The Effect of Sub-division (Two or Three Sub-populations) of a Population on Genetic Gain and Genetic Diversity

T. Oikawa*, H. Matsui and K. Sato

Faculty of Agriculture. Okayama University. Okayama, 700-8530, Japan

ABSTRACT : Breeding efficiencies were compared among three population schemes: a single population, a population with two sub-populations and a population with three sub-populations. 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. Phenotypes of three traits were generated with a model comprising 36 loci, each with additive genetic effects and residuals distributed normally. Among the three population schemes, the single population scheme was definitely superior to the other two with regards to selection response and inbreeding. The multiple sub-population scheme was, however, considered to be an alternative population scheme when the difference in economic weights of the traits was small among the sub-populations, assuming moderate inbreeding depression for traits and crossbreeding. The scheme with two sub-populations had a higher genetic value than that with three sub-populations; however, the genetic values of the schemes were comparable when maternal heterosis was taken into account. The choice of population schemes may depend on the cost-sharing policy between the breeding population and the commercial population rather than just the breeding efficiency. *(Asian-Aust. J. Anim. Sci. 2002. Vol 15, No. 6 : 767-771)*

INTRODUCTION

The objective of animal breeding is to increase the mean genetic value in a population while maintaining genetic diversity as large as possible. To achieve this goal, three selection approaches have been proposed by Cameron (1997): 1) a biased selection criterion, 2) a combined selection criterion of both genetic values and an (predicted) inbreeding coefficient, 3) a modified population structure. In this study, the last approach was investigated with a computer simulation to achieve the above goal. A population scheme with two sub-populations has been compared with a single population scheme, while fundamental properties of the schemes has been also studied under various genetic parameters, selection intensities and economic weights (Oikawa et al., 1997); however, implications of the results are limited because a possible single crossing between the two sub-populations can be realized only for one trait with a direct genetic effect. A population scheme with three sub-populations is an alternative to utilizing both direct and maternal heterosis. The objective of this study was to examine the effect of a population scheme with three sub-populations on the genetic value of animals with a shorter generation horizon under conditions where several levels of the heterosis effect were assumed.

* Address reprint request to T. Oikawa. Tel: +81-86-251-8334,
Fax: +81-86-251-8388.

MATERIALS AND METHODS

Population structure

The population schemes compared in this study are presented in table 1. Size of whole population was set so that dam/sire ratio should be 20, and the effective population size should be around 100. Base population for selection experiments comprised of 30 sires and 600 dams. Then the population was divided into sub-population according to the population schemes. Selection experiment was carried out within (sub-) populations. For each scheme, the selection experiment was carried out by stochastic computer simulation. Genetic gain and a coefficient of inbreeding were compared among three population schemes: a scheme of a single population (POP1), another scheme with two sub-populations (POP2) and the third scheme with three sub-populations (POP3). The coefficient of inbreeding was computed from pedigree information recorded during a simulation by the tabular method described by Tier (1990). The selection experiment was conducted in a simulated animal population by applying a selection index (Hazel, 1943) to the whole population in POP1, while either same or different economic weights in selection indices were applied to each of the sub-populations in POP2 and POP3. The economic weights, Eco1, Eco2 and Eco3 were presented in table 2 for each population scheme. Different weights for the traits were assumed in Eco2 and Eco3, where the difference was larger in Eco3. Phenotypic and genetic (co)variances in the selection indices were computed empirically in each generation. The total number of sires and dams in POP2 and

Table 1. Structure of the three population schemes

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

POP3 was the same as in POP1.

Construction of a trait

Three traits, denoted as Trait-A, -B and -C, were generated by the finite loci model. Each trait was assumed to comprise 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 was assumed to be 0.5 for all loci. Heritabilities were assumed to be 0.3 for all traits with an additive genetic variance of 0.43 and a residual variance of 1.0. "A" and "a" were alleles in a locus, and genotypic values of "AA", "Aa" and "aa" were 0.1546, 0.0 and -0.1546, respectively. All of the genotypic values were summed to form a genetic value for an animal. Genetic correlations between the traits were fixed at zero. The genetic correlations, heritabilities and selection intensity were fixed in the simulation because change of genetic correlation had little effect on the differences among the population schemes, and selection intensity and heritability did not alter the superiority of the single population scheme; only the difference was marginal as in our previous study (Oikawa et al., 1997).

