

Comparison of Breeding System Between Single Population and Two Sub-population Scheme by Computer Simulation

I. Equal genetic level for Sub-populations

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ABSTRACT : Breeding efficiency was investigated to reveal crucial factors for constructing effective breeding system with subdivided populations under equal genetic level. Simulation study of selection experiment was performed for 20 generations with 20 replications each, comparing average breeding values and inbreeding coefficients between the two breeding systems; single population scheme and two population scheme, each of which had the same genetic parameters. Genetic correlations (-0.5 to 0.5) were assumed to be caused only by pleiotropic effect of a gene. Phenotypes of the two traits generated by polygenic effect with additive 36 loci and residuals distributed normally were selected by two traits selection index procedure. Comparing between the single population scheme and the two population scheme, the single population scheme showed higher

genetic gain with lower inbreeding coefficient. This result was confirmed particularly for the situation of high selection intensity, high heritability and high degree of unevenness for economic weight.

Genetic correlations in the single population scheme were significantly lower than the two population scheme when initial genetic correlation was negative.

When terminal crossbreeding for the two population scheme is taken into account, superiority of the two population scheme was suggested. The terminal crossbreeding was effective under the situation of long term selection, existence of moderate inbreeding depression and use of less extreme economic weight.

(Key Words: Simulation, Selection, Crossbreeding, Population Structure, Genetic Level)

INTRODUCTION

A long term objective of animal breeding is not only to achieve high genetic gain but also to keep large genetic variability. Breeding population of beef cattle tends to reduce its population size because of the popularity of AI and crossbreeding for commercial production. Whereas beef production system by pure breeding is common in Japanese Black (Wagyu) cattle because it has a characteristic of high marbled beef. Gama and Smith (1993) indicated that inbreeding levels have impact on the selection program particularly for pure breeds. Whereas, loss of genetic variability is greatly concerned because new technologies such as animal model BLUP (Henderson 1973, Quaas and Pollak 1980) and ET, in addition to the AI, are all expected to accelerate the progress toward genetic uniformity. Quinton et al. (1992) confirmed that selection on BLUP is not necessarily optimum selection criterion when genetic gain is compared under the same level of inbreeding. Then Smith

and Quinton (1993) studied the effect of subdivision of population on selection efficiency and concluded that selection with single line is superior to selection with sublines under restrictions of same level of inbreeding and testing facilities. When the base population was subdivided into many sub-populations, the initial genetic variability among animals in a population can be regarded as being restored as genetic variability among sub-populations after many generations of mating (Falconer 1989) although the theory will be satisfied only under ideal situation. In this study, genetic gain and progress of inbreeding were compared between breeding systems for subdivided populations under equal genetic level to reveal crucial factors for breeding structure.

MATERIALS AND METHODS

Population structure

Parameters for the population structure is summarized in table 1. The number of selected sires, heritability and genetic correlation were varied in the simulation. The

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genetic gain was compared between single population scheme (POP1) and two population scheme (POP2). The breeding plan in the former was applied to the whole population by a selection index. While the latter was designed so that a population can be divided into two sub-populations. Selection was conducted for each sub-population under the specific breeding plan through the selection index (Hazel 1943). This simple selection method is appropriate to study basic act of the model. Initial genetic level (average breeding value) of the two sub-populations in POP2 was same throughout this simulation. Evaluation of the scheme was done by genetic gain, genetic correlation and inbreeding coefficient. The inbreeding coefficient was calculated according to Tier et al. (1990). This inbreeding coefficient was not involved in the model but the effect of inbreeding depression was discussed referring to the inbreeding coefficient.

Table 1. Parameters for the base and alternative conditions representing population structure

	Base	Alternatives
No. of progeny	400	—
No. of dams	100	—
No. of sires	20	4, 10
No. of populations	1	2
No. of traits	2	—
No. of loci	36	—
Gene frequency	0.5	—
Heritability	0.3	0.1, 0.5
Genetic correlation	0.0	-0.5, -0.25, 0.25, 0.5

Traits

The number of traits under selection was two. The two traits in the simulation were generated by polygenic model, where animal's genetic value was determined as a sum of additive genetic effect of a gene. Each trait was assumed to be comprised of unlinked 36 loci with a pair of allele each. Additive genetic effect was only taken into account in this study. Initial gene frequency was 0.5 for each locus. Genetic correlation between the two traits was assumed to be caused by pleiotropic effect of a gene. The genetic correlation was varied such as -0.50, -0.25, 0.0, +0.25 and +0.50.

