Comparison of Breeding System Between Single Population and Two Sub-population Scheme by Computer Simulation II. Different genetic level for Sub-populations

T. Oikawa, Y. Matsura and K. Sato Faculty of Agriculture, Okayama University, Okayama City, 700, Japan

ABSTRACT: The effect of genetic diversity in subpopulations on breeding efficiency was examined with
prospect of potential crossbreeding. Simulation study of
selection was performed for 20 generations with 20
replications each, comparing average breeding values and
inbreeding coefficients between the two breeding
systemes; single population scheme and two population
scheme. The different genetic levels were assumed to be
caused by different gene frequencies. Phenotypes of two
traits generated polygenic effect with additive 36 loci and
residuals distributed normally were selected by selection
index procedure. High genetic gain with less inbreeding
was clearly recognized in the single population scheme,

independently of difference in genetic level, economic weight and genetic correlation. Genetic correlation after selection in the single population scheme was lower than the two population scheme. When crossbreeding between the sub-population was taken into account, superiority of the two population scheme was suggested under those restrictions; difference in genetic level is moderate, selection criterion for the two traits is not far from even economic weight, and genetic correlation is positive with low to moderate value. The use of complementarity increased the possibility of the two population scheme.

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

INTRODUCTION

A long term breeding objective is considered to be an accomplishment of optimum genetic improvement while keeping large genetic variability. Smith and Quinton (1993) concluded that selection with single line is superior to selection with sublines under restrictions of the same level inbreeding and testing facilities. In the previous report (Oikawa et al., 1996), it was confirmed that breeding system with subdivided population was justified by the use of terminal crossbreeding under the situation of long term selection, existence of moderate inbreeding depression and use of less extreme economic weight. As many animal breeds have sublines within a breed, the genetic level is more likely to be different among them. Whereas, this genetic diversity seems to be large for Japanese Black (Wagyu) cattle because each regional sub-population was genetically improved independently, especially at the period of breed foundation. Thus the breeds can be regarded as a combined breed by several sub-populations. Nomura and Sasaki (1988) reported genetical inter-relationship within the breed by cluster analysis. In this study, genetic gain

and progress of inbreeding in the subdivided population were examined to clarify the effect of genetic diversity among sub-populations on efficiency of genetic improvement.

MATERIALS AND METHODS

Population structure during selection experiment was compared between single population scheme (POP1) and two population scheme (POP2). The outline of simulation structure is described in the previous study (Oikawa et al., 1996). A brief description of the simulation design is as follows. The number of selected sires was fixed to be 20. Two traits in the simulation were generated by polygenic model with unlinked 36 loci having a pair of allele each with additive genetic effect. Genotypic values in each locus were assumed to be -0.1546, 0.0 and 0.1546 for recessive homozygote, heterozygote and dom inant homozygote, respectively, which corresponded heritability of 0.3 in a control population. The genetic correlation was varied such as -0.50, -0.25, 0.0, +0.25and +0.50. The number of replication is 20.

The genetic level of base population was assumed to be caused by the difference in gene frequency. The gene

¹ Address reprint requests to T. Oikawa. Received August 20, 1996; Accepted December 16, 1996

frequencies of 0.7 and 0.9 were examined in addition to 0.5. The gene frequencies were assumed to be determined such that the two sub-populations in POP2 were able to have distinctive difference in genetic level. For instance, if the gene frequency in one sub-population is f(A), the gene frequency in the other sub-population is accordingly 1-f(A). Thus the gene frequencies in the first trait were varied just as 0.5, 0.7 and 0.9 in sub-population A and 0.5. 0.3 and 0.1 in sub-population B, and vice versa in the second trait. Expected average of breeding values for various gene frequency is presented in table 1.

Table 1. Expected average breeding values in base population

Init. gene	POP 1	POP 2		
frequency	_	1st trait	2nd trait	
0.5	0.0	0.0	0.0	
0.7	0.0	2.23	-2.23	
0.9	0.0	4.45	-4.45	

The gene frequency was uniformly 0.5 for POP1 because the two sub-populations were combined to form a base population in POP1. Thus the genetic variance in POP1 was different from the one in the previous study (Oikawa et al., 1996), althouth the average genetic level

was same.