Selection

The size of one population comprising 30 sires and 600 dams was constant throughout the simulation study. In POP2 and POP3, the whole population was divided into two and three sub-populations, respectively. The number of progeny for each mating was two-a male and a female animal; thus a total of 1200 offspring were born. Sires for the next generation were then selected from 600 male

offspring. The proportion of selected male animals was 0.05, whereas no selection was assumed in dams. All of the sires and dams were then replaced for the next generation.

The sires and dams were mated at the end of a generation loop then by a formation of offspring for the next generation. Mating was done randomly between selected animals, however, sib-mating was avoided. A genotype of the offspring was determined by two gametes segregated from their respective sires and dams. Breeding values of the offspring were computed by summing up genotypic values over all the loci. A phenotypic value of the animal was then formed by a breeding value and a residual effect (e) generated assuming normal distribution such as e~N(0,1). The discrete generation in the selection experiment was designed to simplify the simulation model.

RESULTS AND DISCUSSION

Figure 1 presents average breeding values of the three population schemes when different sets of economic weights were applied in the selection experiment. In Eco1, breeding values were similar among the population schemes and among the traits. This result reflected the same economic weights for all the traits. Thus genetic gain was similar among three population schemes.

In Eco2, the first sub-populations in POP2 and POP3 showed the highest genetic values among the sub-populations in Trait-A, whereas the third sub-populations showed the highest values in Trait-C in POP3. The two sub-populations of POP2 had similar genetic values in Trait-B because they were weighed equally in the index. Average genetic values of POP1 were slightly higher than the averages of the sub-populations of POP2 and POP3 for all the traits under Eco2.

The superiority of POP1 was more apparent in Eco3 than in Eco2. The average genetic values among the population schemes were negatively related to the number of sub-populations in the schemes-a lower average in the population scheme with more sub-populations. A selection program with subdivided populations using different economic weights for traits was discouraged as far as

Table 2. Economic weights of three traits for the three population schemes

Population[1]	Economic weight	Sub-population 1			Sub-population 2			Sub-population 3		
		Trait-A	Trait-B	Trait-C	Trait-A	Trait-B	Trait-C	Trait-A	Trait-B	Trait-C
POP1	Eco1	1	1	1	-	-	-	-	-	-
POP2	Eco1	1	1	1	1	1	1	-	-	-
	Eco2	3	2	1	1	2	3	-	-	-
	Eco3	10	5	1	1	5	10	-	-	-
POP3	Eco1	1	1	1	1	1	1	1	1	1
	Eco2	2	1	1	1	2	1	1	1	2
	Eco3	10	1	1	1	10	1	1	1	10

[1] POP2 consists of two sub-populations, and POP3 consists of three sub-populations.
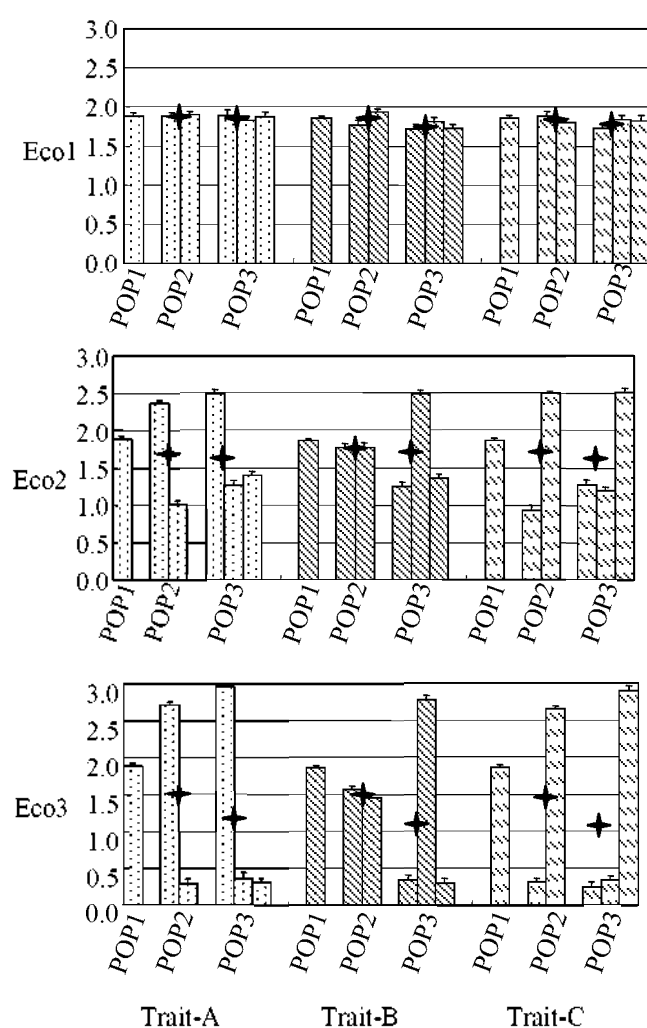
Figure 1. Average breeding values and SEs of the three population schemes at the 10th generation.
Average of the sub-populations are indicated by solid stars for POP2 and POP3.