Initial variances in the populations were 0.43 for additive genetic effect and 1.0 for residual effect corresponding to heritability of 0.3. Let "A" and "a" be a pair of allele in a particular polygenic locus, then genotypic value of "AA", "Aa" and "aa" are 0.1546, 0.0 and -0.1546, respectively. Then this additive genetic

effect was changed according to the heritability from 0.1 to 0.5, whereas the residuals were assumed to follow normal distribution with mean 0 and variance 1.0, because of the residual.

Variance is not affected by the change of additive genetic variance, whereas it is affected under the assumption of constant phenotypic variance.

Selection

The breeding population comprised of 20 sires and 100 dams for each generation. Then the number of selected sires was changed. The number of progeny for each mating was two males and two females, thus 400 offspring were born in total. Then sires and dams for the next generation were selected from 200 males and 200 females. The selected sires and dams were mated at the end of each generation loop. Mating was performed randomly between selected animals. Thus the generation is discrete. Genotypic value of a calf was formed by gametes segregated from its sire and dam, and it was summed for a breeding value. Phenotypic value of a calf was made by the breeding value and a residual effect generated as $e \sim N(0, 1)$. Index selection was carried out for two traits in the simulation.

The economic weights for the two traits in the selection index were assumed to be 1:1, 2:1 and 10:1 for the first trait and second trait. The first trait and second trait in one population are interchangeable because genetic parameters and genetic levels are same between the two traits.

RESULTS AND DISCUSSION

Table 2 presents average breeding values at the generation 20. In the simulation with 20 sires, no significant difference was observed between the average breeding values in POP1 and sub-populations in POP2. If the number of sires is 4 or 10, the breeding values in POP1 were significantly higher than POP2.

The difference in the initial heritability was proportionally related to average breeding values at 20 generation because it parallels with genetic variance under the model with the constant residual variance. The highest breeding values were always obtained for POP1, but significant difference was observed when the heritability was 0.5 in the both traits and 0.1 in the second trait.

Despite the difference of the initial genetic correlation, the breeding values in POP1 were mostly higher than POP2. The only experiment where the breeding value of POP2 was higher than POP1 was the first trait in the genetic correlation of -0.5, however it was statistically

Table 2. Breeding values¹⁾ (mean \pm SD) of animals at generation 20 of simulation

Variables	1st trait			2nd trait		
	POP1	POP2		POP1	POP2	
		A	B		A	B
No. of sires						
20	4.31 \pm 0.14	4.20 \pm 0.26	4.22 \pm 0.25	4.22 \pm 0.19	4.05 \pm 0.38	4.12 \pm 0.30
10	4.39 \pm 0.21 ^a	4.05 \pm 0.32 ^b	4.14 \pm 0.39 ^b	4.45 \pm 0.17 ^a	4.24 \pm 0.25 ^b	4.26 \pm 0.44 ^b
4	4.35 \pm 0.27 ^a	3.65 \pm 0.73 ^b	3.91 \pm 0.58 ^b	4.26 \pm 0.27 ^a	3.75 \pm 0.50 ^b	3.81 \pm 0.69 ^b
h^2						
0.1	1.47 \pm 0.14	1.41 \pm 0.20	1.41 \pm 0.19	1.49 \pm 0.17 ^a	1.39 \pm 0.16 ^{ab}	1.34 \pm 0.26 ^b
0.5	7.44 \pm 0.18 ^a	7.23 \pm 0.24 ^b	7.28 \pm 0.38 ^{ab}	7.56 \pm 0.18 ^a	7.21 \pm 0.24 ^c	7.36 \pm 0.24 ^b
r_g						
-0.5	2.16 \pm 0.32	2.23 \pm 0.40	2.32 \pm 0.65	2.43 \pm 0.34 ^a	2.24 \pm 0.40 ^{ab}	2.10 \pm 0.60 ^b
-0.25	3.36 \pm 0.16	3.25 \pm 0.40	3.30 \pm 0.33	3.42 \pm 0.26 ^a	3.21 \pm 0.33 ^b	3.16 \pm 0.28 ^b
0.25	4.61 \pm 0.17 ^a	4.44 \pm 0.22 ^b	4.54 \pm 0.20 ^{ab}	4.62 \pm 0.12	4.52 \pm 0.24	4.52 \pm 0.25
0.5	4.94 \pm 0.12 ^a	4.83 \pm 0.20 ^b	4.93 \pm 0.16 ^{ab}	4.91 \pm 0.11 ^a	4.83 \pm 0.16 ^{ab}	4.79 \pm 0.18 ^b
Eco. wt. ²⁾						
10:1	5.08 \pm 0.08 ^a	5.02 \pm 0.16 ^{ab}	4.99 \pm 0.13 ^b	1.18 \pm 0.52	1.03 \pm 0.69	1.05 \pm 0.54
2:1	4.71 \pm 0.16	4.62 \pm 0.18	4.61 \pm 0.19	3.64 \pm 0.25 ^a	3.34 \pm 0.41 ^b	3.33 \pm 0.36 ^b