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 the second trait. The first two economic weights, 1:10 and 1:2 equalizing weight, were expected to be effective for averaging the genetic level of the sub-populations, so less weight on a good trait and more weight on a poor trait, thus the weight has an effect to equalize the difference between sub-populations. In contrast, the other two, 10:1 and 2:1 extending weight, were the weight for extending the difference of the sub-population at base generation, which is placing more weight on a good trait and less weight on a poor trait.

RESULTS AND DISCUSSION

Table 2 presents average breeding values at generation 20 for various initial gene frequencies. The breeding values of POP1 increased as the initial gene frequency becomes higher. Because the base population of POP1 in 0.7 and 0.9 gene frequency were formend by the crossbreeding between the two sub-populations that have different initial gene frequecies, large genetic variance is expected to exist in the early generation because of large extent of linkage disequilibulium that was studied theoretically by Bulmer (1971).

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

Init. gene frequency		1st trait			2nd trait		
	Eco. wt. ²⁾	POP 1	POP 2		POP 1	POP 2	
			A	В		A	В
0.5	1:1	4.31 ± 0.14	4.20 ± 0.26	4.22±0.25	4.22±0.19	4.05±0.38	4.12 ± 0.30
0.7	1:1	$4.80 \pm 0.25^{\rm b}$	5.16 ± 0.20^{a}	$3.80 \pm 0.35^{\circ}$	4.81 ± 0.24^{b}	$3.73 \pm 0.41^{\circ}$	5.10 ± 0.19
0.9	1:1	$8.04 \pm 0.25^{\text{b}}$	8.88±0.15°	3.52 ± 0.90°	8.16±0.29 ^b	$3.48 \pm 0.59^{\circ}$	8.86 ± 0.13
0.7	1:10	_	$3.13\pm0.54^{\circ}$	4.50±0.21 ^b	_	4.51 ± 0.37 ⁶	3.00 ± 0.48
	1:2	_	$4.41 \pm 0.36^{\rm b}$	4.28 ± 0.26^{b}	_	4.17 ± 0.41^{c}	4.57 ± 0.33
	2:1	_	5.52 ± 0.15 ^b	$2.83 \pm 0.48^{\circ}$	_	$2.81 \pm 0.34^{\circ}$	5.56 ± 0.14
	10:1	_	5.91 ± 0.06 ^b	$-0.27 \pm 0.84^{\circ}$	_	$-0.24 \pm 0.82^{\circ}$	5.89 ± 0.08
0.9	1:10	_	7.77 ± 0.44 ^b	4.06±0.53°		4.41 ± 0.53°	7.73 ± 0.46
	1:2	_	8.46 ± 0.25 ^b	4.21 ± 0.82°	_	4.06 ± 0.84°	8.49 ± 0.28
	2:1	-	9.03 ± 0.10^{b}	2.37±0.73°	-	$2.46 \pm 0.60^{\circ}$	9.04 ± 0.08
	10:1	_	9.23 ± 0.04^{b}	$-1.28 \pm 1.40^{\circ}$	_	$-0.91 \pm 1.00^{\circ}$	$9.24 \pm 0.04^{\circ}$

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

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

abe Means within a row and within a trait that do not share common superscript letter differ (p < 0.05).

Values in POP 2 are compared with POP 1 with same gene frequency.

430 OIKAWA ET AL.

The expected linkage disequiliblium after merging the sub-populations in POP1 was 0.16 for gene frequency 0.9 and 0.04 for the gene frequency of 0.7. This linkage disequiliblium disappeared approximately after 6 generations for the frequency of 0.7 and 9 generations for 0.9 according to the way in which genetic variance due to linkage disequiliblium was halved every generation (Pirchner, 1983).

For the gene frequencies of 0.7, the breeding values of POP2 by the use of equalizing weight with 1:10 and 1:2 were similar between the two traits, where the breeding

values of POP2 were lower than POP1 under even economic weight. By the use of extending weight with 2: 1 and 10:1, the breeding values of a trait having more weight in POP2 was higher than POP1, however, vice versa for a trait a less weight.

Table 3 presents results of inbreeding coefficient. The inbreeding coefficients was not affected much by the change of initial genetic level and economic weight for the two traits. The inbreeding coefficient POP1 was slightly higher than one half of the inbreeding coefficient in POP2.