Table 3. Coefficient of inbreeding (%. Mean±SE) after the 10th generation of selection

Simulation	Population scheme		
	POP1	POP2	POP3
Eco1	4.21±0.04	8.16±0.11	11.86±0.15
Eco2	4.21±0.04	8.24±0.13	11.85±0.18
Eco3	4.21±0.04	8.14±0.11	11.57±0.14

average genetic value of the traits was a major interest. For the situation such that economic values of traits in a breeding objective were actually different among sub-populations. where the highest genetic gain was achieved in one of the sub-populations of the multiple sub-population scheme, then the multiple population scheme would be optimum because it reflects actual economical condition.

Table 3 presents the average coefficient of inbreeding at the 10th generation for each of the population schemes. The highest coefficient of inbreeding was obtained in POP3 because it had the smallest size of sub-population. The differences of the coefficients of inbreeding between POP3 and POP2. and between POP2 and POP1 were similar (≅ 4.0%). The coefficients of inbreeding (%) estimated by the method of effective population size (Falconer. 1989) based simply on the difference in the number of males and

females were 3.94, 7.87 and 11.81 for POP1. POP2 and POP3. respectively. Thus the values in this simulation were slightly higher than the values computed from the effective population size. This difference may have resulted from the unequal genetic contribution of the ancestry of the animals due to selection.

We examined the effect of crossing between sub-populations which. as suggested by Smith and Banos (1991). is a major benefit that a multiple sub-population scheme can provide. The degree of inbreeding depression was inferred from the literature. The estimates of inbreeding summarized by Falconer (1989) are distributed from 0.7% to 5.1%. an average of about 2.5% of phenotypic SD. On the other hand. Quinton et al. (1992) have conducted a simulation study that examines the effect of inbreeding. assuming different degrees of inbreeding depression from 2.5% to 10.0% of phenotypic SD per 1.0% increase of the coefficient of inbreeding. As the phenotypic SD in this study was approximately 1.2, inbreeding depressions of 1.0%. 3.0% and 5.0% of the phenotypic SD corresponded to 0.012. 0.036 and 0.06 SD units, respectively. The 3.0% inbreeding depression corresponded to the rate of 2.5% of Falconer (1989).

Heterosis. expected to take place when two inbred lines are crossed. is regarded as a phenomenon opposite of inbreeding depression; however. it is not just the other side of inbreeding depression which is caused by the two events of the dominance of an allele and the related epistasis; heterosis, on the other hand, is caused by additive×additive epistasis in addition to the two events (Lynch. 1991). In this study. inbreeding depression was simply assumed to be zero as a result of crossing; therefore. heterosis should be regarded as a minimum value because a non-additive genetic effect was not taken into account in the model.

Table 4 presents results of the average genetic values of POP1. POP2 and POP3 under an assumption of crosses between the sub-populations. Values in the table indicate the advantages of POP1 over POP2 or POP3. When no inbreeding depression was assumed for the traits. the advantage of POP1 over POP3 was larger than its advantage over POP2. The advantage of POP1 over the other population schemes was large when the difference in the economic weights was large among the traits. These results are consistent with the report by Smith and Quinton

Table 4. Advantage of POP1 over POP3 and POP2 in genetic value with crossbreeding between sub-population of POP2 or POP3 after the 10th generation of selection.

