Theoretical and Applied Genetics 44, 63–68 (1974)

Evaluation of Selection Indices under Various Parameter Combinations in Simulated Genetic Populations

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Summary. In a simulation study, the efficiency of some selection indices was tested under various parameter combinations. For the purpose of such comparison a criterion, named as 'evaluation coefficient' was developed. In the evaluation coefficient both the total genetic gain and the relative gains obtained in the individual traits, as a measure of harmony, were taken into consideration.

The results have indicated that the genotypically constructed selection indices were more efficient than the phenotypically constructed selection index of Elston (1963). Furthermore, the effectiveness of selection indices, irrespective of the model used, was found to be decreased in case of tight linkage as compared to that of loose linkage. It was, however, observed that the genotypically constructed indices were more sensitive to linkage and the reduction in their performance was relatively greater if characters included in the index had varying heritability coefficients. The efficiency of the indices was also reduced when the characters incorporated in the index possessed different economic weights. The results, however, suggested that relatively faster rate of improvement in the character having low heritability could be obtained by assigning higher economic weights to that character. This would mean that manipulation of economic weights may help in bringing about the harmonical improvement in all the characters to be selected simultaneously.

The importance of combined selection for several characters has long been realized by plant as well as animal breeders. A mathematical genetic theory fitting to the problems of simultaneous selection was developed by Smith as early as 1936. Eversince, large number of selection indices, as a method for simultaneous selection, has been worked out. However, no reports are available where the selection indices have been incorporated in practical breeding programme. A critical review of the literature on selection index has led to conclude that a large number of theoretical as well as practical problems still exist which make the successful use of this technique impracticable.

All the parameters i.e. variances and covariances, heritability coefficients, and correlation etc. which go into the construction of selection index are affected by a number of factors such as state of dominance at the individual loci, recombination frequencies and epistatic associations between different loci, etc. Experimental designs which permit the estimation of above parameters, generally, do not take these factors into consideration. The presence of different combinations of these factors will definitely affect above parameters and thus, the index also. Different selection models will be affected differently. The present study was, therefore, undertaken to analyse the effect of different parameter combinations on the efficiency of various selection models. It was desired to find out a suitable evaluation criterion which may be recommended for use in breeding projects when a particular set of parameters are available in a population.

Procedural Description

The very first problem in the present study was to create a model population on computer exhibiting a negative correlation between two characters, x and y. The genetic basis of correlation was assumed to be linkage and not pleiotropy. A population of zygotes with $2n = 8$ chromosomes was developed. On each chromosome two loci, each with two alleles, were assumed to be responsible for the expression of each character. For each character, therefore, there were 8 loci (i.e. 16 alleles). For all those loci which were made responsible for the expression of character x, the dominance of one allele over the other was assumed. No dominance was assumed in case of loci governing the character y. In addition, two different recombination values ($r = 0.005$ and 0.05) were considered. The transformation of such a biological genetic system into computer language followed the same principles as described by Singh (1966) and Singh, Bellmann and Ahrens (1967).

The following selection methods were used for selecting superior genotypes in the population described above:

$I^{(A)}$ — Additive genetic selection index,
$I^{(G)}$ — Genotypic selection index,
$I_E^{(P)}$ — Elston's phenotypic selection index.

The first two indices were the genotypically constructed selection indices of the following form

$$I = \sum_{i=1} b_i X_i \qquad (i = 1, 2, \ldots, n)$$

with $b_i = \Sigma C_{ij} A_i$.

where C_{ij} are the elements of the inverted phenotypic variance and covariance matrix and $A_i = \sum_j a_i G_{ij}$ with G_{ij} as additive part of genotypic variance and covariance and a_i as the economic weights assigned to each trait. In $I^{(A)}$ only the additive genetic variances and covariances, whereas in $I^{(G)}$ the total genotypic variances and covariances were considered. $I_E^{(P)}$ is an index in which only the phenotypic values have been incorporated. It is a non-linear selection index proposed by Elston (1963) and has the following form:

$$I_E^{(P)} = \prod_{i=1} (P_i - k_i) \, .$$

The P_i stands for the measurement on the i^{th} trait and k_i for the lowest value in the series of i^{th} trait.