Table 3. Inbreeding coefficient¹⁾ (mean ± SD) of animals in generation 20 of simulation

Init. gene	F	POP 1	PO	P 2
frequency	Eco. wt. ²⁾		A	В
0.5	1:1	0.15 ± 0.01°	0.28 ± 0.02 ^a	0.26±0.02 ^b
0.7	1:1	0.16 ± 0.01^{b}	0.28 ± 0.02^a	$0.28 \pm 0.02^{\circ}$
0.9	1:1	0.16±0.01 ^b	0.29 ± 0.02^{a}	$0.30 \pm 0.02^{\circ}$
0.7	1:10	_	0.28 ± 0.02 ^b	0.29 ± 0.02^{b}
	1:2	_	0.27 ± 0.03^{b}	$0.28 \pm 0.03^{\circ}$
	2:1	_	0.27 ± 0.02^{b}	0.27 ± 0.02^{b}
	10:1	_	0.28 ± 0.02^{b}	0.27 ± 0.02^{b}
0.9	1:10	_	0.29 ± 0.02 ^b	0.28 ± 0.02 ^b
	1:2	_	0.29 ± 0.03^{b}	$0.29 \pm 0.03^{\circ}$
	2:1	-	$0.28\pm0.03^{\text{b}}$	0.28 ± 0.02^{t}
	10:1	_	0.29 ± 0.03^{b}	0.29 ± 0.02^{t}

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

Table 4 presents advantages in breeding values of POP1 over the averages of the sub-populations in POP2 or over the best sub-population of POP2, and percentage of inbreeding depression in phenotypic SD unit. When difference in genetic level exists between the two sub-populations in POP2, advantage of POP1 over average breeding values in POP2 was larger than the situation under equal genetic level.

When the gene frequency was 0.9, advantage of POP1 over the average of POP2 was more than 1.4 SD. Therefore, 3% of inbreeding depression doesn't offset this advantage of POP1. Whereas, for the 0.7 gene frequency, which seems to be more realistic in practice, the advantage of POP1 was 0.27 and 0.33 SD for the first and second trait under even economic weight. The advantage was more than 0.36 SD for moderate economic

weight such as 1:2 or 2:1. Thus the advantage of POP1 under uneven economic weight was larger than even economic weight. For moderate economic weight, the advantage of POP1 is within expected value of inbreeding depression which can be offset by crossbreeding in POP2. Thus these conditions, moderate difference in gene frequency (genetic level) and breeding criterion with moderate weight are necessary to justify the breeding system with subdivided population.

Superiority of POP1 was obvious when initial genetic level is considerably different between the two sub-populations. However the large genetic difference implies that crossbreeding not only offset inbreeding depression but also accompany extensive heterosis effect as Dickerson (1973) illustrated about the performance of inbreds, line crosses and breed crosses. In this simulation,

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

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

Values in POP 2 are compared with POP 1 with same gene frequency.

the genetic level in the base populations is assumed to be resulted only by the difference in gene frequency, although heterosis derived from allelic difference was not taken into account in this study.

Also the advantage of POP1 over the best sub-population in POP2 is presented in table 4. Advantage of POP1 was observed when economic weight is the equalizing weight such as 1:10 and 1:2 in the 0.7 frequency and 1:10 in the 0.9 frequency. When the economic weight is the extending weight, the breeding values in POP2 was higher than POP1, where the difference was more than 0.60 SD.

The utilization of complementarity was considered

under this situation. If one of the traits is assumed to be a reproductive trait of female, the economic weight will be the extending weight with 2:1 weight, where the advantage of the best sub-population in POP2 is approximately 0.6 SD compared with POP1, whereas the disadvantage of POP2 in terms of average of the two traits is 0.5 SD. As these advantage and disadvantage are comparable, inbreeding depression of 0.60 just as observed in 3% of phenotypic SD in POP1 would turn multi-population system into a potential scheme. Thus, for utilizing complementarity, the economic weight should have even weights or moderate extending weight.