Simulation	Advantage	Inbreeding depression (Percentage in SD unit)											
		0%				3%				5%			
		Trait-A	Trait-B	Trait-C	Mean	Trait-A	Trait-B	Trait-C	Mean	Trait-A	Trait-B	Trait-C	Mean
Eco1	POP1-POP3	0.02	0.11	0.06	0.06	-0.13	-0.04	-0.09	-0.09	-0.23	-0.14	-0.19	-0.19
	POP1-POP2	-0.01	0.01	0.01	0.01	-0.16	-0.14	-0.14	-0.51	-0.26	-0.24	-0.24	-0.25
									<u>-0.10</u>				<u>-0.16</u>
Eco2	POP1-POP3	0.18	0.16	0.20	0.18	0.03	0.01	0.05	0.03	-0.07	-0.09	-0.05	-0.07
	POP1-POP2	0.21	0.09	0.15	0.15	0.06	-0.06	0.0	0.0	-0.04	-0.16	-0.10	-0.10
									<u>0.05</u>				<u>-0.02</u>
Eco3	POP1-POP3	0.69	0.73	0.71	0.71	0.54	0.58	0.56	0.56	0.44	0.48	0.46	0.46
	POP1-POP2	0.39	0.35	0.38	0.37	0.24	0.20	0.23	0.22	0.14	0.10	0.13	0.12
									<u>0.27</u>				<u>0.20</u>

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.

(1993) and with our previous report (Oikawa et al., 1997). The advantage of POP1 was apparent under the assumption of no inbreeding depression; therefore, multiple sub-population schemes and the subsequent crossbreeding are not recommended, although the assumption is undoubtedly unrealistic for most of the genetic traits.

Under the assumption of 3% depression, which is almost the average inbreeding depression in the literature, the advantage of multiple sub-population schemes was suggested when a similar economic weight was applied for the traits in the multiple sub-population schemes. When unequal economic weights were applied for the traits, the average genetic values in POP1 were virtually comparable (Eco2) or higher than the population schemes with multiple sub-populations (Eco3).

In comparing the average genetic values between POP2 and POP3, POP2 showed a higher genetic value than POP3. This superiority of POP2 may be caused by the higher averages of breeding values. When, however, one of the traits was related to the dam's maternal effect because a breeding program often included it in the breeding objectives, the average genetic values of POP2 were those underlined in the table. The lower advantage was due to the fact that maternal heterosis is not realized by the two-way crossbreeding in POP2. Thus the inbreeding depression for one of the three traits was neglected in POP2, and the advantage of POP1 over POP2 was then comparable with the advantage of POP1 over POP3 under the inbreeding depression of 3%.

Under the inbreeding depression of 5%, the population schemes with multiple sub-populations showed higher genetic values than POP1 in Eco1 and Eco2; however, when the economic weights were very different among the traits as in Eco3, POP1 had higher genetic values than the

population schemes with multiple sub-populations. Thus the population schemes with multiple sub-populations had an advantage for traits with similar economic weights.

A related topic is about costs for maintaining breeding population under different population structures. The economic loss in multiple sub-populations may be higher than that in a single population scheme because severe inbreeding depression is expected to occur in the former. A commercial population can, however, expect heterosis when crossbreeding is carried out between sub-populations. Thus a breeding population mainly suffers adverse effects of inbreeding, whereas a commercial population is free of such effects. In a single population scheme, the effect of inbreeding is less severe in a breeding population; however, heterosis cannot be utilized in a commercial population. Therefore the choice of population schemes is closely related to a breeding policy of how to share the costs of the adverse effects of inbreeding between breeding population and commercial population.

REFERENCES

Cameron, N. D. 1997. Selection indices and prediction of genetic merit in animal breeding. 103-105. CAB International. Wallingford. UK.

Falconer, D. S. 1989. Introduction to quantitative genetics (3rd Ed.). 248-253. Longman, London. UK.

Hazel, L. N. 1943. The genetic basis for constructing selection indexes. Genetics 28:476-490.

Lynch, M. 1991. The genetic interpretation of inbreeding depression and outbreeding depression. Evolution 45:622-629.

Oikawa, T., Y. Matsura and K. Sato. 1997. Comparison of breeding system between single and two sub-population scheme by computer simulation I. Equal genetic level for sub-populations. Asian-Aus. J. Anim. Sci. 10:422-427.

Quinton, M., C. Smith and M. E. Goddard. 1992. Comparison of

selection methods at the same level of inbreeding. J. Anim. Sci. 70:1060-1067.

Smith, C. and G. Banos. 1991. Selection within and across populations in livestock improvement. J. Anim. Sci. 69:2387-2394.

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.

Tier, B. 1990. Computing inbreeding coefficients quickly. Genet. Sel. Evol. 22:419-430.