Table 1. *Variant populations and used indices*

Indices	Variant 1 $h_y^2 = h_x^2;\ a = \binom{1}{1}$		Variant 2 $h_y^2 > h_x^2;\ a = \binom{1}{1}$		Variant 3 $h_y^2 > h_x^2;\ a = \binom{1}{4}$
	$r = 0.005$	$r = 0.05$	$r = 0.005$	$r = 0.05$	$r = 0.05$
$I^{(A)}$	×	×	×	×	×
$I^{(G)}$	×	×	×	×	×
$I_E^{(P)}$	×	×	×	×	×

These indices were used for making selection in populations with three different parameter combinations (Table 1). The parameter combinations (variants) which could be studied, have been marked with the sign '×' in Table 1. In Table 1, h_x^2 and h_y^2 mean the heritability coefficients of characters x and y, respectively, $a = \binom{1}{1}$ means that both the traits have been equally evaluated whereas in $a = \binom{1}{4}$, the character x has been weighted four times to y. r stands for recombination frequencies between loci.

Results

1. *Maximum Genetic Gain* (ΔG_T)

Assuming that x and y are two components of yield, which are additive i.e. $x + y = t$, the sum of the genetic gains obtained in the individual traits (i.e. $\Delta G_x + \Delta G_y = \Delta G_T$) may be used as a basis for comparing selection indices. In order to estimate the maximum genetic gain in both traits, the total genetic gain was obtained in that generation in which one of the characters had reached its maximum. This criterion was important, because any selection beyond that will mean selection on one character only. The maximum genetic gain obtained by different indices are given in Fig. 1. From the figure, it was evident that in case of variant 1 the index $I^{(A)}$ was superior to $I^{(G)}$ and $I_E^{(P)}$ for both loose as well as tight linkage. $I^{(G)}$ was, in turn, more effective than $I_E^{(P)}$. So far as the variant 2 was concerned the order of superiority of indices remained the same for tight linkage. In the case of loose linkage, the performance of Elston's index $I_E^{(P)}$, was, however, at par with the $I^{(A)}$, whereas the performance of index $I^{(G)}$ was the poorest. It may, however, be mentioned that this figure does not provide a correct basis for comparison, because in case of different selection indices the maximum genetic gain (ΔG_T) was obtained in different generations. This means that the time required by different indices to achieve the maximum gain was different. It was, therefore, preferred to determine the genetic gain per generation which could be compared without any reservation. As it is evident from Fig. 2, the three indices performed equally good in case of variant 1 with loose linkage. The genotypically constructed indices ($I^{(A)}$ and $I^{(G)}$) were, however, superior to $I_E^{(P)}$ in case of tight linkage (i.e. $r = 0.005$). In case of loose linkage of variant 2, $I^{(A)}$ was found superior to other two methods. For tight linkage, there did not seem to be any difference regarding the performance of the different indices. The two genotypically constructed selection indices, $I^{(A)}$ and $I^{(G)}$, were equally efficient in case of variant 3.

2. *The 'Harmonieziffer' as an Evaluation Criterion*

Assuming independent loci, i.e. no linkage, on principal these values are attainable by an appro-

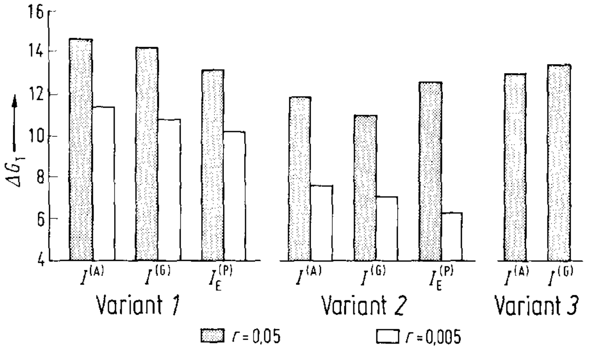

Fig. 1. Genetic gain realized by application of three different selection indices depending on two degrees of linkage