¹⁾ Base condition for the simulation; No. of sires = 20, $h^2 = 0.3$, $r_g = 0.0$, Eco. wt. $\approx 1:1$.

²⁾ The economic weight of "x:y" is "1st trait:2nd trait".

^{a,b} Means within a row and within a trait that do not share common superscript letter differ ($p < 0.05$).

insignificant. The standard deviation was considerably large when the initial genetic correlation was negative. This phenomenon seems to be caused by repulsion association between the traits. The breeding value in POP1 was higher than POP2 in general, however, the significant difference was observed only partially.

The result of average inbreeding coefficients is presented table 3.

If the number of selected sires decreased, the inbreeding coefficient showed large increase, where the inbreeding coefficient in POP1 was significantly lower than POP2. Other variables didn't affect the inbreeding coefficient much, because the inbreeding coefficient is mostly determined by population size.

Table 4 presents the change of genetic correlation at the generation 20 for various initial genetic correlations. The genetic correlation of POP1 was significantly lower than POP2 when initial genetic correlation was negative. This tendency was also observed for the positive initial genetic correlation.

Comparing overall results between POP1 and POP2, advantage of POP1 was suggested because POP1 showed higher genetic gain, while sustaining lower inbreeding coefficient than POP2. These results were consistent with the report by Smith and Quinton (1993). If the results in

Table 3. Inbreeding coefficient¹⁾ (mean \pm SD) at generation 20 of simulation

Variables	POP1	POP2	
		A	B
No. of sires			
20	0.15 \pm 0.01 ^c	0.28 \pm 0.02 ^a	0.26 \pm 0.02 ^b
10	0.27 \pm 0.02 ^b	0.44 \pm 0.04 ^a	0.45 \pm 0.04 ^a
4	0.51 \pm 0.04 ^b	0.72 \pm 0.03 ^a	0.72 \pm 0.02 ^a
h^2			
0.1	0.14 \pm 0.01 ^b	0.25 \pm 0.01 ^a	0.25 \pm 0.01 ^a
0.5	0.15 \pm 0.01 ^b	0.28 \pm 0.02 ^a	0.28 \pm 0.03 ^a
r_g			
-0.5	0.14 \pm 0.01 ^b	0.27 \pm 0.02 ^a	0.26 \pm 0.02 ^a
-0.25	0.15 \pm 0.01 ^b	0.27 \pm 0.02 ^a	0.27 \pm 0.02 ^a
0.25	0.15 \pm 0.01 ^b	0.28 \pm 0.02 ^a	0.28 \pm 0.02 ^a
0.5	0.15 \pm 0.01 ^b	0.28 \pm 0.02 ^a	0.28 \pm 0.02 ^a
Eco. wt. ²⁾			
10:1	0.15 \pm 0.01 ^b	0.27 \pm 0.02 ^a	0.26 \pm 0.02 ^a
2:1	0.15 \pm 0.01 ^b	0.28 \pm 0.02 ^a	0.27 \pm 0.02 ^a

¹⁾ Base condition for the simulation; No. of sires = 20, $h^2 = 0.3$, $r_g = 0.0$, Eco. wt. = 1:1.

²⁾ The economic weight of "x:y" is "1st trait:2nd trait".

^{a,b,c} Means within a row and within a trait that do not share common superscript letter differ ($p < 0.05$).

this study were compared on the same inbreeding level, the superiority of POP1 for genetic gain was even larger.

The increase of selection intensity and higher heritability especially increased the advantage of POP1. By contrast, the advantage of POP2 was observed in the higher genetic correlation when the initial genetic correlation was negative. Other advantage of POP2 is a potential use of crossbreeding between the two sub-populations.