Table 4. Advantage¹⁾ of POP1 in breeding values over POP2 and expected inbreeding depression for various gene frequencies (SD unit)

Init. gene frequency	Eco. wt. ²⁾	Advantage of POP1 over the average		Advantage of POP1 over the best		% depression ³⁾ on SD basis
		1st trait	2nd trait	1st trait	2nd trait	3%
0.5	1:1	0.084	0.113	0.092	0.084	0.5
0.7	1:1	0.268	0.330	-0.301	-0.243	0.6
0.9	1:1	1.539	1.664	-0.702	-0.585	0.6
0.7	1:10	0.824	0.882	1.397	1.514	0.6
	1:2	0.380	0.368	0.326	0.201	0.6
	2:1	0.523	0.523	-0.602	-0.627	0.6
	10:1	1.656	1.660	-0.928	<u> </u>	0.6
0.9	1:10	1.777	1.748	0.226	0.360	0.6
	1:2	1.462	1.576	-0.351	-0.276	0.6
	2:1	1.957	2.015	-0.828	-0.736	0.6
	10:1	3.399	3.341	-0.995	-0.903	0.6

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

Table 5 presents breeding values at 20 generation when the initial genetic correlations between the two traits were varied. In POP2, selection was undertaken favoring a trait of higher genetic level by the extending weight of 2:1, while, the economic weight was fixed to be 1:1 in POP1. In POP1, higher breeding values were observed for the increase of the initial genetic correlation. Whereas, in POP2, difference among these genetic correlations was small in a more weighted trait, however it varied more in a less weighted trait.

Table 6 presents the comparisons of inbreeding coefficients and genetic correlations at 20 generations.

Little difference was observed in inbreeding coefficients. The genetic correlation in POP1 was lower than the both sub-populations in POP2. The difference was particularly large when the initial genetic correlation was negative.

Table 7 presents gene frequencies at independent loci. The gene frequencies of the both traits in POP1 were similar, while the gene frequencies in POP2 were different between the two traits because of the different economic weight. The gene frequencies of a more weighted trait in POP2 were higher than POP1, but the average gene frequencies of both traits were lower than POP1.

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

³⁾ Depression in SD unit per increase of 1% inbreeding coefficient.

432 OIKAWA ET AL.

		1st trait	2nd trait			
Initial	POP1 ³⁾ POP2 ⁴)P2 ⁴⁾	POP1	POP2	
$\mathbf{r}_{\mathbf{g}}$		A	В		A	В
-0.5	2.94 ± 0.68 ^b	5.73 ± 0.15°	$-5.19 \pm 0.52^{\circ}$	3.07 ± 0.69 ^b	$-4.92\pm0.45^{\circ}$	5.83±0.13°
-0.25	4.33 ± 0.25^{b}	5.09 ± 0.20^{a}	0.38±0.52°	4.40 ± 0.23^{b}	$0.24 \pm 0.64^{\circ}$	5.09 ± 0.32^a
0.0	4.80 ± 0.25 ^b	5.52 ± 0.15^{a}	$2.83 \pm 0.48^{\circ}$	4.81 ± 0.24^{b}	$2.81 \pm 0.34^{\circ}$	5.56±0.14°
0.25	4.99 ± 0.31^{b}	5.70 ± 0.11^{a}	$3.11 \pm 0.62^{\circ}$	$5.04 \pm 0.17^{\circ}$	$3.12 \pm 0.60^{\circ}$	5.70 ± 0.13^{a}
0.5	5.26 ± 0.27^{b}	5.91 ± 0.07^{a}	2.64 ± 0.44°	5.25 ± 0.30^{b}	$2.57 \pm 0.49^{\circ}$	$5.91 \pm 0.06^{\circ}$

Table 5. Breeding values 0.25 (mean ± SD) for various initial genetic correlations

Table 6. Inbreeding coefficient and genetic correlation^{1,2)} (mean ± SD) for various initial genetic correlations