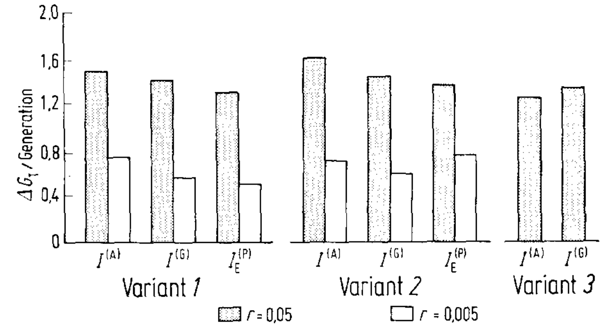

Fig. 2. Genetic gain per generation realized by three different selection indices depending on two degrees of linkage

priate selection procedure in a time interval (t_1, t_2). Because no superdominant relations are assumed the process converges to $\bar{G}_{\max}$, i.e. to the homozygote population. It is the realisation of a negative correlation (by linkage conditions) the reason that during selection on one of the two traits, increase in $\bar{G}$s of the character under selection and decrease in $\bar{G}$s of the other character is to be observed. If selection acts on both traits simultaneously in the desired direction no pronounced genetic gain is evident in both of the characters (providing $h_x^2 = h_y^2$). If $h_y^2 > h_x^2$ one can observe increasing of $\bar{G}_y$ and decreasing of $\bar{G}_x$.

To overcome these difficulties it is worthful to use a selection index as an evaluation criterion in selection.

In some cases the aim of simultaneous selection is to go for a selection model by which harmonical improvement in all the traits may be obtained and at the same time the selection gain is maximum. To be more precise, there is need for a selection procedure which ensures $\Delta G_x/\Delta G_y = 1$ and at the same time, maximizes ΔG_T also. This means, for comparing different selection models, one has to evolve a criterion which takes care of both the symmetrical improvement of all the characters included in the index as well as the maximization of ΔG_T. The following expression was, therefore, suggested as a measure of harmonical development of the different traits and was named as 'Harmonieziffer' (HZ):

$$\mathrm{HZ} = [\{\bar{G}_{\max}^{(x)} + \bar{G}_{\max}^{(y)} + 1\} - |\Delta G^{(x)} - \Delta G^{(y)}|]\,. \quad (1)$$

In the present study maximum genotypic mean was assumed to be

$$\bar{G}_{\max}^{(x)} = \bar{G}_{\max}^{(y)} = 8\,.$$

Thus

$$\bar{G}_{\max}^{(x)} + \bar{G}_{\max}^{(y)} + 1 = 17\,.$$

Selection was continued until one of the characters x, y reached its maximum and hence there was no point in continuing the selection, as thereafter the selection would have been based on one character only, leading to additional asymmetry.

It is t_2 the point where in every run one of the both characters has achieved the maximum value, $\bar{G}_{\max} = 8$. All the following considerations based on the results: $t_1 = 0^{\text{th}}$ generation, $t_2 = 7^{\text{th}}$ generation. Starting in t_1 with $\bar{G}_x = \bar{G}_y = 0$, it is

$$\bar{G}_{\min} < \Delta G < \bar{G}_{\max}$$
$$-8 < \Delta G < 8\,,$$

i.e. with improvement in one character decreasing of $\bar{G}$ of the other is possible.

As a measure of disharmonic development of the two traits during selection serves

$$d = |\Delta\bar{G}^{(x)} - \Delta\bar{G}^{(y)}|\,.$$

Only in the case of $\Delta\bar{G}^{(x)} - \Delta\bar{G}^{(y)}$, i.e. $d = 0$, the procedure used for genetic improvement was most effective relating to harmony. It is

$$0 \leq d \leq |G_{\min}^{(x)} - G_{\max}^{(y)}| = |G_{\min}^{(y)} - G_{\max}^{(x)}| = 16\,.$$

In the case considered

$$\mathrm{HZ} = 17 - d, \quad \text{i.e.} \quad 1 \leq \mathrm{HZ} \leq 17\,.$$

Because it is obvious that maximum of HZ is a function of population structure, the comparison of a selection procedure in different genotypic populations (i.e. evaluation of a selection index applied to different populations) HZ may be used in a somewhat different manner:

$$\mathrm{HZ}^* = \frac{\mathrm{HZ}}{\mathrm{HZ}_{\max}}\,.$$

In our case we did not need HZ*, because in every variant population $G_{\max} = 8$ and $G_{\min} = -8$ does hold for each trait.

For final evaluation the 'evaluation coefficient' E. C. was used. E. C. is a function of total genetic gain $\Delta\bar{G}_T = \Delta\bar{G}^{(x)} + \Delta\bar{G}^{(y)}$ in an interval (t_1, t_2) and of HZ and is calculated by

$$\text{E. C.} = \Delta\bar{G}_T \cdot \mathrm{HZ}\,.$$

Starting with $\bar{G}_x = \bar{G}_y = 0$ the maximum of $\Delta\bar{G}_T$ attainable by selection on both traits in positive direction is

$$\Delta G_{T_{\max}} = \Delta G_{\max}^{(x)} + \Delta G_{\max}^{(y)} = 8 + 8 = 16\,.$$

For this we get

$$\text{E. C.}_{\max} = 16 \cdot 17 = 272\,.$$

Using HZ* we would get E. $\text{C.}_{\max} = 16$.

