time. However, such low gains were not impossible given that the maximum genetic gain potential estimated in this study was only 0.004 kg per year. For ADG, the annual genetic gains of TBV, EBV, and PH selection in the MHPPT were 0.007 kg, 0.005 kg, and 0.004 kg, respectively, and those in the SHPT were 0.007 kg, 0.004 kg, and 0.004 kg, respectively. These genetic gains were similar or higher than those of the CHPPT.

For both ULMA and UMS traits in the MHPPT scheme, the relative efficiencies were greater than those of CLMA and CMS. This could be explained by the lack of genetic and error correlations between ULMA and UMS, whereas for CLMA and CMS, these values were -0.02 for the genetic correlation and 0.17 for the error correlation. Therefore, the accuracy of EBV for ULMA and UMS could be higher than CLMA or CMS, largely due to a lack of an error correlation between the two ultrasound traits.

Overall, for the SHPT scheme, the responses of EBV selection were slightly higher than those of PH selection. This could be explained as follows. First, the selection was made based on the performance of the animal itself, which caused the performance of selection on PH to be relatively high in comparison to the other two schemes, in which carcass traits were measured via progeny. Second, the variation between the level of fixed effect was very low in this simulation (Table 9), which might have made the

Table 5. Genetic gain per year and relative efficiency of the true breeding value for each trait according to the selection method for each scheme

Scheme		BW12[1]			BW24			ADG[1]			CWT[2]			CLMA[2]			CMS[2]			ULMA			UMS		
		Selection method			Selection method			Selection method			Selection method			Selection method			Selection method			Selection method			Selection method		
		TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH
CHPPT	dG[3]	1.995	1.285	1.079	3.406	2.124	1.800	0.007	0.004	0.004	2.108	1.340	1.132	0.364	0.205	0.193	0.050	0.036	0.035	0.336	0.199	0.173	0.035	0.026	0.026
	RE[4]	1.00	0.64	0.54	1.00	0.62	0.53	1.00	0.64	0.54	1.00	0.64	0.54	1.00	0.56	0.53	1.00	0.72	0.71	1.00	0.59	0.51	1.00	0.74	0.74
MHPPT	dG[3]	2.046	1.462	1.147	3.268	2.389	1.853	0.007	0.005	0.004	1.986	1.488	1.148	0.323	0.241	0.187	0.045	0.038	0.033	0.292	0.230	0.172	0.032	0.027	0.023
	RE[4]	1.00	0.71	0.56	1.00	0.73	0.57	1.00	0.70	0.56	1.00	0.75	0.58	1.00	0.75	0.58	1.00	0.84	0.73	1.00	0.79	0.59	1.00	0.85	0.71
SHPT	dG[2]	2.437	1.501	1.317	4.422	2.840	2.538	0.007	0.004	0.004	3.098	2.037	1.862	0.544	0.359	0.322	0.140	0.096	0.093	0.733	0.499	0.448	0.200	0.138	0.136
	RE[3]	1.00	0.62	0.54	1.00	0.64	0.57	1.00	0.59	0.54	1.00	0.66	0.60	1.00	0.66	0.59	1.00	0.69	0.67	1.00	0.68	0.61	1.00	0.69	0.68

[1] Trait for the selection index of young bulls. [2] Trait for the selection index of proven bulls.
[3] Genetic gain per year. [4] Relative efficiency to TBV selection.
BW12 and BW24 = Body weight at age of 12 and 24 months, respectively; ADG = Average daily gain tested from 6 to 12 months; CWT = Carcass weight at finish (24 months); CLMA = Carcass LMA; CMS = Carcass marbling score; ULMA = Ultrasound longissimus muscle area; UMS = Ultrasound marbling score; TBV = True breeding value; EBV = Estimated breeding value; PH = phenotypic value.

phenotypic value close to the TBV. Particularly in UMS, the high heritability would overestimate the performance of PH selection. However, EBV selection was 5% more efficient on average for PH selection in the SHPT scheme. If the accuracy of ultrasound measurements were secured, PH selection could be used. In other cases, EBV selection should be recommended because it should maximize the use of the relatives' performance for predicting the EBV.

Trend of additive genetic variance (Supplementary Figure TBV-1-PH-8)

Ju (2001) investigated the reduction of additive genetic variance while simulating various selection methods for Hanwoo cattle. He reported that the additive genetic variance was reduced at the initial stages of simulation (until the 3rd generation of proven bulls was selected) but remained stable thereafter. Similar to the results of Ju (2001), we observed that the additive genetic variance decreased during the first 10 years of simulation. The trait under selection pressure tended to show more reduction in genetic variance, which was also observed by Ju (2001).

The additive genetic variance computed for each trait and each breeding scheme, and selected using each selection method is summarized in Table 6.

Within the CHPPT and MHPPT schemes, young bulls were selected based on BW12 and ADG, and proven bulls were chosen based on CWT, CLMA, and CMS. Particularly in the MHPPT scheme, BW12 and ADG were used to select heifers. In the SHPT scheme, BW12, ULMA, and UMS were used to select proven bulls. The traits under selection showed more reduction of additive genetic variance over all the schemes. Across all growth traits, the genetic variances of the CHPPT and MHPPT decreased more than that of the SHPT. However, the SHPT scheme showed a larger reduction in ULMA and UMS traits than the other two schemes.

In the TBV selection, additive genetic variance decreased, as well when the selection was made, based on the EBV. However, the magnitude of the reduction on EBV was lower than that of TBV selection. Therefore, the reductions in those traits were larger than in the other traits. For all growth traits, the genetic variance of the CHPPT and

Table 6. Trend of additive genetic variance calculated from the TBV of the population by each selection method

		BW12			BW24			ADG			CWT		
		Breeding scheme			Breeding scheme			Breeding scheme			Breeding scheme		
		CHPPT	MHPPT	SHPT	CHPPT	MHPPT	SHPT	CHPPT	MHPPT	SHPT	CHPPT	MHPPT	SHPT
TBV	R[1]	-1.186	-1.082	0.060	-2.210	-2.778	0.010	-1.48E-05	-1.76E-05	1.35E-06	-1.007	-1.129	-0.258
	Rsq[2]	0.734	0.304	0.001	0.505	0.438	0.001	0.7515	0.5746	0.0237	0.617	0.541	0.151
	R88[3]	-1.161	-0.407	0.665	-2.550	-1.630	1.324	-1.30E-05	-1.15E-05	4.97E-06	-1.028	-0.760	0.169
	Rsq88[4]	0.752	0.062	0.629	0.650	0.193	0.507	0.6833	0.3503	0.5460	0.662	0.310	0.073
EBV	R[1]	-0.729	-0.305	-0.156	-1.935	-1.135	-0.521	-9.04E-06	-6.82E-06	2.62E-07	-0.744	-0.586	-0.483
	Rsq[2]	0.752	0.214	0.015	0.644	0.372	0.065	0.7265	0.4289	0.0096	0.698	0.519	0.368
	R88[3]	-0.696	-0.006	0.186	-2.318	-0.493	0.457	-8.36E-06	-3.59E-06	3.30E-06	-0.850	-0.337	-0.242
	Rsq88[4]	0.662	0.004	0.298	0.694	0.138	0.111	0.6080	0.1624	0.3871	0.715	0.320	0.120
PH	R[1]	-0.334	-0.383	-0.014	-1.173	-0.711	-0.263	-5.47E-06	-3.97E-06	-3.09E-06	-0.504	-0.365	-0.320
	Rsq[2]	0.515	0.337	0.002	0.624	0.269	0.087	0.5242	0.2427	0.1576	0.682	0.461	0.465
	R88[3]	-0.273	-0.167	0.223	-1.072	-0.348	0.201	-3.43E-06	-1.09E-06	-1.55E-06	-0.439	-0.249	-0.145
	Rsq88[4]	0.444	0.140	0.384	0.649	0.109	0.057	0.3390	0.0257	0.0080	0.684	0.296	0.319

		CLMA			CMS			ULMA			UMS		
		Breeding scheme			Breeding scheme			Breeding scheme			Breeding scheme		
		CHPPT	MHPPT	SHPT	CHPPT	MHPPT	SHPT	CHPPT	MHPPT	SHPT	CHPPT	MHPPT	SHPT
TBV	R[1]	-0.026	-0.034	-0.014	-0.002	-0.002	-0.001	-0.007	-0.001	-0.030	-0.001	-0.001	-0.002
	Rsq[2]	0.216	0.536	0.180	0.656	0.455	0.525	0.012	0.467	0.357	0.467	0.232	0.600
	R88[3]	-0.036	-0.028	0.004	-0.002	-0.001	-0.001	-0.006	-0.001	-0.012	-0.001	0.000	-0.001
	Rsq88[4]	0.447	0.377	0.009	0.478	0.212	0.450	0.004	0.375	0.071	0.375	0.027	0.493
EBV	R[1]	-0.003	-0.028	-0.035	-0.002	-0.002	-0.039	-0.030	-0.001	-0.037	-0.001	-0.001	-0.001
	Rsq[2]	0.002	0.364	0.505	0.640	0.677	0.572	0.461	0.698	0.566	0.698	0.591	0.605
	R88[3]	-0.007	-0.028	-0.021	-0.001	-0.002	-0.038	-0.042	-0.001	-0.021	-0.001	-0.001	-0.001
	Rsq88[4]	0.003	0.361	0.266	0.464	0.716	0.500	0.691	0.643	0.375	0.643	0.653	0.500
PH	R[1]	-0.020	-0.008	-0.013	-0.001	-0.001	-0.002	-0.010	-0.001	-0.026	-0.001	0.000	-0.001
	Rsq[2]	0.412	0.070	0.117	0.414	0.312	0.640	0.057	0.100	0.317	0.100	0.002	0.296
	R88[3]	-0.016	-0.004	-0.004	-0.001	-0.001	-0.002	-0.009	-0.001	-0.028	-0.001	0.000	-0.001
	Rsq88[4]	0.281	0.007	0.005	0.536	0.357	0.682	0.044	0.411	0.301	0.411	0.022	0.122

[1] Regression coefficient of the additive genetic variance from 1983 to 2020. [2] Coefficient of determination of the linear regression (R).
[3] Regression coefficient of the additive genetic variance from 1988 to 2020 (regression coefficient).
[4] Coefficient of determination of the linear regression (R88). [5] Relative efficiency to CHPPT.
BW12 and BW24 = Body weight at the age of 12 and 24 months, respectively; ADG = Average daily gain tested from 6 to 12 months; CWT = Carcass weight at finish (24 months); CLMA = Carcass LMA; CMS = Carcass marbling score; ULMA = Ultrasound longissimus muscle area; UMS = Ultrasound measure of the marbling score.