Falconer (1989) reported degree of inbreeding depression per 1% increase of inbreeding coefficient from 0.7% to 5.1% of phenotypic SD, where the average would be approximately 2.5% of SD. While Quinton et al. (1992) examined various degree of inbreeding depression such as from 0.025 to 0.1 SD unit per 1% increase of inbreeding depression in their simulation study. As the phenotypic SD is approximately 1.2 in this study, inbreeding depression of 1%, 3% and 5% correspond with 0.012, 0.036 and 0.06 SD unit, respectively. The 3% inbreeding depression in this study seems to be a center value for inbreeding depression.

The effective population size was summarized to be approximately 100 for several breeds of cattle and horse by Pirchner (1983). However it seems to be reduced in recent situation because of the popularity of AI and other new technologies. It is also recognized that the population under selection reduced the effective population size (Wray et al. 1990, Santiago and Caballero 1995). Nomura (personal communication) estimated approximately 35% smaller effective population size for population under selection. For Japanese Black cattle, the effective population size seems to be reduced considerably because the breeding populations are mostly restricted within a prefectural district. The effective population size in this simulation are 66.7 for 20 sires, 36.4 for 10 sires and 15.4 for 4 sires.

Table 4. Genetic correlations¹⁾ (mean \pm SD) between two traits at generation 20 of simulation

Initial r_g	POP1		POP2	
			A	B
-0.5	-0.761 \pm 0.048 ^b	-0.718 \pm 0.059 ^a	-0.691 \pm 0.062 ^a	
-0.25	-0.495 \pm 0.075 ^b	-0.428 \pm 0.079 ^a	-0.453 \pm 0.075 ^{a,b}	
0.0	-0.055 \pm 0.086	-0.015 \pm 0.138	-0.024 \pm 0.121	
0.25	0.025 \pm 0.093	0.042 \pm 0.107	0.040 \pm 0.131	
0.5	0.103 \pm 0.093	0.094 \pm 0.163	0.160 \pm 0.161	

¹⁾ Base condition for the simulation; No. of sires = 20, $h^2 = 0.3$, Eco. wt. = 1:1.

^{a,b} Means within a row and within a trait that do not share common superscript letter differ ($p < 0.05$).

Table 5 presents advantage of POP1 over POP2 in terms of breeding values and expected phenotypic depression at the generation 20 when percentages of inbreeding depression per 1% increase of inbreeding coefficient were assumed to occur such as 1%, 3% and 5% of phenotypic SD. The largest advantage of POP1 took place under high selection intensity (4 sires), where advantage more than 0.40 SD were obtained in the simulation. While the simulation with 20 sires brought only 0.01 SD advantage for POP1.

Then, taking into account the inbreeding coefficient of POP1 and duplicity of the population in POP2, the overall performance was compared between the breeding systems. POP2 is able to restore its inbreeding depression by crossbreeding between the two sub-populations whereas it is not for POP1. For instance, in the situation on of high selection intensity such as 4 sires, 1% depression is more than the advantage of POP1. Thus, in all the selection intensity, low percentage of inbreeding depression such as 1% of SD seems to be sufficient to offset the genetic advantage of POP1.

When the heritability was low like 0.1, the advantage of POP1 was less than the expected inbreeding depression of 1% SD. Whereas, if the heritability was 0.5, the inbreeding depression of 1% SD is slightly less than the advantage of POP1. Thus, inbreeding depression more than 1% of SD would be necessary to utilize efficacy of crossbreeding for a trait of high heritability.

When the advantage of POP1 is compared among various initial genetic correlations, the advantage of POP1 was uneven between the two traits when the correlation was negative. Even in the simulation with negative initial genetic correlations, crossbreeding within POP2 has a prospective method to offset the advantage of POP1. Thus, 1% of inbreeding depression was suggested to be sufficient for POP2 to offset the advantage of POP1.

The different advantage of POP1 was also observed between the two traits when economic weight is uneven, where larger advantage of POP1 was observed in a less weighted trait. The advantage of POP1 in a more weighted trait was less than a value of 1% SD inbreeding depression.

The advantage of POP1 under the economic weight of 1:1 was compared with POP2 under the uneven economic weight. If the economic weight for the traits are extreme like 10:1, the results were contrasted; very large advantage of POP1 in less weighted trait and vice versa in more weighted trait. In 10:1 economic weight, the advantage of POP1 is more than 1% SD. The discussion was focused mostly on the economic weight 2:1 because it is considered to be close to the real situation.

