EFFICIENCY OF INDIRECT SELECTION WITH A FINITE NUMBER OF LOCI

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SUMMARY

The effect of continued selection on the efficiency of indirect selection relative to direct selection when a finite number of loci is considered was studied through Monte Carlo simulation. Computer results were compared with predictions based on an infinitesimal model. Theoretical expectations which account only for changes in relative efficiency due to the generation of linkage disequilibrium indicate a loss in efficiency of indirect selection when more than one cycle of selection is practised. Results of this study show that indirect selection is relatively less efficient when changes in gene frequencies are also considered. Caution should be taken in applying indirect selection procedure in practice.

INTRODUCTION

The efficiency of indirect selection relative to that of direct selection was studied in detail by Searle (1965). The conclusions of his work were based on the conventional equations to predict genetic responses (e.g. Falconer, 1981). However, those equations are strictly valid for only one generation of selection. If selection is continued, expected responses are altered as a consequence of changes in genetic parameters. In large populations, these changes are due solely to linkage disequilibrium generated by selection, if an infinite number of loci is assumed (Bulmer, 1980).

Under repeated cycles of directional selection, change in genetic parameters continues until an equilibrium is achieved after several generations. Villanueva and Kennedy (1990b) have re-examined the relative efficiency of indirect selection when this equilibrium is reached. For all cases in which indirect selection was relatively superior to direct selection, the relative efficiency was smaller at the equilibrium than in the first generation of selection. For some combinations of genetic parameters, the ranking of the two selection procedures changed. A basic assumption in their work was that there is an infinite number of loci each with infinitely small effect segregating for each trait. The objective of this study was to investigate, through computer simulation, if these predictions hold when the assumption of an infinite number of loci is relaxed.

METHODS

Genetic response of the trait we want to improve (desired trait) from direct selection on it was compared with correlated genetic response of that trait from indirect selection on another trait (alternative trait). The initial heritabilities of desired and alternative traits were 0.1 and 0.5 respectively and the genetic correlation between the traits was 0.5. Assuming an infinite number of loci this particular combination of parameters leads theoretically to a change in the ranking of the two selection procedures (Villanueva and Kennedy, 1990b). In the first generation, indirect selection is more efficient than direct selection but the reverse occurs when the equilibrium is achieved.

Each trait was determined by n unlinked loci acting additively. Two experiments were carried out; one with 10 loci and another one with 30 loci. Each locus had two alleles with effects α and $-\alpha$, respectively with α defined such that initial genetic variance was equal to 5. Initial gene frequencies were 0.5 for both alleles at each locus. Pleiotropy was the only cause of correlation. Half of the loci affected both traits in the same direction. Genotypic value of the individual for each trait was obtained by summing values at each locus over all loci. Phenotypic value was obtained by adding a normally distributed environmental component with mean zero and variance of 45 for the desired trait and of 5 for the alternative trait. Environmental variance was maintained constant over generations.

The base population was in Hardy-Weinberg and linkage equilibrium. One thousand individuals (500 males and 500 females) were sampled to constitute generation zero. In each generation 100 males and 100 females with the highest phenotypic values were selected to be parents of the next generation. Direct selection was based on phenotypic performance for the desired trait and indirect selection was based on phenotypic performance for the alternative trait. Selected individuals were randomly mated and each pair produced 10 offspring (5 males and 5 females). Selection was continued for 10 generations. One hundred replicates were run for each simulation.

The criterion to evaluate the relative efficiency of indirect selection was the ratio of correlated to direct genetic response for the desired trait. Values greater than one for this ratio indicate that indirect selection is more effective than direct selection. Expected values under an infinitesimal model for genetic variances and covariance required for predicting responses were computed at each generation of selection using the expressions described by Villanueva and Kennedy (1990a).

RESULTS AND DISCUSSION

Table 1 shows simulated and predicted correlated response of the desired trait by selecting on the alternative trait as well as the ratio of that response to direct response by selecting on the desired trait itself. Simulated values are the mean of 100 replicates. As expected, indirect selection was more efficient than direct selection ($CR_d/R_d > 1$) in the first generation of selection for both 10 and 30 loci. Predicted and simulated values were in good agreement at this generation. After the first generation, the predicted and observed ranking of both selection procedures changed (i.e. direct selection became more efficient than indirect selection). Under the infinitesimal model, the ratio of predicted responses achieved an equilibrium value after a few cycles of selection. However, the observed ratio of responses with finite loci decreased each generation with the larger reduction in the 10 loci experiment. Both observed direct and correlated responses were reduced more than those expected but the proportional change in correlated response was greater than in direct response. This led to a decrease in the ratio of responses with each generation of selection. The low predictability of correlated responses over several generations of selection was pointed out by Bohren et al. (1966).