MHPPT on EBV decreased more than that of the SHPT. However, similar to TBV selection, the SHPT scheme on the EBV showed larger reduction on ULMA and UMS traits than the other two schemes. Additionally, similar to TBV and EBV selection, additive genetic variance was reduced as well when the selection was made based on PH. However, the magnitude of reduction on PH was much lower than that of TBV or EBV selection. Except for ULMA and UMS, the reduction in all three schemes on PH showed similar patterns over the three breeding schemes. In ULMA and UMS, the SHPT scheme on PH showed larger reduction compared to the CHPPT and MHPPT schemes because the selection pressure of those traits in the SHPT was higher than that in other breeding schemes.

According to these simulations, the MHPPT scheme showed satisfying results when animals were selected based on the EBV. However, in terms of genetic gains, the SHPT was superior to both the CHPPT and MHPPT schemes. Although the SHPT scheme was the most efficient, in practice, the selection of Hanwoo gives more attention to its appearance rather than its performance, which proved to be the very reason not to replace the CHPT or MHPPT with the SHPT. Thus, our data suggest that the MHPPT and SHPT schemes performed better than the CHPPT in terms of genetic gain and population size and could be used in place of the CHPPT scheme. However, the simulation had many limitations for mimicking realistic conditions, and numerous assumptions were made that differed from actual practice. Therefore, the results of this research should be cautiously interpreted.

In this study, we developed an Integrated General Model (IGM), which consisted of three different schemes and suggested that the MHPPT was superior to the CHPPT, which mimicked the currently used Hanwoo improvement system. In addition, by modeling the new scheme, SHPPT, we were able to compare it with two different schemes. Furthermore, users could select the performance test step and the progeny test step according to their circumstances so that they can control the breeding schemes and selection methods of this system, IGM, by only manipulating the input parameters.

ACKNOWLEDGMENTS

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- Supplementary Data -

< General Assumption >

All female animals with age greater than or equal to one year were mated once per year simultaneously hence all mated cows calved once a year. Therefore all mature female can be mated once a year. As a result it sets limitation to simulate real situation in which every day some cows can be inseminated and give birth. The use of random mating strategy prevented the utilization of planned mating and mimicking artificial insemination taken place in real Hanwoo farms.

The simulation program was facilitated to run Tsuruta et al. (2001)'s BLUPF90IOD for estimation of breeding values. In simulation the record of animal was generated using linear model as follows:

$$Y_{ijkl} = Year_i + Sex_j + Herd_k + animal_{ijkl} + error_{ijkl}$$

Where, Y_{ijkl} = observation of lth animal in i^{th} year, j^{th} sex, k^{th} herd
$Year_i = i^{th}$ year effect (1978-2020)
$Sex_j = j^{th}$ sex effect (male and female)
$Herd_k = k^{th}$ herd effect (1, 2, 3)
$animal_{ijkl}$ = additive genetic effect of lth animal
$error_{ijkl}$ = random residual effect.

The value of each level for year and herd effects was chosen at the beginning of simulation and used throughout the process. The average value of sex effect was given as a parameter and only the sex was determined at random. In Table 1, the number of levels and level value ranges of each effect are listed.

Table 1. Parameters assumed in the simulation

Trait[1]	h^2	Variance component		Phenotype sex mean		Genetic and phenotypic correlation[2]							
		σ_a^2	σ_e^2	M	F	BW12	BW24	ADG	CWT	CLMA	CMS	ULMA	UMS
BW12	0.20	250	970	315	210		0.82	0.78	0.67	0.30	-0.03	0.30	-0.03
BW24	0.22	620	2,140	580	330	0.59		0.73	0.90[3]	0.64	0.00[4]	0.64	0.00[4]
ADG	0.19	0.0032	0.0140	1.00	0.45	0.72	0.64		0.60	0.21	0.01	0.21	0.01
CWT	0.26	255	720	300	300	0.44	0.88	0.38		0.51	0.22	0.51	0.22
CLMA	0.34	22	42	77	77	0.17	0.41	0.15	0.56		-0.02	0.70	-0.02
CMS	0.46	0.77	0.92	2.40	2.40	0.04	0.06	0.13	0.15	0.17		0.00	0.70
ULMA	0.34	22	42	77	77	0.17	0.41	0.15	0.56	0.70	0.00		0.00[5]
UMS	0.46	0.77	0.92	2.30	2.30	0.04	0.06	0.13	0.15	0.00	0.70	0.00[5]	

[1] BW12 and BW24 = Body weight at age of 12 and 24 months, ADG = Average daily gain tested from 6 to 12 months, CWT = Carcass weight at finish (24 months), CLMA = Carcass LMA, CMS = Carcass marbling score, ULMA = Ultrasound measure of longissimus muscle area, UMS = Ultrasound measure of marbling score.

[2] Genetic correlations are above diagonal, phenotypic correlations are below diagonal.

[3] Genetic correlation was adjusted from 0.93 to 0.90 to make genetic variance-covariance matrix to be positive definite.

[4] Genetic correlation between BW24 and MS was assumed 0 because there was only one estimate with 0.25 and it had been known that it was negative (Koots, 1994).

[5] The correlation between ULMA and UMS was assumed 0, while those with other traits are assumed to be same as CLMA and CMS.

Table 2. Additive genetic (co)variances used in the simulation

Trait[1]	Additive genetic variance-covariance							
	BW12	BW24	ADG	CWT	CLMA	CMS	ULMA[2]	UMS[2]
BW12	250.000	322.834	0.696	167.904	21.878	-0.382	21.878	-0.382
BW24	322.834	620.000	1.028	357.856	74.746	0.000	74.746	0.000
ADG	0.696	1.028	0.003	0.537	0.056	0.000	0.056	0.000
CWT	167.904	357.856	0.537	255.000	38.484	3.126	38.484	3.126
CLMA	21.878	74.746	0.056	38.484	22.000	-0.074	15.400	-0.074
CMS	-0.382	0.000	0.000	3.126	-0.074	0.770	0.000	0.539
ULMA	21.878	74.746	0.056	38.484	15.400	0.000	22.000	0.000
UMS	-0.382	0.000	0.000	3.126	-0.074	0.539	0.000	0.770

[1] BW12 and BW24 = Body weight at age of 12 and 24 months, ADG = Average daily gain tested from 6 to 12 months, CWT = Carcass weight at finish (24 months), CLMA = Carcass longissimus muscle area, CMS = Carcass marbling score, ULMA = Ultrasound measure of longissimus muscle area, UMS = Ultrasound measure of marbling score.

[2] The correlations between ULMA, UMS with other traits were assumed to be same as those of CLMA and CMS, respectively, and the correlation between two ultrasound measures was set to be zero.

Table 3. Residual error (co)variances used in the simulation

Trait[1]	Residual error variance-covariance[2]							
	BW12	BW24	ADG	CWT	CLMA	CMS	ULMA	UMS
BW12	970.000	759.812	2.602	306.525	25.625	2.311	25.625	2.311
BW24	759.812	2,140.000	3.381	1,085.719	97.571	4.098	97.571	4.098
ADG	2.602	3.381	0.014	0.998	0.104	0.021	0.104	0.021
CWT	306.525	1085.719	0.998	720.000	100.294	2.862	100.294	2.862
CLMA	25.625	97.571	0.104	100.294	42.000	1.816	29.400	0.074
CMS	2.311	4.098	0.021	2.862	1.816	0.920	0.000	0.644
ULMA	25.625	97.571	0.104	100.294	29.400	0.000	42.000	0.000
UMS	2.311	4.098	0.021	2.862	0.074	0.644	0.000	0.920

[1] BW12 and BW24 = Body weight at age of 12 and 24 months, ADG = Average daily gain tested from 6 to 12 months, CWT = Carcass weight at finish (24 months), CLMA = Carcass longissimus muscle area, CMS = Carcass marbling score, ULMA = Ultrasound measure of longissimus muscle area, UMS = Ultrasound measure of marbling score.

[2] Residual variance-covariances were calculated by subtracting additive genetic variance-covariances from phenotypic variance-covaraiances, and phenotypic variance-covaraiances were calculated from phenotypic correlations and variances listed in Table 1.

Table 4. Age distribution at equilibrium, average age of cows in herd, and herd size growth rate

Source	Age of cow					
	1	2	3	4	5	6
Probability of culling	0.300	0.100	0.100	0.100	0.100	1.000
Probability of surviving	0.700	0.900	0.900	0.900	0.900	0.000
Age distribution	0.259	0.181	0.163	0.147	0.132	0.119
Cull distribution	0.300	0.070	0.063	0.057	0.051	0.459
Average age in herd, yr	3.07					
Average age of culled cows, yr	3.87					
Herd size growth rate, yr[1]	1.0009					

[1] Herd size growth rate was calculated from eigenvalue.

Table 5. Fixed effects used in the simulation

Effect	No of Level	Level	Level value of each effect by trait							
			BW12	BW24	ADG	CWT	CLMA	CMS	ULMA	UMS
Sex[1]	2	Male	315	580	1	300	77	2.4	77	2.3
		Female	210	330	0.45	300	77	2.4	77	2.3
Herd[2]	3	Min	0	0	0	0	0	0	0	0
		Max	2.5	5	0.05	5	0.5	0.1	0.5	0.1
Year[2]	43	Min	0	0	0	0	0	0	0	0
		Max	2.5	5	0.05	5	0.5	0.1	0.5	0.1

[1] The value of each level was fixed throughout the simulation. [2] The value for each level was chosen at random at every each year.

