

Genetic Advantage of Three Sub-Populations under Genetic Parameters of Realistic Traits and Fluctuated Breeding Objectives

Takuro Oikawa, Hiroyoshi Matsui and Katsunori Sato

(Field Science Center)

Breeding efficiency was compared among three population schemes: a single population, a population with two sub-populations and a population with three sub-populations when sets of realistic genetic parameters were assumed, and when breeding objectives were changed in the middle of selection program. A simulation experiment of selection was carried out for 10 generations with 20 replications each by comparing average breeding values and inbreeding coefficients among the three population schemes. Genetic gain of growth trait was the largest, then that of meat quality trait was the second largest, and that of reproductive trait was the smallest. The amount of the genetic gain was dependent on their genetic variance. Among the three population schemes, the single population scheme had similar genetic level with the other two schemes under a selection with same economic weights for the traits, however, the multiple sub-populations scheme had the highest genetic level after crossbreeding between sub-populations when inbreeding depression was assumed. The population scheme with three sub-populations can enjoy full advantage of heterosis when different economic weights were applied to the traits. The change of breeding objective made impact on genetic gain of the population scheme when different economic weights were applied to the traits, where the population scheme with three sub-populations had higher genetic gain than the other population schemes.

Key words : Computer simulation, Selection, Crossbreeding, Population structure, Breeding objective

Introduction

In order to balance genetic response and genetic diversity, three approaches are possible: 1) a biased selection criterion, 2) a combined selection criterion of both genetic values and an (predicted) inbreeding coefficient, 3) a modified population structure¹⁾. Modification of population structure in the selected population has been investigated using computer simulation approach. Our previous studies²⁻⁴⁾ revealed that a single population scheme had better genetic response and less progress of inbreeding than a multiple sub-population scheme. However, advantage of the multiple sub-population scheme is expected if inbreeding depression within a sub-population is cancelled out by cross breeding among them. This advantage is practically realized if breeding objectives and genetic levels in base population are similar among sub-populations within a population scheme. The study of a population scheme with three sub-populations suggested that it is potentially an appropriate population scheme if breed-

ing program includes a trait of reproductive performance. The aims of this study were to compare population schemes with/without sub-populations if traits in interest are growth performance, meat quality and reproductive performance and to examine the effects of future change of breeding objective on the population schemes.

Materials And Methods

Population scheme

Three population schemes in this study are presented in Table 1. Dam/sire ratio was 20 in each population scheme with the effective population size being around 100. Computer simulation of selection experiments based on different population schemes, economic weights and selection policies were evaluated by average genetic level of a population scheme at 10th generation of the selection and subsequent cross-

breeding between the sub-populations. The coefficient of inbreeding (CIB) was computed with the tabular method⁵⁾ from pedigree information recorded during a simulation.

Generation of a record

Three traits for genetic improvement were assumed to be growth trait (GRTH), meat quality trait (MEAT) and reproductive trait (REPR). The genetic parameters of the traits were taken from averages of post-weaning gain, lean meat percentage and ease of birth in review articles^{6,7)}. Table 2 presents these heritabilities and genetic correlations for the traits in the selection experiments. The REPR records of male animals were assumed to be phenotypic averages of their six half-sib females. The phenotype of MEAT was assumed to be estimated on an individual animal by live measuring technique. Each trait comprises 36 unlinked loci with a pair of alleles in each locus. The simulation method assumed an additive gene action for each allele in the simulation. The initial gene frequency in each locus was 0.5. Genotypic value in a locus was assigned according to the given genetic variance, while residual variance of the traits was fixed at 1.0. Genetic correlation between two traits was assumed to be caused by pleiotropic effect of a gene on them. The proportion of genes with pleiotropic effect for a trait was determined according to the genetic correlation between traits.

Table 1 The number of factors in the three population schemes

Item	Population scheme		
	POP1	POP2	POP3
Sub-populations	1	2	3
Sires per a sub-population	30	15	10
Dams per a sub-population	600	300	200
Offspring per a sub-population	1,200	600	400
Traits of interest	3	3	3

Table 2 Genetic parameters¹⁾ assumed for the traits²⁾ in the simulation

	GRTH	MEAT	REPR
GRTH	0.40	-0.03	-0.34
MEAT		0.35	-0.18
REPR			0.16

¹⁾Heritabilities on diagonal and genetic correlations above diagonal.

²⁾GRTH: growth, MEAT: meat quality, REPR: reproductive performance.