Table 5. Advantage of POP1 in breeding values over POP2 and expected inbreeding depression (SD unit)

	Advantage of POP1 over POP2		Percentage of depression ¹⁾ on SD basis		
	1st trait	2nd trait	1%	3%	5%
No. of sires					
20	0.084	0.113	0.2	0.5	0.9
10	0.247	0.167	0.3	1.0	1.6
4	0.477	0.401	0.6	1.8	3.0
h ²					
0.1	0.050	0.105	0.2	0.5	0.8
0.5	0.155	0.230	0.2	0.5	0.9
r _g					
-0.5	-0.096	0.217	0.2	0.5	0.8
-0.25	0.071	0.197	0.2	0.5	0.9
0.25	0.100	0.084	0.2	0.5	0.9
0.5	0.050	0.084	0.2	0.5	0.9
Eco. wt. ²⁾					
10:1	0.063	0.117	0.2	0.5	0.9
2:1	0.079	0.255	0.2	0.5	0.9
Comparison with 1:1 ³⁾					
10:1	-0.581	2.659	0.2	0.5	0.9
2:1	-0.255	0.740	0.2	0.5	0.9
Comparison with 1:1 trans-wt. ⁴⁾					
10:1	1.066	1.012	0.2	0.5	0.9
2:1	0.280	0.205	0.2	0.5	0.9

¹⁾Depression in SD unit per increase of 1% inbreeding coefficient.

²⁾The economic weight of "x:y" is "1st trait : 2nd trait".

³⁾Breeding value of POP1 under 1:1 economic weight was compared with POP2 under 10:1 or 2:1 economic weight.

⁴⁾Same as 3), but economic weight for POP2 had a trans-weight, x:y for POP-A and y:x for POP-B.

Suppose two breeding strategies; one is a breeding strategy for single population scheme like POP1 using equal economic weight, 1:1, for two traits. The other is a breeding strategy for two population scheme like POP2 using trans-weight for two traits in the two sub-populations; 2:1 in sub-population A and 1:2 in sub-population B for 'first trait : second trait', thus, specific selection criteria for each sub-population. The result about the advantage of POP1 over POP2 is presented in the last two rows in the table 5. Thus the advantage of POP1 for the first trait and second trait was 0.28 SD and 0.21 SD larger than POP2. If inbreeding depression of 3% is assumed, POP2 was better than POP1. Therefore, as far as these conditions; equal genetic level, moderate inbreeding depression and moderate economic weight are met, the breeding strategy of the two population scheme

with specific breeding criterion was more advantageous than single population scheme, however the margin of the advantage was less than the selection scheme with equal economic weight.

If reproductive trait is assumed for one of the traits under selection, it is known to be a system using complementarity for dam line as discussed by Dickerson (1973). The advantage of 0.255 SD in POP2, in the third row from the last, will be realized by the 2:1 economic weight if the first trait is assumed to be a reproductive trait of female. But this scheme needs additional condition for population structure because inbreeding depression is expected to lower its reproductive performance considerably. So an additional sub-population for dam is needed to restore inbreeding depression and to maximize genetic progress.

During 20 generations of selection, the inbreeding coefficient increased linearly. Whereas the difference of genetic gain between POP1 and POP2 was approximately constant during the selection except for first few generations. Thus the advantage of POP2 will be reduced as the generation of selection shortend. For instance, the amount of inbreeding depression at 10 generations of selection was halved whereas genetic difference between POP1 and POP2 is almost same.

Under the situation of equal genetic level between the sub-populations, simple comparison showed superiority of POP1 in both genetic progress and genetic variability whether or not inbreeding coefficient is taken into account. However, POP2 is equivalent to or superior to POP1 if terminal crossbreeding is assumed. This result was valid under the situation of long term selection, existence of moderate inbreeding depression and less extreme economic weight. Use of specific economic weight for a sub-population was suggested to bring less benefit to the crossbreeding system alone but more potentiality for the breeding system together with use of complementarity for reproductive traits.

In the actual situation where the breeding population was maintained or subsidized by government or public organization like population of beef cattle, dairy cattle or swine in Japan. This fact acts being advantageous for multi-population scheme like POP2 because producers are allowed to be reluctant to the high degree of inbreeding in the breeding populations. This inbreeding coefficient in POP2 can be reduced to zero by crossbreeding in the commercial population. Whereas the inbreeding coefficient of the commercial population is as high as the breeding population in POP1.

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