Table 6. Age distribution and sex ratio of base population for program test

Sex	Age of animal						Total
	1	2	3	4	5	6	
Male	12,908	9,261	8,284	7,335	6,577	5,874	50,239
Row percentage	25.69	18.43	16.49	14.60	13.09	11.69	50.24
Female	12,926	8,924	8,114	7,301	6,518	5,978	49,761
Row percentage	25.98	17.93	16.31	14.67	13.10	12.01	49.76
Total	25,834	18,185	16,398	14,636	13,095	11,852	100,000
Row percentage (a)	25.83	18.19	16.40	14.64	13.10	11.85	100.00
Given parameter (p)	25.90	18.10	16.30	14.70	13.20	11.90	100.00
Difference (a-p)	-0.07	0.09	0.10	-0.06	-0.10	-0.05	0.09[1]

[1] Standard deviation of differences.

Table 7. Comparison of genetic (above diagonal) and phenotypic (below diagonal) correlations between traits of female

Source	Trait	Trait							
		BW12	BW24	ADG	CWT	CLMA	CMS	ULMA	UMS
Simulated[1]	BW12		0.821	0.781	0.665	0.297	-0.031	0.294	-0.029
	BW24	0.591		0.732	0.900	0.640	-0.002	0.638	-0.004
	ADG	0.719	0.643		0.597	0.213	-0.003	0.210	-0.001
	CWT	0.438	0.882	0.380		0.515	0.221	0.514	0.218
	CLMA	0.176	0.414	0.157	0.557		-0.015	0.699	-0.018
	CMS	0.043	0.060	0.127	0.147	0.172		0.003	0.699
	ULMA	0.176	0.415	0.158	0.559	0.699	0.005		0.001
	UMS	0.043	0.058	0.123	0.145	-0.001	0.696	0.003	
Given parameter	BW12		0.820	0.778	0.665	0.295	-0.028	0.295	-0.028
	BW24	0.590		0.730	0.900	0.640	0.000	0.640	0.000
	ADG	0.720	0.640		0.595	0.213	0.005	0.213	0.005
	CWT	0.435	0.880	0.375		0.514	0.223	0.514	0.223
	CLMA	0.170	0.410	0.153	0.556		-0.018	0.700	-0.018
	CMS	0.043	0.060	0.125	0.148	0.168		0.000	0.700
	ULMA	0.170	0.410	0.153	0.556	0.700	0.000		0.000
	UMS	0.043	0.060	0.125	0.148	0.000	0.700	0.000	
Difference	BW12		0.001	0.003	0.000	0.002	-0.003	-0.001	-0.001
	BW24	0.001		0.002	0.000	0.000	-0.002	-0.002	-0.004
	ADG	-0.001	0.003		0.002	0.000	-0.008	-0.003	-0.006
	CWT	0.003	0.002	0.005		0.001	-0.002	0.000	-0.005
	CLMA	0.006	0.004	0.004	0.001		0.003	-0.001	0.000
	CMS	0.000	0.000	0.002	-0.001	0.004		0.003	-0.001
	ULMA	0.006	0.005	0.005	0.003	-0.001	0.005		0.001
	UMS	0.000	-0.002	-0.002	-0.003	-0.001	-0.004	0.003	

[1] The phenotypic correlations of simulated data were estimated separately by sex because trait 1 and 2 have different mean of sex. There were no differences between sex on phenotypic correlation. Therefore only female estimates were prepared. Total 100,000 animals were generated
BW12 and BW24 = Body weight at age of 12 and 24 months, ADG = Average daily gain tested from 6 to 12 months, CWT = Carcass weight at finish (24 months), CLMA = Carcass LMA, CMS = Carcass marbling score, ULMA = Ultrasound measure of longissimus muscle area, UMS = Ultrasound measure of marbling score.
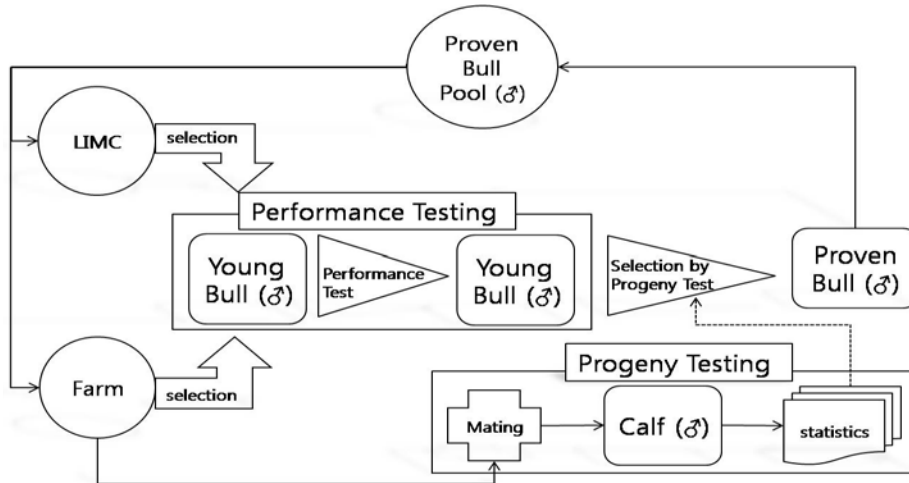
Figure 1. Model I (CHPPT). The current HPPT module in IGM with performance and progeny tests.
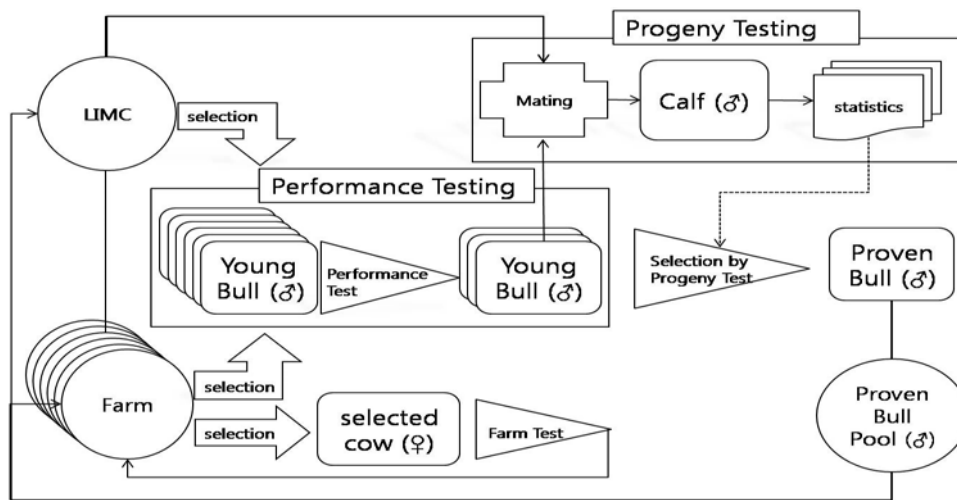

Figure 2. Model II (MHPPT). The modified HPPT module in IGM with performance and progeny tests.

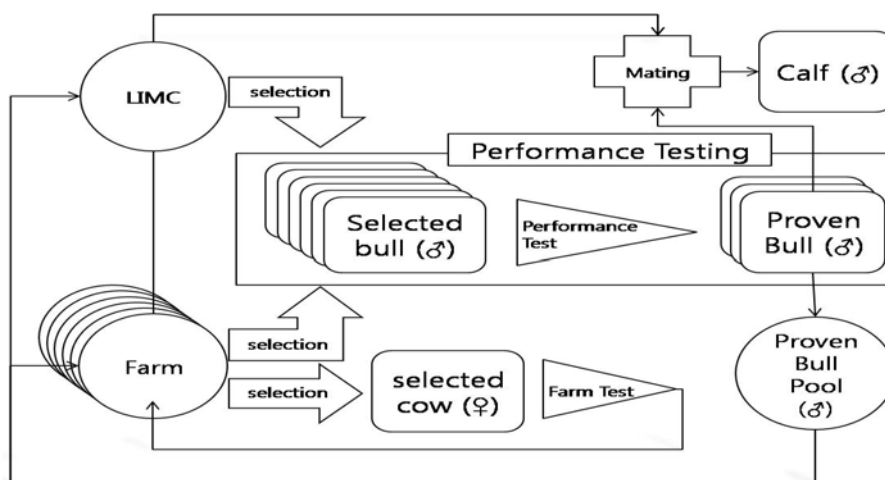**Figure 3.** Model III (SHPT). New breeding scheme, SHPT module in IGM, utilized ultrasound techniques with performance test only.

<Comparison of the selection response of TBV, EBV, and PH for each scheme>

Table 8. Genetic gain of true breeding value for each trait according to selection method in CHPPT scheme