Selection experiment

The total number of animals was the same in the population schemes; 30 sires and 600 dams during the simulation. The number of progeny for each mating was two—a male and a female animal; thus 1,200 offspring in total. For the next generation, thirty male offspring was selected as sires from 600 male offspring by their indices, whereas selection of dams was random.

Random mating was performed among animals whereas sib mating was avoided. A genotype of offspring was formed by two alleles segregated from its sire and dam. All loci were assumed to be unlinked in the simulation. Breeding values of the offspring were computed by summation of genotypic values over all loci. A phenotypic value of the animal was then formed by the breeding value and a residual effect (e) generated assuming that it followed normal distribution such as $e \sim N(0, 1)$. The discrete generation in the selection experiment was designed to simplify the simulation model.

The selection was conducted by a selection index⁸⁾ based on three traits. Either same or different selection indices were applied to each sub-population in POP2 and POP3. Economic weights applied to the indices are summarized in Table 3. In terms of selection objectives, this study was composed of two breeding experiments; a selection based on a consistent objective (Experiment I) and a selection based on variable objectives (Experiment II). The former applied the same economic weight (Phase I weight) to the selection index throughout 10 generations, whereas, in the later, the economic weight was changed from a Phase I weight to a Phase II weight at the 6th generation. During Phase I, the same economic weights were applied for all the traits in Eco1 whereas different weights were applied for each sub-population in Eco2. The economic weight in Phase II was assumed to place larger weight on MEAT because improvement of meat quality tends to be a primary interest once improvement of meat quantity reaches a satisfactory level.

Results And Discussion

Experiment I

Figure 1 presents average genetic values of the three population schemes under Eco1 and Eco2 when the economic weights of Phase I were applied to the traits in the index throughout the selection experiment. The genetic values were similar among the population schemes within each trait under Eco1. Largest genetic gain was observed in GRTH, then in

Table 3 Economic weights of three traits for the three population schemes in two different phases

Scheme ¹⁾	Weight	Phase	Sub-population 1			Sub-population 2			Sub-population 3		
			GRTH	MEAT	REPR	GRTH	MEAT	REPR	GRTH	MEAT	REPR
POP1	Eco1	I	1	1	1	—	—	—	—	—	—
		II	1	2	1	—	—	—	—	—	—
POP2	Eco2	I	1	1	1	—	—	—	—	—	—
		II	1	2	1	—	—	—	—	—	—
POP2	Eco1	I	1	1	1	1	1	1	—	—	—
		II	1	2	1	1	2	1	—	—	—
POP3	Eco2	I	3	2	1	1	2	3	—	—	—
		II	1	2	1	1	2	1	—	—	—
POP3	Eco1	I	1	1	1	1	1	1	1	1	1
		II	1	2	1	1	2	1	1	2	1
POP3	Eco2	I	2	1	1	1	2	1	1	1	2
		II	1	2	1	1	2	1	1	2	1

¹⁾POP2 consists of two sub-populations, and POP3 consists of three sub-populations.

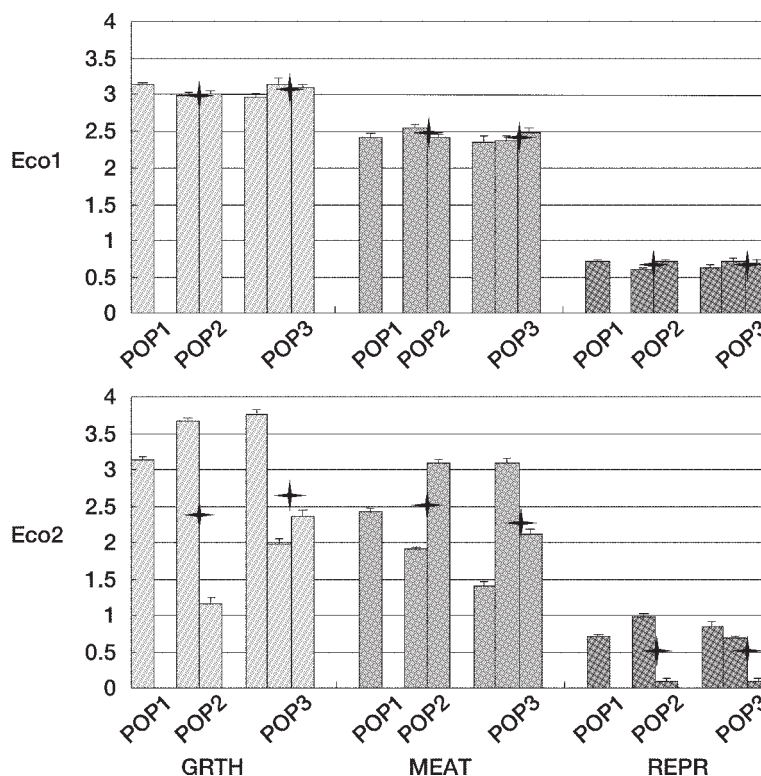


Fig. 1 Average breeding values and SEs of the three population schemes (constant breeding objectives) at the 10th generation.