The data for HZ and E. C. for different indices under various parameter combinations were given in Table 2. A variantwise comparison of selection indices did not indicate significant differences between their HZ-values in case of loose linkage. The values for harmonieziffer, in case of tight linkage (r=0.005), were higher for the genetic indices (i.e. 14.31 and 13.30 for variant 1 and 8.03 and 8.52 for variant 2) as compared to their values for phenotypic index which was 11.72 for variant 1 and 6.93 for variant 2. It may, however, be mentioned that the additive genetic index, $I^{(A)}$, had the maximum HZ-values for all the variants studied under two different linkages.

Table 2. *Harmonieziffer (HZ) and evaluation coefficient (E. C.)*

Indices		$I^{(A)}$		$I^{(G)}$		$I_E^{(P)}$	
Criteria of comparison		HZ	E. C.	HZ	E. C.	HZ	E. C.
Loose linkage	Variant 1	16.59	226.26	15.30	187.58	14.54	159.65
(r = 0.05)	Variant 2	12.51	144.49	11.75	126.65	11.49	119.74
	Variant 3	13.47	125.14	13.73	120.96	—	—
Tight linkage	Variant 1	14.31	101.03	13.30	92.83	11.72	72.36
(r = 0.005)	Variant 2	8.03	43.60	8.52	50.43	6.93	41.30

Further, irrespective of the linkage values, the HZ-values were less in variant 2 as compared to the values in variant 1. This means, if the characters with unequal heritability coefficients were included in the index, the improvement in the means of traits would not be symmetrical. This was true both for genotypically as for phenotypically constructed selection indices. This suggests that even the genotypically constructed selection indices were not in a position to bring about harmonical improvement, in case the characters with unequal heritabilities were incorporated in the index.

A comparison of these indices can also be made on the basis of 'Evaluation Coefficients' given in Table 2. The performances of the indices were, in general, better in variant 1 than in variant 2 and 3. This was true both for loose as well as for tight linkage. As indicated by its maximum evaluation coefficient, the additive genetic index was found to be the most efficient. The index $I^{(G)}$ with its evaluation coefficient values higher than those for $I_E^{(P)}$, was found in turn superior over Elston's index. For all the variants studied here the order of performance of these three indices remained the same.

3. Linkage Sensitivity of Selection Indices

The following expression was used to measure the 'linkage sensitivity' of the indices and was, therefore, termed as 'linkage sensitivity coefficient' (Singh 1969):

Linkage sensitivity coefficient

$$(\mathrm{LSC}) = 100 - \left[\frac{\Delta G\,(0.005)}{\Delta G\,(0.05)}\right] \cdot 100 \,.$$

Here $\Delta G(0.005)$ and $\Delta G(0.05)$ stand for the E. C.-values for tight and loose linkages, respectively. As evident from the above expression, the higher values of linkage sensitivity coefficient (LSC) would mean more sensitivity to linkage.

Table 3. *Linkage sensitivity coefficient (LSC)*

Indices	Variant 1	Variant 2
$I^{(A)}$	58.80	69.97
$I^{(G)}$	50.60	60.70
$I_E^{(P)}$	55.40	65.55

A perusal of the LSC-values given in Table 3 indicated that the genetic index, $I^{(A)}$, was the most sensitive among all the three indices studied here. From the table it was further evident that the sensitivity of the indices was more in variant 2 (i. e. in case of unequal heritabilities) than in variant 1.

4. Effect of Unequal Heritability Coefficients on 'Evaluation Coefficient'

The extent of sensitivity of selection indices against unequal heritability coefficients was measured by the following ratio (R):

$$\mathrm{R} = \frac{\mathrm{E.\,C.}\,(\neq)}{\mathrm{E.\,C.}\,(=)} \cdot 100 \,.$$

Here E. C. ($\neq$) and E. C. ($=$) stand for evaluation coefficients in variant 2 and variant 1, respectively. As it is evident from Table 2, the genetic gain in variant 2 was always lesser than that of variant 1 and therefore, the value of above expression would always be less than 100. Larger value for this ratio would, therefore, mean less sensitivity of the index against unequal heritabilities.