Birth year	BW12[1]			BW24			ADG[1]			CWT[2]			CLMA[2]			CMS[2]			ULMA			UMS		
	Selection method			Selection method			Selection method			Selection method			Selection method			Selection method			Selection method			Selection method		
	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH
1983	-0.16	0.20	-0.07	-0.33	0.33	0.17	-0.001	0.001	0.000	0.07	0.63	0.51	-0.02	0.01	0.01	0.070	0.053	0.077	-0.09	0.01	0.05	0.064	0.066	0.083
1984	10.02	4.32	5.15	21.00	8.88	9.90	0.032	0.015	0.017	12.67	5.43	6.30	2.67	1.00	1.08	0.079	0.005	0.055	2.71	1.13	1.22	0.088	0.030	0.086
1985	10.86	4.90	5.42	22.09	9.46	10.50	0.034	0.016	0.019	13.27	5.75	6.67	2.80	1.09	1.17	0.119	0.028	0.077	2.80	1.11	1.24	0.088	0.057	0.102
1986	22.13	10.63	11.15	43.53	20.44	20.91	0.071	0.037	0.037	25.62	11.83	12.68	5.32	2.31	2.26	0.083	0.026	0.054	5.36	2.48	2.39	0.119	0.036	0.121
1987	24.53	12.40	12.35	48.15	23.58	24.05	0.079	0.042	0.040	28.36	13.98	14.28	5.73	2.62	2.90	0.106	0.052	0.066	5.91	2.75	2.97	0.111	0.063	0.106
1988	31.64	15.53	15.42	62.15	29.50	29.50	0.102	0.052	0.051	37.04	17.20	17.33	7.49	3.34	3.43	0.160	0.037	0.046	7.52	3.50	3.50	0.178	0.069	0.084
1989	26.39	13.45	10.75	52.39	23.84	17.93	0.086	0.045	0.038	31.78	14.11	10.13	6.54	2.35	1.70	0.335	0.053	0.056	6.38	2.57	1.87	0.295	0.073	0.098
1990	31.30	15.85	13.47	62.76	28.56	24.15	0.101	0.054	0.046	38.26	17.14	15.08	7.86	2.98	2.57	0.385	0.174	0.255	7.71	3.19	2.64	0.332	0.154	0.246
1991	36.08	16.72	14.64	71.63	29.99	26.36	0.117	0.056	0.049	44.07	18.04	16.43	8.78	3.22	2.87	0.502	0.247	0.248	8.68	3.35	2.95	0.417	0.225	0.241
1992	38.50	18.73	16.70	75.34	33.69	30.43	0.126	0.064	0.056	46.36	20.14	18.43	9.07	3.56	3.42	0.540	0.250	0.262	8.89	3.72	3.54	0.445	0.220	0.243
1993	38.98	19.36	18.78	73.13	35.21	34.25	0.129	0.066	0.064	44.11	21.23	20.70	8.38	3.76	3.88	0.437	0.279	0.286	8.38	3.95	3.97	0.361	0.229	0.257
1994	39.77	20.10	18.53	75.54	36.11	33.40	0.133	0.068	0.063	46.00	21.85	20.23	9.00	3.77	3.66	0.580	0.285	0.294	8.74	4.04	3.81	0.478	0.255	0.270
1995	41.08	21.88	18.73	77.10	38.39	32.77	0.136	0.074	0.063	46.53	23.35	20.02	9.27	3.77	3.51	0.595	0.324	0.356	8.78	4.18	3.54	0.484	0.289	0.320
1996	45.11	23.63	20.58	85.14	42.25	36.20	0.148	0.080	0.070	51.80	25.98	22.36	10.13	4.29	3.87	0.645	0.394	0.428	9.70	4.53	3.92	0.510	0.324	0.371
1997	47.28	24.69	21.89	88.83	43.90	38.81	0.158	0.084	0.073	54.50	26.93	23.95	10.36	4.52	4.16	0.751	0.448	0.433	9.85	4.68	4.29	0.564	0.361	0.373
1998	48.54	25.99	23.35	90.35	45.52	41.36	0.163	0.087	0.077	55.22	27.74	25.42	10.42	4.67	4.53	0.771	0.458	0.455	10.01	4.82	4.56	0.581	0.357	0.399
1999	49.76	26.85	23.99	91.94	47.51	42.15	0.166	0.090	0.081	55.94	28.99	26.02	10.56	4.99	4.51	0.790	0.473	0.499	10.26	5.15	4.53	0.605	0.370	0.438
2000	50.86	28.16	24.04	94.02	49.67	42.13	0.171	0.096	0.082	57.42	30.57	25.99	10.92	5.10	4.52	0.883	0.510	0.528	10.45	5.33	4.44	0.686	0.426	0.451
2001	53.43	29.59	24.93	98.34	51.64	43.96	0.179	0.101	0.086	60.12	31.77	27.15	11.21	5.17	4.72	0.909	0.562	0.566	10.78	5.44	4.68	0.704	0.462	0.472
2002	56.17	31.39	26.42	102.92	54.53	46.13	0.185	0.106	0.089	62.93	33.63	28.76	11.55	5.54	4.91	0.972	0.626	0.618	11.32	5.62	4.92	0.741	0.485	0.500
2003	57.93	32.26	27.98	105.94	56.13	48.62	0.194	0.110	0.093	64.92	34.69	30.29	11.92	5.76	5.27	1.041	0.676	0.651	11.67	5.90	5.07	0.787	0.532	0.535
2004	58.77	33.01	29.40	107.60	57.09	51.07	0.197	0.112	0.099	66.05	35.26	31.50	12.27	5.79	5.59	1.099	0.677	0.687	11.87	5.90	5.25	0.805	0.534	0.571
2005	60.22	34.54	29.67	109.80	59.61	51.78	0.202	0.118	0.101	67.31	37.19	32.08	12.59	5.89	5.64	1.135	0.719	0.751	12.05	6.11	5.41	0.869	0.567	0.610
2006	62.53	35.74	30.39	113.26	61.71	52.93	0.210	0.122	0.103	69.61	38.33	32.81	12.74	6.07	5.82	1.183	0.769	0.786	12.12	6.41	5.56	0.942	0.589	0.626
2007	64.78	36.97	32.02	116.59	63.92	55.04	0.216	0.126	0.110	71.64	39.53	34.11	12.93	6.43	5.91	1.250	0.795	0.816	12.42	6.55	5.59	0.945	0.610	0.654
2008	66.52	38.26	33.45	119.94	66.33	57.55	0.221	0.130	0.113	73.37	41.36	35.81	13.42	6.74	6.14	1.277	0.832	0.852	12.91	6.67	5.83	0.958	0.642	0.681
2009	68.06	39.61	34.03	123.17	68.10	58.42	0.228	0.134	0.115	75.65	42.22	36.30	13.87	6.91	6.22	1.310	0.864	0.878	13.31	6.91	5.87	0.997	0.670	0.708
2010	69.29	40.53	35.21	124.62	69.44	60.25	0.233	0.137	0.119	76.47	43.10	37.47	14.07	7.01	6.37	1.350	0.872	0.904	13.43	7.05	6.03	1.004	0.691	0.744
2011	70.99	41.67	36.17	127.32	71.03	62.29	0.239	0.141	0.122	77.98	44.12	38.77	14.41	7.02	6.83	1.380	0.902	0.949	13.51	7.07	6.44	1.030	0.692	0.763
2012	72.74	42.81	36.79	131.11	72.80	63.22	0.246	0.146	0.125	80.67	45.12	39.21	14.72	7.13	6.97	1.428	0.964	0.988	13.78	7.21	6.54	1.024	0.735	0.796
2013	74.74	44.37	38.49	133.67	75.65	65.74	0.251	0.151	0.131	81.95	47.07	40.82	14.96	7.50	6.99	1.514	1.012	1.023	14.15	7.49	6.67	1.079	0.768	0.812
2014	76.45	45.39	39.47	136.32	77.63	67.61	0.257	0.154	0.134	83.61	48.18	42.12	15.21	7.82	7.15	1.560	1.025	1.070	14.49	7.81	6.88	1.157	0.768	0.812
2015	77.64	46.17	39.75	138.81	78.55	68.38	0.262	0.157	0.136	85.20	48.87	42.65	15.60	7.82	7.31	1.604	1.081	1.088	14.81	7.81	6.94	1.195	0.831	0.841
2016	79.28	47.64	40.81	141.21	80.39	70.00	0.269	0.162	0.139	86.44	50.00	43.84	15.89	7.97	7.53	1.634	1.134	1.115	14.99	7.88	7.06	1.185	0.863	0.865
2017	80.95	48.78	41.66	144.13	82.78	71.65	0.275	0.166	0.142	88.61	51.59	45.00	16.07	8.17	7.80	1.673	1.139	1.170	15.12	8.14	7.31	1.211	0.854	0.920
2018	82.85	50.12	43.44	147.61	84.91	74.66	0.279	0.170	0.149	90.99	52.89	46.35	16.44	8.39	8.22	1.740	1.182	1.192	15.50	8.39	7.67	1.268	0.888	0.948
2019	84.36	51.35	44.83	150.05	87.02	76.50	0.286	0.175	0.152	92.09	54.18	47.45	16.80	8.68	8.29	1.797	1.234	1.215	15.84	8.59	7.77	1.300	0.926	0.941
2020	85.97	52.06	45.03	152.37	88.26	77.25	0.293	0.177	0.153	93.53	55.10	48.38	16.98	8.80	8.38	1.837	1.249	1.270	15.98	8.71	7.84	1.336	0.946	0.957
dG[3]	1.995	1.285	1.079	3.406	2.124	1.800	0.007	0.004	0.004	2.108	1.340	1.132	0.364	0.205	0.193	0.050	0.036	0.035	0.336	0.199	0.173	0.035	0.026	0.026
RE[4]	1.00	0.64	0.54	1.00	0.62	0.53	1.00	0.64	0.54	1.00	0.64	0.54	1.00	0.56	0.53	1.00	0.72	0.71	1.00	0.59	0.51	1.00	0.74	0.74

[1] Trait for selection index of Young Bull. [2] Trait for selection index of Proven Bull. [3] Genetic gain per year. [4] Relative efficiency to TBV selection.
BW12 and BW24 = Body weight at age of 12 and 24 months, ADG = Average daily gain tested from 6 to 12 months, CWT = Carcass weight at finish (24 months), CLMA = Carcass LMA, CMS = Carcass marbling score, ULMA = Ultrasound longissimus muscle area, UMS = Ultrasound marbling score, TBV = True breeding value, EBV = Estimated breeding value, PH = Phenotypic value.

Table 9. Genetic gain of true breeding value for each trait according to selection method in MHPPT scheme