1) Averages of the sub-populations are indicated by solid stars for POP2 and POP3.

MEAT (20% less than GRTH), and the smallest genetic gain was observed in REPR. This result reflected the genetic variance of the traits because genetic gain is dependent on selection intensity, accuracy of selection and genetic standard deviation according to the standard expression of selection response¹⁾.

In Eco2, the first sub-populations in POP2 and POP3 showed the highest genetic values in GRTH, whereas the highest values were observed in the second sub-populations in MEAT. The average genetic values in POP2 and POP3 were lower than POP1 in GRTH but they were similar to POP1 in MEAT. In REPR, the last sub-populations showed the smallest

loss in genetic value (higher value indicates higher loss in genetic level) and the average genetic loss in POP2 and POP3 were lower than POP1. The lower genetic loss in POP2 and POP3 seemed to be caused by the same reason as with the low genetic gains in the other traits.

Table 4 presents averages and standard errors of CIB at the 10th generation for each of the population schemes. Highest CIB was estimated for POP3, medium for POP2, and lowest CIB was observed in POP1. The increases of CIB from POP1 to POP2 and from POP2 to POP3 were close to 4%. The difference in the economic weight has little effect on the progress of inbreeding. Thus the CIB level was different among the population schemes and inbreeding depression is the largest factor which lowers population mean in a selected population⁹⁾.

The benefit of multiple sub-populations scheme is associated with crossbreeding between sub-populations followed by selection^{2,10)}. So we evaluated the population schemes when crossbreeding was incorporated into the breeding system. The amount of inbreeding depression was referred as average values in literatures. One value reviewed in a literature¹¹⁾ indicated the average inbreeding depression to be 2.5% of phenotypic SD. More recent research¹²⁾ used a range of inbreeding depression from 2.5% to 10.0% of

phenotypic SD per 1.0% increase of the coefficient of inbreeding. Other research⁹⁾ used 5.0% of the phenotypic SD as a value of inbreeding depression in their simulation study. In this study, genetic level after crossbreeding was compared, assuming inbreeding depressions of 3.0% and 5.0% of the phenotypic SD.

Table 5 presents deviation of average genetic level of POP1 from that of POP2 or POP3 after crossbreeding between the sub-populations. When no inbreeding depression was assumed, the genetic level of POP1 was similar to the other population schemes under Eco1. Looking at an individual trait, the genetic level of REPR in the schemes with multiple sub-populations was slightly higher than the single population scheme.

When 3% of inbreeding depression was assumed, the average levels in POP2 and POP3 were higher than that in POP1. The similar averages of POP2 and POP3 are not practically applicable because only a two-way terminal cross is possible in POP2. In order to realize heterosis in REPR of POP2, criss cross is necessary in POP2, where heterosis will be one third of full heterosis in direct genetic effect and two thirds for maternal genetic effect¹³⁾. Then the advantage of POP2 reduced to -0.08 because of inbreeding depression in the third trait, REPR. Thus the advantage of POP3 was larger than POP2 after considering this restriction. When 5% inbreeding depression was assumed, the advantage of the schemes with multiple sub-populations was larger. Thus the advantage of POP3 was suggested among the population schemes.

With Eco2, the average genetic levels of the schemes with multiple sub-populations were equal or smaller than POP1 under the assumption of the inbreeding depression less than 3%. Theoretical research¹⁴⁾ concluded that the average index should be applied for concurrent selection when breeding objectives were varied among sub-populations and moderately correlated. Our result is consistent with their

Table 4 Coefficient of inbreeding (mean%±SE) after the 10th generation of selection (constant breeding objective)

Simulation	Population scheme ¹⁾		
	POP1	POP2	POP3
Eco1	4.22±0.04	8.19±0.10	12.27±0.17
Eco2	4.22±0.04	8.35±0.12	11.77±0.16

¹⁾The coefficient of inbreeding within a simulation was significantly ($P<0.01$) different among the population schemes.