Table 1. Simulated (S) and predicted (P) genetic response from indirect selection (CR_d) and ratio of CR_d to genetic response from direct selection (R_d) for the desired trait.

	CR_d			CR_d/R_d		
	No. of loci			No. of loci		
	10	30	∞	10	30	∞
Generation	S	S	P	S	S	P
1	1.10	1.08	1.11	1.12	1.09	1.12
2	.88	.94	.94	.95	.99	.99
3	.74	.84	.90	.84	.90	.96
4	.67	.82	.89	.82	.91	.96
5	.54	.78	.89	.66	.91	.96
6	.39	.69	.89	.51	.86	.96
7	.26	.64	.89	.39	.79	.96
8	.16	.56	.89	.25	.72	.96
9	.07	.47	.89	.14	.62	.96
10	.08	.44	.89	.17	.64	.96

Changes in genetic variances and covariance across generations are presented in table 2. The smaller the number of loci, the larger was the difference between observed and predicted values. This difference increased each generation for both 10 and 30 loci simulations. Prediction of genetic variances and covariances for each generation of selection accounts for changes by linkage disequilibrium but not for changes in gene frequencies. Changes in genetic parameters due to linkage disequilibrium are important in the early generations whereas those due to changes in gene frequencies are more important in the latter generations.

In both the 10 and 30 loci experiments, under indirect selection the genetic covariance decreased from generation 0 to generation 10 in the same proportion as the genetic variance of the alternative trait. This percentage reduction was much larger than that in the genetic variance of the desired trait under direct selection due to the higher heritability of the alternative trait with respect to that of the desired trait. This is however a basic requirement for indirect selection be more effective than direct selection to improve the desired trait.

Under the infinitesimal model the relative efficiency of indirect selection at the equilibrium is expected to be smaller than in the first generation of selection. Results from the simulations show that when the number of loci is finite the loss in efficiency is even greater. Also the smaller the number of loci involved, the smaller the value of indirect selection. These results together with problems related to errors in parameter estimations which affect prediction of responses (Searle, 1965; Sales and Hill, 1976) suggest caution in applying indirect selection in practice.

Table 2. Simulated (S) and predicted (P) genetic variances of desired (Var(d)) and alternative (Var(a)) traits and genetic covariance between both traits (Cov(a,d)) per generation (Gen) under direct and indirect selection.

	Direct selection			Indirect selection								
	Var(d)			Var(a)			Var(d)			Cov(a,d)		
	No. of loci			No. of loci			No. of loci			No. of loci		
	10	30	∞	10	30	∞	10	30	∞	10	30	∞
Gen	S	S	P	S	S	P	S	S	P	S	S	P
0	5.02	4.99	5.00	5.04	4.99	5.00	5.03	4.96	5.00	2.50	2.48	2.50
1	4.72	4.72	4.80	3.85	3.97	4.02	4.65	4.73	4.76	1.91	2.00	2.01
2	4.56	4.63	4.72	3.26	3.70	3.81	4.36	4.57	4.70	1.64	1.84	1.91
3	4.29	4.47	4.69	2.75	3.44	3.76	4.03	4.37	4.69	1.38	1.72	1.88
4	4.05	4.32	4.67	2.15	3.15	3.75	3.67	4.25	4.69	1.09	1.60	1.87
5	3.80	4.25	4.66	1.59	2.82	3.75	3.27	4.07	4.69	0.78	1.44	1.87
6	3.35	4.12	4.66	1.07	2.51	3.75	2.94	3.87	4.69	0.53	1.29	1.87
7	3.04	3.94	4.66	0.66	2.22	3.75	2.71	3.61	4.69	0.33	1.13	1.87
8	2.70	3.80	4.66	0.39	1.88	3.75	2.54	3.42	4.69	0.18	0.94	1.87
9	2.36	3.61	4.66	0.22	1.58	3.75	2.47	3.26	4.69	0.11	0.80	1.87
10	2.06	3.38	4.66	0.12	1.29	3.75	2.40	3.05	4.69	0.06	0.64	1.87

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