Birth year	BW12[1]			BW24			ADG[1]			CWT[2]			CLMA[2]			CMS[2]			ULMA			UMS		
	Selection method			Selection method			Selection method			Selection method			Selection method			Selection method			Selection method			Selection method		
	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH
1983	-0.31	0.27	0.08	-0.42	0.50	0.37	0.000	0.001	0.000	0.13	0.51	0.36	-0.08	0.07	0.09	0.081	0.062	0.045	-0.06	0.12	0.11	0.068	0.063	0.042
1984	4.80	5.20	5.00	9.68	9.59	9.77	0.015	0.015	0.016	5.94	5.46	5.72	1.18	1.16	1.28	0.045	0.024	0.048	1.27	1.21	1.29	0.075	0.011	0.036
1985	4.93	5.69	5.21	10.06	10.30	10.22	0.017	0.017	0.016	6.26	5.84	6.28	1.16	1.19	1.19	0.073	0.003	0.062	1.36	1.25	1.28	0.105	0.012	0.053
1986	9.23	8.94	8.38	17.45	16.79	16.46	0.031	0.028	0.027	10.40	9.67	9.59	1.94	2.02	2.12	0.037	0.056	0.033	2.01	1.98	2.06	0.082	0.021	0.029
1987	10.48	10.08	10.48	19.61	19.20	19.60	0.035	0.032	0.033	11.44	11.07	11.43	2.14	2.25	2.36	0.042	0.023	0.048	2.33	2.28	2.35	0.075	-0.001	0.053
1988	12.92	12.60	12.71	24.18	24.05	23.73	0.043	0.041	0.040	14.16	13.73	13.67	2.69	2.90	2.87	0.045	0.014	0.037	2.90	2.80	2.87	0.085	0.002	0.042
1989	13.10	12.79	10.87	24.60	24.49	18.64	0.044	0.041	0.036	15.28	14.61	10.40	2.86	3.08	2.07	0.288	0.193	0.066	2.85	3.22	2.13	0.262	0.172	0.054
1990	16.51	15.71	13.88	31.34	29.89	24.88	0.055	0.050	0.046	19.47	17.88	14.74	3.67	3.73	2.91	0.326	0.245	0.184	3.66	3.75	2.82	0.296	0.220	0.139
1991	21.33	17.69	15.12	38.08	32.16	25.75	0.071	0.055	0.048	22.96	19.51	15.16	4.29	3.84	2.84	0.345	0.285	0.178	4.19	3.67	2.74	0.291	0.252	0.135
1992	24.30	20.97	18.10	42.73	37.17	31.18	0.080	0.066	0.057	25.72	22.25	18.30	4.75	4.17	3.48	0.370	0.308	0.220	4.63	4.20	3.34	0.314	0.256	0.169
1993	25.37	23.04	20.26	43.32	40.10	34.22	0.082	0.072	0.064	25.84	23.56	19.88	4.56	4.52	3.85	0.386	0.261	0.249	4.64	4.39	3.65	0.310	0.175	0.183
1994	29.03	24.43	21.75	49.25	42.72	36.45	0.095	0.077	0.069	29.21	25.32	21.29	5.30	4.89	3.94	0.445	0.312	0.285	5.22	4.60	3.79	0.362	0.250	0.248
1995	32.73	26.08	22.06	54.59	44.92	36.44	0.107	0.082	0.071	32.68	27.07	21.43	5.79	4.94	3.92	0.524	0.427	0.324	5.34	4.85	3.71	0.448	0.343	0.233
1996	36.48	28.52	23.83	60.79	48.88	40.30	0.119	0.088	0.078	36.52	29.15	23.94	6.22	5.48	4.37	0.578	0.440	0.372	5.96	5.38	4.17	0.474	0.354	0.277
1997	38.73	30.11	25.50	64.13	50.55	42.29	0.125	0.094	0.081	38.04	30.31	24.88	6.75	5.49	4.49	0.586	0.479	0.365	6.55	5.35	4.43	0.475	0.359	0.279
1998	40.13	31.70	26.76	66.21	53.60	44.58	0.130	0.102	0.086	39.16	31.92	26.37	6.92	5.77	4.75	0.604	0.486	0.430	6.71	5.75	4.57	0.465	0.370	0.332
1999	41.33	33.31	27.99	68.22	55.45	46.09	0.134	0.105	0.089	40.76	33.09	27.12	7.02	5.83	5.00	0.656	0.516	0.460	6.75	5.71	4.79	0.519	0.380	0.346
2000	43.48	34.66	28.68	71.54	58.89	47.41	0.143	0.112	0.093	42.82	35.32	28.22	7.22	6.30	4.96	0.702	0.561	0.468	7.07	6.25	4.78	0.554	0.450	0.371
2001	46.01	36.18	29.42	75.42	61.13	48.05	0.151	0.115	0.095	45.03	36.75	28.48	7.73	6.59	4.99	0.788	0.609	0.524	7.33	6.49	4.83	0.596	0.484	0.374
2002	47.79	37.23	30.56	79.20	63.03	50.95	0.158	0.121	0.100	47.37	37.92	30.24	8.18	6.78	5.47	0.819	0.627	0.540	7.80	6.59	5.26	0.627	0.494	0.407
2003	49.18	38.43	31.55	80.92	64.64	52.28	0.161	0.122	0.103	48.47	38.82	31.26	8.29	6.93	5.45	0.848	0.697	0.580	7.98	6.78	5.35	0.644	0.523	0.457
2004	50.14	39.58	32.59	82.71	66.65	54.39	0.166	0.128	0.106	49.69	40.44	32.72	8.50	7.00	5.79	0.884	0.711	0.638	8.01	6.90	5.49	0.650	0.557	0.468
2005	51.84	40.79	32.88	85.01	68.60	54.26	0.169	0.130	0.107	51.09	41.70	32.53	8.69	7.28	5.71	0.951	0.752	0.674	8.23	7.10	5.45	0.691	0.558	0.479
2006	54.14	41.21	34.02	88.97	69.41	56.27	0.180	0.135	0.112	53.35	42.01	34.00	9.07	7.44	5.89	0.966	0.809	0.697	8.62	7.30	5.61	0.712	0.599	0.518
2007	55.73	42.73	34.78	91.96	71.69	57.99	0.187	0.138	0.113	55.43	43.56	35.08	9.32	7.67	6.16	1.031	0.858	0.753	8.80	7.44	5.91	0.756	0.624	0.534
2008	57.52	44.05	35.62	94.82	73.85	59.63	0.192	0.143	0.118	57.16	45.17	36.06	9.72	7.78	6.49	1.091	0.919	0.773	9.13	7.51	6.10	0.819	0.679	0.568
2009	58.63	45.22	36.79	96.31	76.55	61.12	0.194	0.147	0.121	58.03	46.62	36.99	9.88	8.14	6.50	1.109	0.914	0.813	9.29	7.94	6.15	0.821	0.666	0.571
2010	60.16	45.83	37.43	98.15	77.32	61.87	0.200	0.149	0.122	59.22	47.53	37.54	10.03	8.20	6.53	1.160	0.965	0.846	9.23	8.06	6.17	0.838	0.710	0.603
2011	61.85	46.80	38.32	100.92	78.82	63.47	0.206	0.152	0.127	60.87	48.37	38.42	10.17	8.40	6.73	1.229	1.012	0.855	9.58	8.26	6.29	0.891	0.733	0.607
2012	64.17	48.45	38.93	104.73	81.38	65.14	0.215	0.160	0.129	63.29	49.71	39.69	10.54	8.57	6.83	1.266	1.062	0.896	9.82	8.37	6.46	0.928	0.759	0.618
2013	65.77	49.18	40.11	107.57	82.49	66.53	0.221	0.161	0.133	65.34	50.29	40.59	10.81	8.76	6.88	1.318	1.054	0.932	10.08	8.35	6.46	0.975	0.744	0.639
2014	67.14	50.86	41.67	110.02	85.35	68.60	0.226	0.165	0.137	66.77	52.37	41.63	11.18	9.07	7.13	1.362	1.125	0.970	10.44	8.63	6.79	1.014	0.793	0.685
2015	68.56	51.32	41.59	112.06	85.99	69.34	0.229	0.167	0.137	67.92	52.83	42.28	11.43	9.08	7.46	1.402	1.140	0.998	10.62	8.74	6.97	1.015	0.809	0.688
2016	70.22	53.02	42.64	115.06	89.24	70.62	0.236	0.173	0.142	69.71	55.02	43.20	11.76	9.37	7.35	1.435	1.195	1.054	10.82	9.13	6.87	1.057	0.861	0.740
2017	71.90	53.65	43.53	117.50	90.15	72.41	0.241	0.178	0.144	71.37	55.39	44.21	11.93	9.40	7.62	1.521	1.212	1.060	11.21	9.08	7.19	1.110	0.878	0.740
2018	73.59	54.40	45.05	120.38	91.50	74.48	0.249	0.179	0.148	73.27	56.55	45.26	12.02	9.68	7.92	1.558	1.271	1.079	11.28	9.26	7.33	1.151	0.911	0.727
2019	75.02	56.60	45.72	122.88	94.22	75.42	0.253	0.185	0.151	74.92	57.82	46.22	12.39	9.85	7.82	1.613	1.306	1.161	11.48	9.41	7.37	1.186	0.937	0.794
2020	76.70	57.61	46.47	125.69	96.07	76.96	0.258	0.188	0.155	76.57	59.55	47.18	12.82	9.92	8.05	1.626	1.391	1.185	11.86	9.62	7.52	1.201	1.009	0.817
dG[3]	2.046	1.462	1.147	3.268	2.389	1.853	0.007	0.005	0.004	1.986	1.488	1.148	0.323	0.241	0.187	0.045	0.038	0.033	0.292	0.230	0.172	0.032	0.027	0.023
RE[4]	1.00	0.71	0.56	1.00	0.73	0.57	1.00	0.70	0.56	1.00	0.75	0.58	1.00	0.75	0.58	1.00	0.84	0.73	1.00	0.79	0.59	1.00	0.85	0.71

[1] Trait for selection index of Young Bull. [2] Trait for selection index of Proven Bull. [3] Genetic gain per year. [4] Relative efficiency to TBV selection.
BW12 and BW24 = Body weight at age of 12 and 24 months, ADG = Average daily gain tested from 6 to 12 months, CWT = Carcass weight at finish (24 months), CLMA = Carcass LMA, CMS = Carcass marbling score, ULMA = Ultrasound longissimus muscle area, UMS = Ultrasound marbling score, TBV = True breeding value, EBV = Estimated breeding value, PH = Phenotypic value.