Table 5 Advantages¹⁾ of POP 1 in average genetic levels after crossbreeding between sub-populations of POP 2 or POP 3 (constant breeding objective)

Simulation	Advantage	Inbreeding depression (Percentage in SD unit)											
		0%				3%				5%			
		GRTH	MEAT	REPR	Mean	GRTH	MEAT	REPR	Mean	GRTH	MEAT	REPR	Mean
Eco1	POP1-POP3	0.06	0.03	-0.04	0.02	-0.10	-0.13	-0.18	-0.14	-0.21	-0.23	-0.27	-0.24
	POP1-POP2	0.13	-0.06	-0.06	0.0	-0.03	-0.22	-0.20	-0.15	-0.14	-0.32	-0.29	-0.25
								<u>-0.08</u>					<u>-0.15</u>
Eco2	POP1-POP3	0.43	0.22	-0.18	0.16	0.27	0.06	-0.32	0.0	0.16	-0.04	-0.41	-0.10
	POP1-POP2	0.72	-0.07	-0.18	0.16	0.56	-0.23	-0.32	0.0	0.45	-0.33	-0.41	-0.10
									<u>0.11</u>				<u>0.04</u>

¹⁾The underlined values indicate the advantage of POP1 over POP2 when one of the traits is assumed to be a trait related to the dam's reproductive performance from which POP2 realizes no benefit of the crossbreeding between the two sub-populations.

conclusion. When 5% of inbreeding depression was assumed, POP3 showed genetic values higher than POP1. Thus a single population scheme is a better choice than the multiple sub-population scheme if they have different breeding criteria. This result is consistent with our previous report^{2,4)} in which genetic properties of the sub-populations were same.

Experiment II

Figure 2 presents average genetic values under a situation where the breeding objective was changed during the selection experiment. The difference in the

average genetic value was negligible among the population schemes under Eco1. The difference among the sub-populations was also small. This result was similar to that in Experiment I. Genetic gain of MEAT was similar to GRTH under Eco1 because greater weight on MEAT in Phase II seemed to cause greater genetic gains of MEAT in this experiment. The average genetic gain of REPR was similar to that in the Experiment I.

Under Eco2, POP1 showed higher average genetic value than POP2 and POP3 for GRTH, similar value

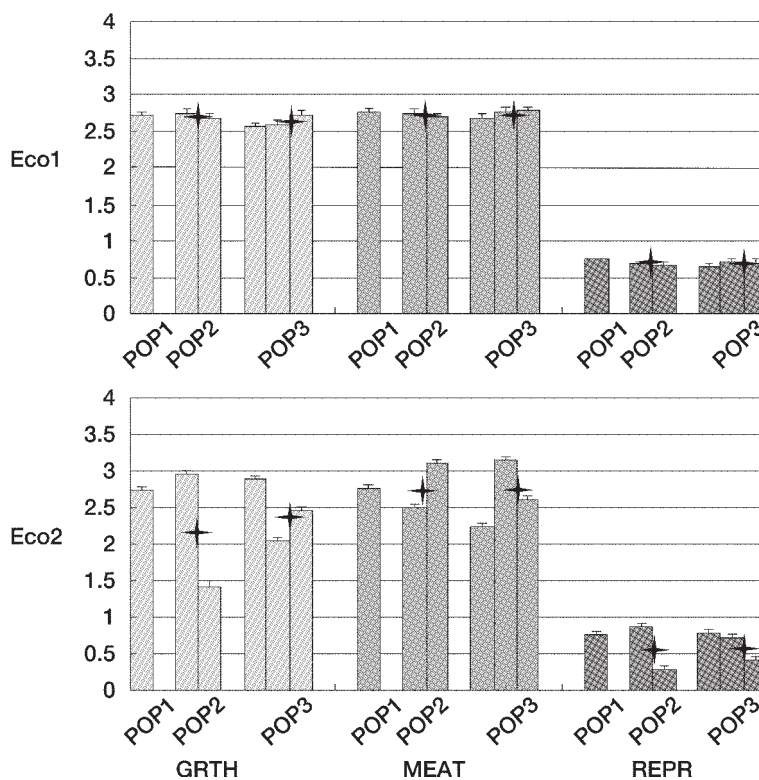


Fig. 2 Average breeding values and SEs of the three population schemes (fluctuated breeding objectives) at the 10th generation.

1) Averages of the sub-populations are indicated by solid stars for POP2 and POP3.