Initial	POP13)	POP2®					
r_{g}		A	В				
	Inbreeding	Inbreeding coefficient					
-0.5	0.14 ± 0.01^{b}	0.26 ± 0.02^a	0.26 ± 0.02^{a}				
-0.25	0.14 ± 0.01^{b}	$0.27 \pm 0.02^{\circ}$	0.27 ± 0.02^{a}				
0.0	0.16 ± 0.01^{b}	$0.28~\pm~0.02^a$	0.27 ± 0.02^{a}				
0.25	0.15 ± 0.01^{b}	$0.29\ \pm\ 0.02^a$	0.28 ± 0.02^{a}				
0.5	$0.15 \pm 0.01^{\circ}$	0.27 ± 0.02^{b}	0.28 ± 0.02^a				
	Genetic c	orrelaton					
-0.5	-0.977±0.012b	-0.525 ± 0.135^{a}	-0.581 ± 0.086^{a}				
-0.25	-0.793 ± 0.045	-0.468 ± 0.122^a	-0.445 ± 0.100^{4}				
0.0	-0.065 ± 0.089	-0.008 ± 0.091	-0.004 ± 0.114				
0.25	0.006 ± 0.079	0.011 ± 0.137	0.032 ± 0.103				
0.5	0.064 ± 0.088^{b}	0.192 ± 0.121^{a}	0.159 ± 0.115°				

¹⁾ Initial gene frequencies are 0.7 for trait 1 of A and trait 2 of B in POP 2, 0.5 in POP 1.

Table 8 presents summary of comparison between POP1 and POP2 under various initial genetic correlations. When the breeding values of POP1 were compared with the averages of POP2 on phenotypic SD basis, the advantage of POP1 was clearly recognized when the correlation was high with either positive or negative sign. Whereas, comparing with the best sub-population of

POP2, the breeding value of the sub-population was higher than POP1.

Taking into account the complementarity, advantage of POP2 was realized when the initial genetic correlation was positive with low to moderate value becaues the advantage of POP2 observed in the best sub-population is comparable with the disadvantage of POP2 observed in the average of the two traits. Thus only the margin of inbreeding depression POP1 becomes the advantage in POP2. However three population scheme is additionally required to fullfil this prospective, because reproductive traits tend to suffer inbreeding depression more severely.

According to the review article by Koots et al. (1994a) about heritability of beef cattle, weighted average heritabilities of reproductive traits are low in general. At low heritability, the subdivided population was suggested to be superior to single population scheme (Oikawa et al., 1996). Koots et al. (1994b) also reviewed genetic correlations between reproductive traits and growth traits or carcass traits. At present, very few genetic correlations were reported for the reproduction traits except for the relationship between calving ease and birth weight, calving ease and weaning weight (Koots et al., 1994b). Thus the situation with various genetic correlations need to be taken into account.

Consequently, the straight comparison simply indicates that single population scheme has an overall advantage in terms of genetic gain and genetic variability within population whether or not the genetic level of the sub-populations is different. If crossbreeding is assumed for the two population scheme, equal economic weight was advantageous under the existence of moderate genetic difference between sub-populations. Whereas the single population scheme is superior to the subdivided

¹⁾ Initial gene frequencies are 0.7 for trait 1 of A and trait 2 of B in POP2, 0.5 in POP1.

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

³⁾ For POP1, Econmic weight for traits is 1:1.

⁴⁾ For POP2, Econmic weight for traits is 2:1 favouring high frequency genotype.

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

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

³⁾ For POP 1 Economic weight for traits is 1:1.

⁴⁾ For POP 2 Economic weight for traits is 2:1 favouring high frequency genotype.

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

population scheme if the genetic difference is extreme. As most of major breeds have sub populations or sub lines within them, the situation under moderate genetic difference among the sub populations is common in

practice. Thus POP2 scheme can be justifiable in this case. We don't need to consider the situation with large genetic difference because breeding program is mostly undertaken within a breed.

Table 7. Gene frequency^{1, 2)} (mean ± SD) in independent loci for various initial genetic correlations