Table 10. Genetic gain of true breeding value for each trait according to selection method in SHPT scheme

Birth year	BW12[1]			BW24			ADG			CWT			CLMA			CMS			ULMA[1]			UMS[1]		
	Selection method			Selection method			Selection method			Selection method			Selection method			Selection method			Selection method			Selection method		
	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH	TBV	EBV	PH
1983	0.32	-0.12	0.28	0.65	-0.13	0.41	0.001	0.000	0.001	0.53	0.34	0.41	0.15	-0.03	0.03	0.062	0.066	0.056	0.19	-0.06	0.06	0.055	0.072	0.061
1984	2.91	3.28	2.43	5.71	6.39	4.78	0.010	0.010	0.008	4.68	4.91	3.89	0.74	0.81	0.59	0.289	0.276	0.273	0.94	1.13	1.03	0.408	0.410	0.417
1985	3.84	3.58	3.20	6.92	7.07	5.92	0.013	0.011	0.010	5.33	5.28	4.75	0.84	0.98	0.62	0.286	0.283	0.312	1.05	1.20	1.07	0.410	0.406	0.458
1986	4.73	4.60	4.42	8.49	8.62	7.82	0.015	0.013	0.013	6.55	6.46	5.92	1.01	1.02	0.90	0.369	0.342	0.362	1.37	1.41	1.32	0.501	0.486	0.510
1987	13.02	8.48	7.57	22.55	15.86	14.18	0.039	0.022	0.023	15.89	10.98	10.28	2.45	2.11	1.77	0.697	0.513	0.558	3.40	3.01	2.53	1.002	0.737	0.787
1988	15.29	9.19	9.71	26.88	17.09	17.39	0.045	0.024	0.028	18.69	12.31	12.61	3.06	2.27	2.01	0.777	0.610	0.647	4.09	3.06	2.83	1.118	0.877	0.909
1989	17.62	11.89	11.35	30.69	21.91	20.24	0.052	0.030	0.034	21.04	15.49	14.61	3.57	2.87	2.40	0.882	0.705	0.711	4.91	3.84	3.13	1.284	1.010	1.039
1990	21.87	13.87	13.03	38.27	25.81	23.14	0.065	0.035	0.039	26.22	18.17	16.62	4.45	3.40	2.66	1.077	0.857	0.806	5.89	4.70	3.54	1.536	1.181	1.184
1991	25.24	15.56	14.77	43.57	29.18	26.40	0.075	0.039	0.045	29.71	20.22	18.92	4.98	3.94	2.94	1.197	0.909	0.902	6.55	5.22	4.04	1.738	1.270	1.296
1992	28.02	17.61	15.92	48.18	33.45	28.76	0.081	0.047	0.049	32.93	23.27	20.63	5.58	4.34	3.25	1.359	1.004	0.985	7.50	5.91	4.48	1.940	1.410	1.427
1993	31.15	19.48	17.57	53.86	36.67	32.23	0.090	0.050	0.054	36.95	25.49	23.01	6.30	4.77	3.74	1.537	1.124	1.097	8.39	6.54	5.10	2.198	1.594	1.591
1994	34.65	22.12	19.39	59.81	41.11	35.81	0.102	0.059	0.058	40.72	28.21	25.57	6.85	5.19	4.22	1.652	1.196	1.184	9.16	7.18	5.69	2.383	1.693	1.710
1995	37.19	23.75	21.30	64.54	43.98	38.66	0.108	0.062	0.065	43.79	30.26	27.58	7.62	5.55	4.41	1.808	1.301	1.282	10.11	7.84	6.11	2.599	1.828	1.850
1996	40.21	25.60	23.18	70.07	47.76	42.10	0.118	0.068	0.069	47.56	32.86	29.98	8.29	6.04	4.84	1.935	1.409	1.394	11.01	8.39	6.64	2.800	1.977	1.991
1997	42.57	27.62	25.38	74.56	50.93	46.92	0.125	0.074	0.077	50.85	35.06	33.28	8.83	6.31	5.49	2.109	1.494	1.492	11.73	8.82	7.36	3.013	2.109	2.138
1998	44.71	29.00	26.02	78.21	53.49	48.12	0.130	0.076	0.078	53.39	36.90	34.21	9.38	6.73	5.76	2.273	1.582	1.592	12.37	9.37	7.79	3.219	2.247	2.275
1999	47.26	30.69	26.78	83.27	55.90	49.09	0.139	0.080	0.079	56.79	38.52	35.29	9.97	6.96	5.97	2.384	1.674	1.706	13.24	9.62	8.05	3.398	2.370	2.440
2000	49.18	31.86	28.23	86.81	58.80	51.74	0.144	0.083	0.083	59.53	40.73	37.02	10.33	7.50	6.15	2.509	1.770	1.761	13.80	10.27	8.49	3.589	2.511	2.542
2001	51.43	32.58	29.05	91.00	60.21	53.59	0.151	0.086	0.086	62.38	42.05	38.49	10.90	7.61	6.46	2.645	1.896	1.847	14.51	10.56	8.90	3.790	2.682	2.680
2002	53.41	34.06	30.64	94.31	62.96	56.90	0.157	0.090	0.090	64.95	43.98	40.87	11.30	7.96	6.92	2.799	2.011	1.936	15.12	11.01	9.45	3.992	2.818	2.811
2003	55.20	35.56	31.31	97.96	66.12	58.70	0.162	0.095	0.093	67.95	46.21	42.29	11.61	8.51	7.10	2.936	2.091	2.033	15.78	11.48	9.90	4.186	2.940	2.941
2004	57.34	36.46	32.38	101.55	68.01	60.67	0.167	0.097	0.095	70.45	47.86	43.91	12.10	8.66	7.37	3.084	2.198	2.109	16.31	11.90	10.19	4.395	3.097	3.074
2005	59.72	37.60	33.67	106.13	70.06	62.81	0.174	0.102	0.098	73.45	49.29	45.35	12.76	8.90	7.66	3.218	2.305	2.204	17.21	12.17	10.60	4.563	3.246	3.205
2006	61.88	39.47	35.51	110.07	73.86	65.58	0.182	0.106	0.103	76.04	52.06	47.17	13.23	9.42	7.80	3.334	2.390	2.280	17.78	12.87	11.02	4.759	3.365	3.342
2007	63.85	40.59	36.36	113.88	75.72	67.94	0.185	0.109	0.105	79.23	53.58	49.18	13.69	9.55	8.25	3.487	2.491	2.380	18.41	13.21	11.44	4.983	3.501	3.480
2008	65.70	41.62	37.72	117.82	77.78	70.48	0.191	0.113	0.111	81.99	54.92	50.69	14.26	9.94	8.54	3.614	2.585	2.432	19.14	13.59	11.94	5.158	3.640	3.567
2009	67.41	42.97	38.53	121.19	80.43	72.24	0.196	0.116	0.112	84.60	57.23	52.43	14.68	10.20	8.84	3.770	2.676	2.563	19.86	14.05	12.34	5.355	3.755	3.735
2010	69.83	43.59	39.26	125.22	81.92	73.73	0.203	0.118	0.115	87.51	58.40	53.59	15.12	10.45	9.06	3.884	2.769	2.653	20.42	14.45	12.66	5.555	3.922	3.864
2011	72.48	45.15	40.38	130.56	84.50	76.60	0.210	0.122	0.118	90.94	60.43	55.53	15.88	10.77	9.51	4.013	2.858	2.746	21.27	14.72	13.21	5.726	4.050	3.997
2012	74.76	46.55	41.56	133.92	87.23	78.64	0.217	0.126	0.120	93.48	62.06	57.34	16.16	11.05	9.81	4.164	2.895	2.820	21.78	15.27	13.56	5.933	4.152	4.125
2013	76.58	47.61	42.47	137.89	90.00	80.86	0.222	0.130	0.124	96.24	64.16	58.82	16.75	11.40	10.18	4.269	3.018	2.912	22.57	15.90	14.06	6.121	4.295	4.239
2014	78.06	48.82	43.76	140.50	92.53	83.24	0.225	0.133	0.129	98.57	66.30	60.87	17.05	11.82	10.27	4.440	3.110	3.027	22.98	16.31	14.34	6.349	4.455	4.392
2015	81.35	50.80	44.78	146.12	96.07	85.29	0.235	0.138	0.132	102.28	68.38	62.49	17.78	12.13	10.50	4.565	3.180	3.124	23.74	16.93	14.69	6.518	4.554	4.534
2016	83.26	51.62	45.55	149.90	97.96	87.45	0.241	0.140	0.134	104.57	70.10	64.24	18.23	12.35	10.89	4.675	3.288	3.235	24.59	17.37	15.29	6.687	4.707	4.681
2017	84.78	52.99	46.56	153.05	100.15	89.06	0.245	0.144	0.136	107.08	71.77	65.63	18.66	12.71	11.09	4.822	3.378	3.360	25.18	17.69	15.53	6.916	4.850	4.852
2018	87.57	54.25	48.12	157.90	102.85	91.90	0.252	0.148	0.140	110.58	73.49	67.39	19.28	13.12	11.62	4.960	3.439	3.417	25.96	18.13	16.04	7.100	4.977	4.960
2019	89.66	56.02	49.14	161.90	105.82	93.90	0.259	0.153	0.143	113.44	75.96	68.97	19.79	13.40	11.82	5.110	3.599	3.511	26.58	18.49	16.43	7.285	5.159	5.106
2020	91.86	57.29	50.32	166.00	108.46	96.37	0.265	0.156	0.147	116.08	77.65	70.95	20.42	13.81	12.18	5.231	3.655	3.611	27.46	19.17	16.75	7.490	5.270	5.247
dG[3]	2.437	1.501	1.317	4.422	2.840	2.538	0.007	0.004	0.004	3.098	2.037	1.862	0.544	0.359	0.322	0.140	0.096	0.093	0.733	0.499	0.448	0.200	0.138	0.136
RE[4]	1.00	0.62	0.54	1.00	0.64	0.57	1.00	0.59	0.54	1.00	0.66	0.60	1.00	0.66	0.59	1.00	0.69	0.67	1.00	0.68	0.61	1.00	0.69	0.68

[1] Relative efficiency to TBV selection. [2] Trait for selection index of Proven Bull. [3] Genetic gain per year. [4] Relative efficiency to TBV selection.
BW12 and BW24 = Body weight at age of 12 and 24 months, ADG = Average daily gain tested from 6 to 12 months, CWT = Carcass weight at finish (24 months), CLMA = Carcass LMA, CMS = Carcass marbling score, ULMA = Ultrasound longissimus muscle area, UMS = Ultrasound marbling score, TBV = True breeding value, EBV = Estimated breeding value, PH = Phenotypic value.
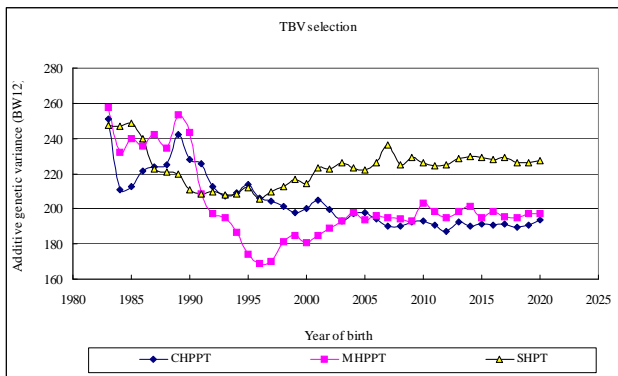
<Trend of additive genetic variance>

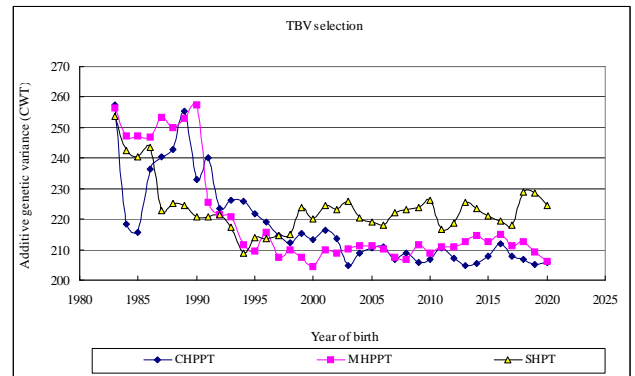**Figure TBV-1.** Change of additive genetic variance of BW12 in TBV selection population.