Table 6 Advantages¹⁾ of POP1 in average genetic levels after crossbreeding between sub-populations of POP2 or POP3 (fluctuated breeding objectives)

Simulation	Advantage	Inbreeding depression (Percentage in SD unit)											
		0%				3%				5%			
		GRTH	MEAT	REPR	Mean	GRTH	MEAT	REPR	Mean	GRTH	MEAT	REPR	Mean
Eco1	POP1-POP3	0.11	0.03	-0.07	0.02	-0.05	-0.13	-0.21	-0.13	-0.16	-0.24	-0.31	-0.24
	POP1-POP2	0.02	0.05	-0.07	0.0	-0.14	-0.11	-0.21	-0.15	-0.25	-0.22	-0.31	-0.26
									<u>-0.08</u>				<u>-0.16</u>
Eco2	POP1-POP3	0.27	0.10	-0.12	0.08	0.11	-0.06	-0.26	-0.07	-0.0	-0.17	-0.36	-0.18
	POP1-POP2	0.56	-0.04	-0.19	0.11	0.39	-0.20	-0.33	-0.05	0.28	-0.31	-0.43	-0.15
									0.06				<u>-0.01</u>

¹⁾The underlined values indicate the advantage of POP1 over POP2 when one of the traits is assumed to be a trait related to the dam's reproductive performance from which POP2 realizes no benefit of the crossbreeding between the two sub-populations.

to them for MEAT and lower value than them for REPR. These results were the same tendency as in Experiment I but the difference of the averages between POP1 and multiple sub-populations schemes was smaller than Experiment I. Thus the change of breeding objectives in the middle of the selection program had an effect to reduce the differences among the population schemes.

Average CIB in Experiment II showed similar results as in experiment I. The CIBs (%) in this experiment were around 4.3 in POP1, 8.3 in POP2 and 12.0 in POP3. Thus the change of breeding objective had no effect on the level of CIB. Table 6 presents deviations of genetic level of POP1 from that of POP2 or POP3 after crossbreeding between sub-populations was assumed. Under Eco1, the results of this experiment were similar to the results in Experiment I. When no inbreeding depression was assumed, the difference in genetic levels of the three population schemes was small. Whereas advantage of the multiple sub-populations schemes was observed when either 3% or 5% of inbreeding depression was assumed. Among the multiple sub-populations schemes, POP3 showed higher genetic level than POP2 because of the heterosis in REPR as described above.

Under Eco2, the genetic level in POP1 was higher than POP2 and POP3 when no inbreeding depression was assumed, however the difference was less than Experiment I. The deviation in REPR showed that genetic levels of the multiple sub-populations schemes were higher than POP1. Comparing between the multiple sub-populations schemes, POP3 showed higher genetic level under the situation with inbreeding depression of 3%. This result was due to the high genetic level of REPR in POP3. The superiority of POP3 was more apparent under the assumption of inbreeding depression of 5%. Thus, the population scheme with three sub-populations seemed to be superior to single population scheme even under the situation where every sub-population has its own breeding objective if the inbreeding depression is expected for traits in interest, and the breeding objective was changed in the middle of the breeding system.

The change of breeding objective during the selection program caused different effects on the genetic levels of the population schemes depending on the type of economic weight. Under Eco1, the change of breeding objective had no effect on the comparison of the population schemes. The advantage of the multiple sub-populations schemes is due to heterosis by crossing between sub-populations. Under Eco2, POP3 showed higher genetic level after crossing because the

superiority of POP1 in the traits with smaller economic weight in Phase II was reduced compared with Experiment I, whereas the genetic values of the multiple sub-populations schemes and also the difference in CIB among the population schemes stayed at similar levels. When the breeding objective is expected to be changed in future, the population scheme with three sub-populations seems to be superior to the other population schemes.

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実際の遺伝的パラメータ，育種目標の変更を仮定した場合での3集団モデルの遺伝的有利性

及川 卓郎・松井 宏吉・佐藤 勝紀

(山陽圏フィールド科学センター)

実際の遺伝的パラメータ，選抜の途中で育種目標の変更を仮定した場合における育種効率を3つの集団計画（1集団計画，2分集団計画，3分集団計画）間で比較検討した。選抜期間が10世代のシミュレーション実験を各実験区で20回繰り返して，遺伝的改良量と近交係数を比較した。成長形質の改良量が最も大きく，次いで肉質形質，繁殖形質の順であった。これらの順番は遺伝的分散の大きさに依存していた。これら3つの集団計画間で1集団計画は，同じ経済的加重付けを3形質に対して行ったとき，他の2つの計画と同様の遺伝的水準を示した。しかし近交退化を仮定すると，交雑後，複数集団計画は最も高い遺伝的水準を示した。3つの形質に異なる経済的加重付けを行った場合には3集団計画が最もヘテロシス効果を利用していた。各形質に異なる経済的加重付けを行った場合，選抜途中における育種目標の変更は集団計画の遺伝的改良量に大きく影響した。そしてそこでは，3集団計画が他の計画に比較して高い改良量を記録した。