Initial r _g	-	1st trait			2nd trait		
	POP13)	POP2 ⁴⁾ A B		POP1	PC	P2	
					A	В	
-0.5	0.995 ± 0.003 ^b	0.997±0.003°	$0.109 \pm 0.068^{\circ}$	0.996±0.003b	0.141 ± 0.057°	0.996±0.005°	
-0.25	0.979 ± 0.007^{b}	$0.984 \pm 0.007^{\circ}$	$0.616 \pm 0.047^{\circ}$	0.980 ± 0.006^{b}	$0.601 \pm 0.071^{\circ}$	0.984 ± 0.007^a	
0.0	0.895 ± 0.020^{b}	$0.955 \pm 0.017^{\circ}$	0.733 ± 0.032^{c}	0.896 ± 0.020^{b}	$0.731 \pm 0.030^{\circ}$	$0.958 \pm 0.015^{\circ}$	
0.25	0.885 ± 0.033^{b}	0.962 ± 0.013^a	$0.678 \pm 0.069^{\circ}$	0.891 ± 0.019^{b}	$0.678 \pm 0.066^{\circ}$	0.963 ± 0.012^{a}	
0.5	0.877 ± 0.044^{b}	0.984 ± 0.008^a	$0.447 \pm 0.073^{\circ}$	0.877 ± 0.050^{b}	$0.434 \pm 0.083^{\circ}$	-0.986 ± 0.010^{a}	

¹⁾ Initial gene frequencies are 0.7 for trait 1 of A and trait 2 of B in POP2, 0.5 in POP1.

Table 8. Advantage of POP1 in breeding values over POP2 for various initial genetic correlations (SD unit)

Intial	Advantage of POP	l over the average	Advatage of POP	% depression ²⁾ on SD basis	
r_{g}	1st trait	2nd trait	1st trait	2nd trait	0.3%
-0.5	2.233	2.187	-2.333	-2.308	0.6
-0.25	1.334	1.451	-0.636	-0.577	0.6
0.0	0.523	0.523	-0.602	-0.627	0.6
0.25	0.489	0.527	-0.594	-0.552	0.6
0.5	0.824	0.845	-0.544	-0.552	0.6

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

Japanese Black (Wagyu) cattle is a typical breed which has several sub-populations within the breed. If this result is applied to them, the important traits among production traits seem to be meat quantity and meat quality. They have low genetic correlation according to Koots et al. (1994b). Thus the weights for the traits are almost even because they are equally important in terms of economic value of final products. In this situation, two population structure will be advantageous without use of complementarity. This system may realize additional advantage when the economic situation is changed because its multi-population system bring more flexibility. Thus the application of this result depends on the difference of genetic parameters, inbreeding depression, initial genetic level and relative importance of the traits.

However, the key point for the decision for the breeding scheme would be a prospect for long term breeding strategy; constant breeding goal vs variable breeding goal, in other words, optimism or pessimism for future requirement for genetic improvement.

REFERENCES

Bulmer, M. 1971. The Effect of Selection on Genetic Variability. Am. Nat. 105:201-211.

Dickerson, G. 1973. Inbreeding and Heterosis in Animals. In: Proc. of the Animal Breeding and Genetics Symp. in Honor of Dr. Jay L. Lush. ASAS and ADAS, Champaign, IL. USA.

Koots, K. R., J. P. Gibson, C. Smith and J. W. Wilton. 1994a.
Analyses of published Genetic Parameter Estimates for

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

³⁾ For POP1, Economic weight for traits is 1:1.

⁴⁾ For POP2, Economic weight for traits is 2:1 favoring high frequency genotype.

abe Means within a row and within a trait that do not share mommon superscript letter differ (p < 0.05).

²⁾ Depression in SD unit per increase of 1% inbreeding coefficient.

- Beef Production Traits, 1. Heritability. Anim. Breed. Abstr. 62:309-338.
- Koots, K. R., J. P. Gibson and J. W. Wilton. 1994b. Analyses of published Genetic Parameter Estimates for Beef Production Traits. 2. Phenotypic and Genetic Correlations. Anim. Breed. Abstr. 62:825-853.
- Nomura, T. and Y. Sasaki. 1988. Studies on Genetic Differentiation of Japanese Black Cattle by Means of Multivariate Analysis. Jpn. J. Zootech. Sci. 59:952-960.
- Oikawa, T., Y. Matsura and K. Sato. 1996. Comparison of Breeding System between Single Population and two subpopulation Scheme. I. Equal genetic level for subpopulations (in this Journal).
- Pirchner, F. 1983 Population Genetics in Animal Breeding (2nd Ed.). Plenum Press, NY, USA.
- Smith, C. and M. Quinton. 1993. The effect of selection in sublines and crossing on genetic response and inbreeding. J. Anim. Sci. 71:2631-2638.