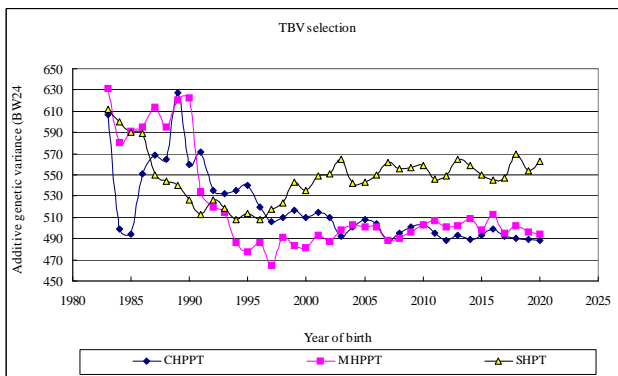**Figure TBV-4.** Change of additive genetic variance of CWT in TBV selection population.

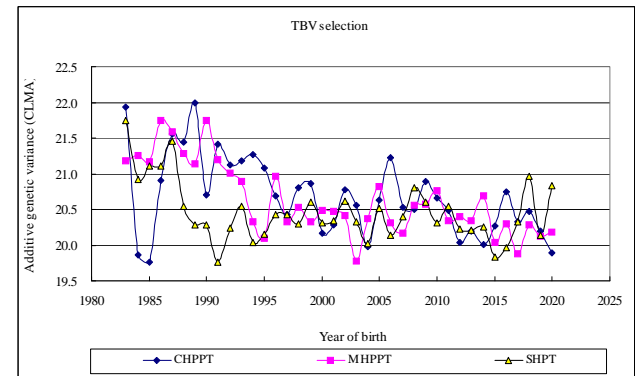**Figure TBV-2.** Change of additive genetic variance of BW24 in TBV selection population.

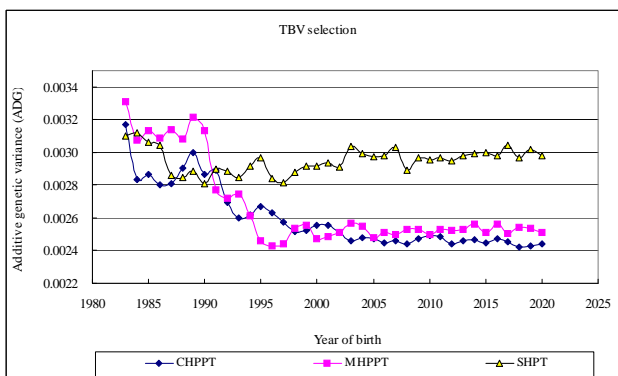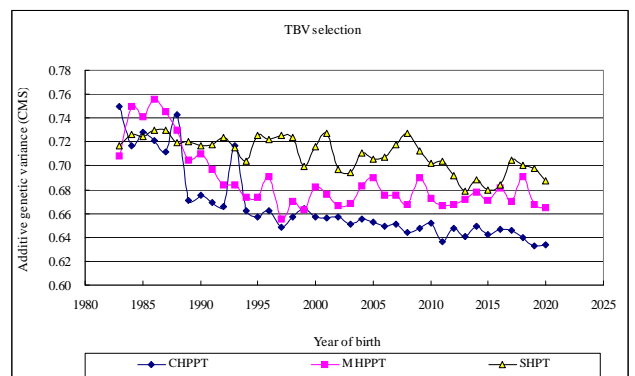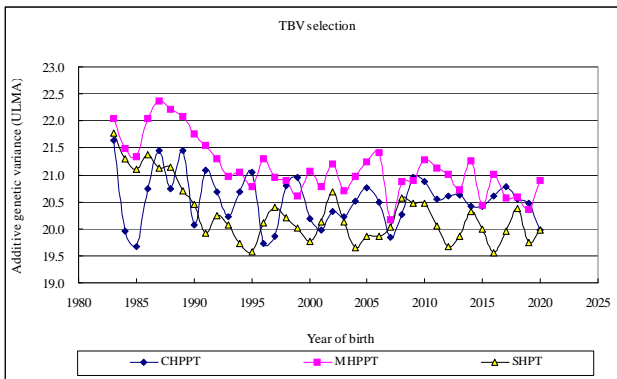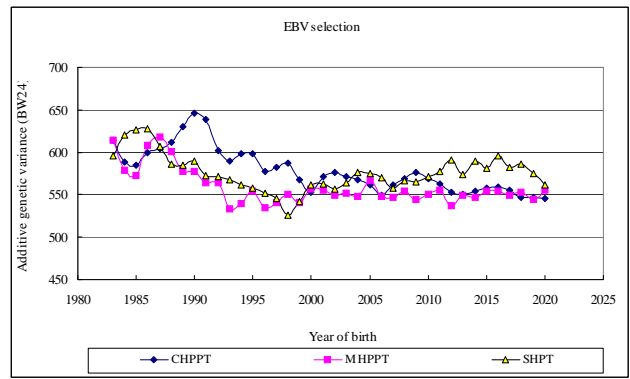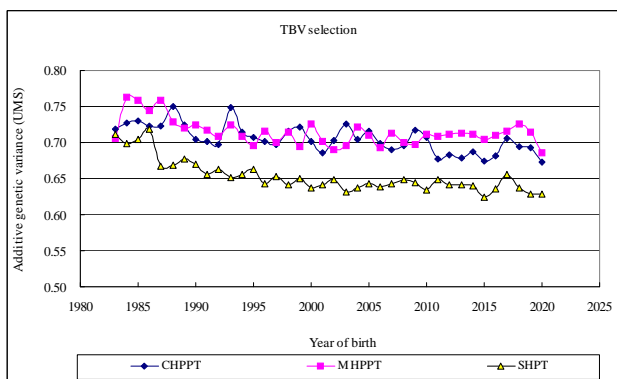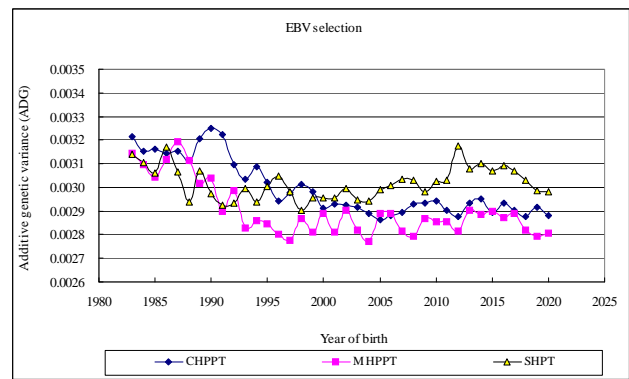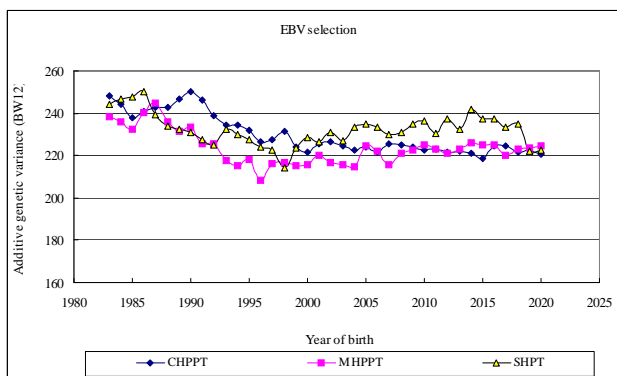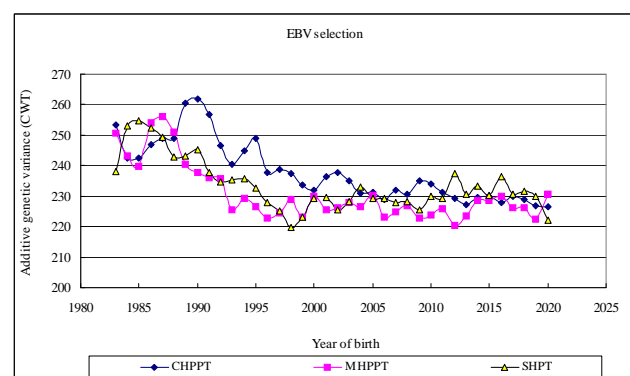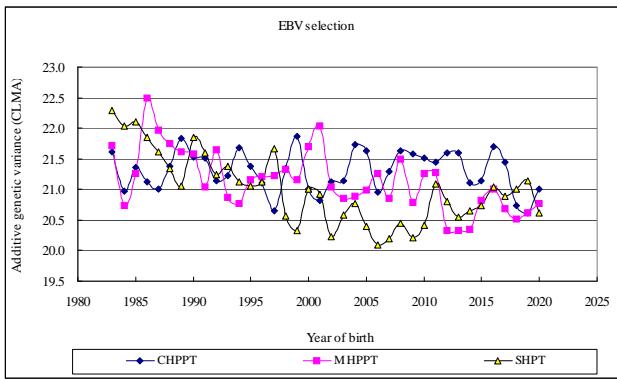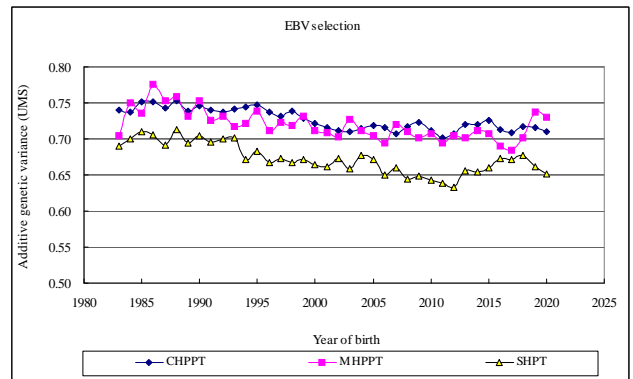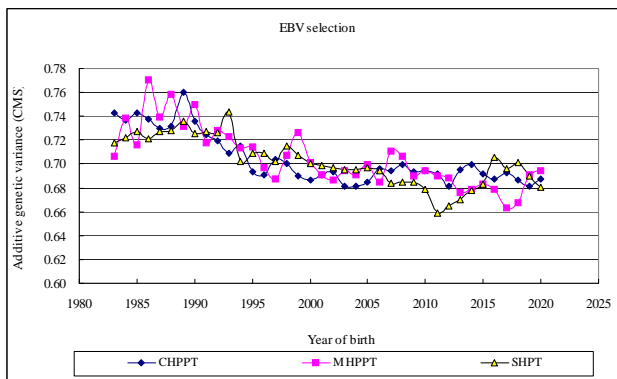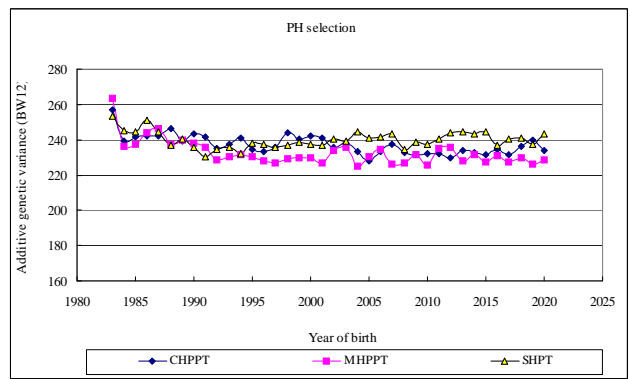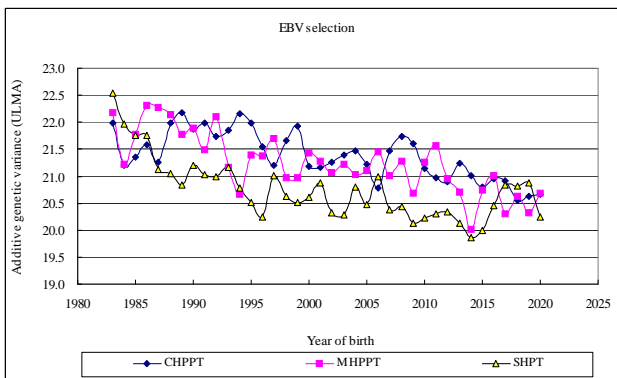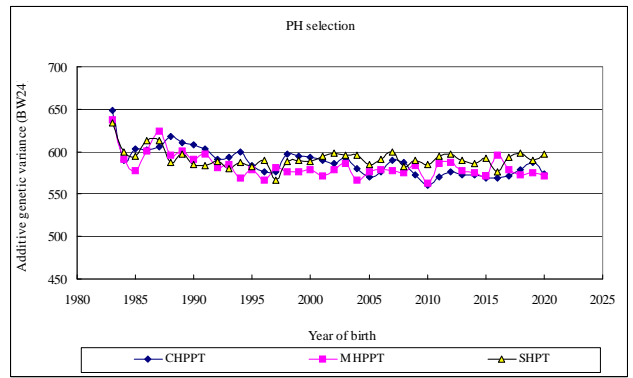**Figure TBV-5.** Change of additive genetic variance of CLMA in TBV selection population.

Figure TBV-3. Change of additive genetic variance of ADG in TBV selection population.

Figure TBV-6. Change of additive genetic variance of CMS in TBV selection population.

Figure TBV-7. Change of additive genetic variance of ULMA in TBV selection population

Figure EBV-2. Change of additive genetic variance of BW24 in EBV selection population
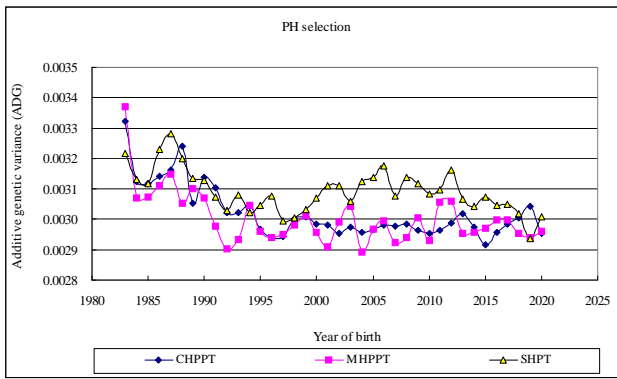

Figure TBV-8. Change of additive genetic variance of UMS in TBV selection population.

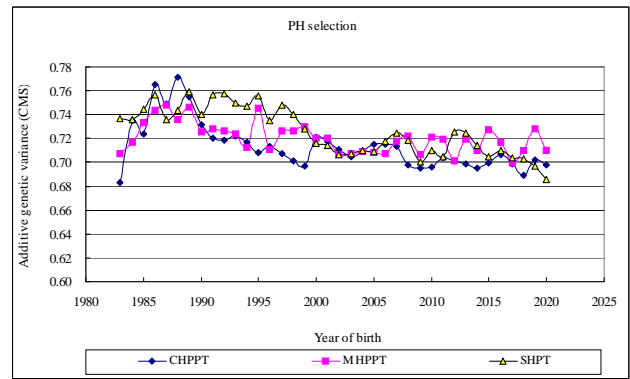**Figure EBV-3.** Change of additive genetic variance of ADG in EBV selection population.

Figure EBV-1. Change of additive genetic variance of BW12 in EBV selection population.

Figure EBV-4. Change of additive genetic variance of CWT in EBV selection population.

Figure EBV-5. Change of additive genetic variance of CLMA in EBV selection population.

Figure EBV-8. Change of additive genetic variance of UMS in EBV selection population.

Figure EBV-6. Change of additive genetic variance of CMS in EBV selection population.

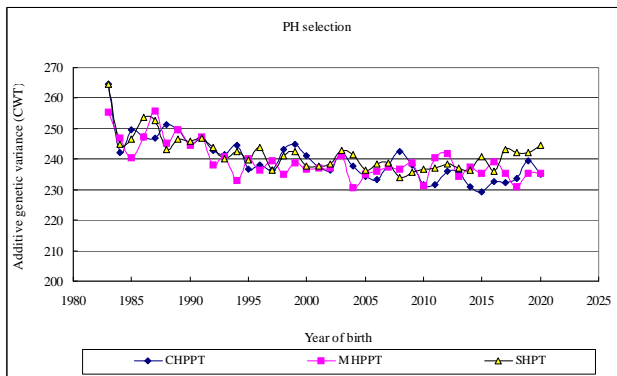**Figure PH-1.** Change of additive genetic variance of BW12 in PH selection population.

Figure EBV-7. Change of additive genetic variance of ULMA in EBV selection population.

Figure PH-2. Change of additive genetic variance of BW24 in PH selection population.

Figure PH-3. Change of additive genetic variance of ADG in PH selection population

Figure PH-6. Change of additive genetic variance of CMS in PH selection population.

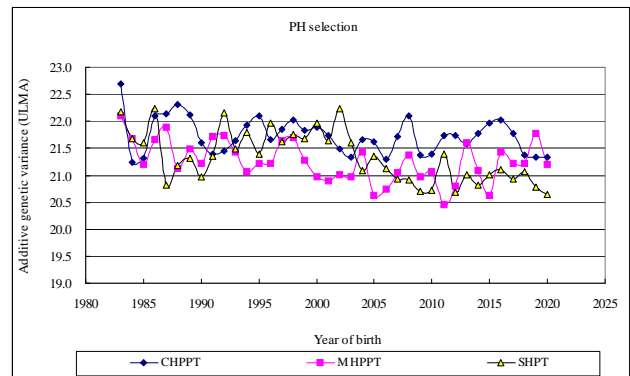**Figure PH-4.** Change of additive genetic variance of CWT in PH selection population

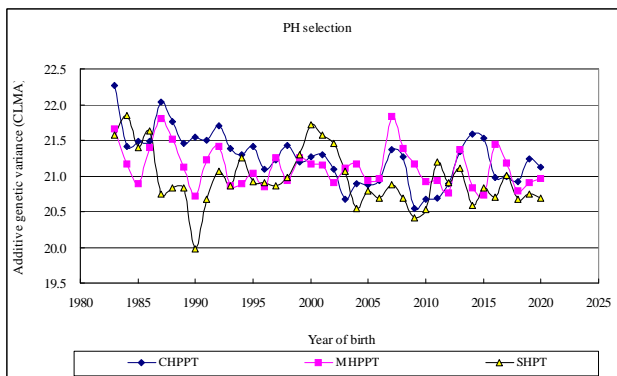**Figure PH-7.** Change of additive genetic variance of ULMA in PH selection population.

Figure PH-5. Change of additive genetic variance of CLMA in PH selection population.
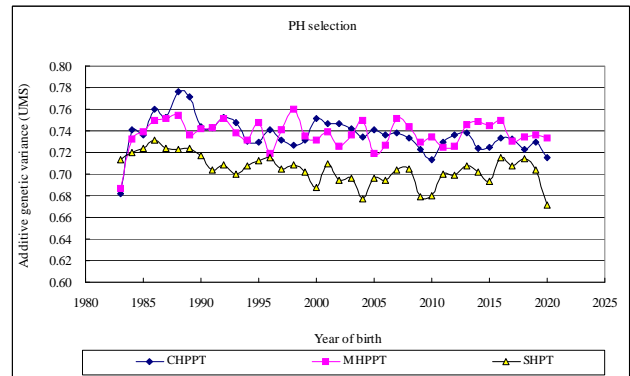

Figure PH-8. Change of additive genetic variance of UMS in PH selection population.