Table 4. *Sensitivity R of the indices against unequal heritabilities r*

Indices	recombination	
	$r = 0.05$	$r = 0.005$
$I^{(A)}$	63.8	43.1
$I^{(G)}$	63.3	54.3
$I_E^{(P)}$	75.1	57.7

A perusal of the R-values given in Table 4 indicated that index $I^{(A)}$ was the most sensitive selection procedure to the variations in heritability coefficients. In general, the R-values were lower in case of tight linkage as compared to loose linkage. This suggests that the efficiency of selection indices would be reduced if the characters included in the index have unequal heritabilities and at the same time tight linkage prevailed between the loci governing these characters.

5. Effect of Differential Assignment of Economic Weights on the Efficiency of Indices

A comparison of the genetic gains obtained in variant 2 and variant 3 provides a direct evidence on the effect of the differential evaluation of the characters. In variant 2 both the characters x and y, were assigned equal weights i. e. $a = \binom{1}{1}$, whereas in variant 3, the character x was weighted four times of the character y (Table 1). Only the indices $I^{(A)}$ and $I^{(G)}$ could be compared here because a-vector was not involved in the phenotypic index of Elston.

A comparison of the data for E. C. given in Table 2, clearly indicated that the efficiency of the index $I^{(A)}$ in case of variant 2 was about 16 per cent greater than its performance in variant 3. Similarly, in case of Index $I^{(G)}$ the selection gain in variant 2 was 5 per cent more than that of variant 3. These results clearly indicate that the efficiency of selection index is decreased, in case the characters included in an index are assigned different economic weights.

Another interesting observation could be made by comparing the harmonical improvement of the characters (i. e. HZ-values) for different indices in variant 2 and 3. For index $I^{(A)}$, there was an increase in HZ-value from 12.51 in variant 2 to 13.47 in variant 3, whereas for $I^{(G)}$, the increase was from 11.75 to 13.75 (Table 2).

From the foregoing results it was evident that by manipulating the economic weights to be assigned to each character, it seems possible to affect harmonical development of the characters. It may, however, be added that such differential assignment of economic weights reduce the total genetic gain.

If a comparison of E. C. values for variant 1 and variant 3 was made, the simultaneous effect of unequal heritabilities and differential economic weights on the performances of selection indices may be determined. As evident from Table 2, the gain obtained in variant 3 as compared to variant 1 was 45 per cent lesser in case of $I^{(A)}$ and 36 per cent in case of $I^{(G)}$. The results clearly support that the reduction in gain depends on the restriction(s) posed on heritability and the economic weights.

Discussion

For the construction of selection indices a number of parameters, depending on the selection model, are required such as phenotypic and genotypic variances and covariances and heritability etc. It will, in general, be the case where population variances and covariances will be unknown, and we will have only estimates of them. Thus, the efficiency of selection indices is directly correlated with the accuracy of these estimates. These estimates do suffer, as do most second degree statistics from large sampling errors (Harris, 1964; Herrendörfer, 1968; Cockerham, 1963) and they are generally affected by linkages and hence the efficiency of selection indices is also likely to be affected. The results in the present investigations have indicated that the effectiveness of the selection indices, irrespective of the model used, is decreased in case of tight linkage. Though the gains obtained by the index $I^{(A)}$ in case of tight linkage were higher than those of $I^{(G)}$ and $I_E^{(P)}$, the relative decrease in gain by the former index was more indicating its high sensitivity to linkage conditions. Similar results have been reported earlier also (Fraser 1960, 1962; Martin and Cockerham, 1960; Gill, 1965a; 1965b; Bellmann and Ahrens, 1966 and Singh et al. 1967).

Martin and Cockerham (1960) established that the selection gain was a function of n, N, m and r with n = number of individual/group, N = size of the population, m = number of loci per chromosome and r = frequency of recombination.

Both by simulation studies as well as by the studies on real biological populations it has been shown that the selection gain expected by any method of selection depends directly on heritability coefficients of the characters to be selected (Heidhues, 1961; Singh, 1969; Singh et al., 1967; and Falconer, 1960, etc.). In selection index where selection is exercized on several characters simultaneously, the gain obtained in the individiual trait as well as the total gain depends, as per present investigations, on whether or not the characters have equal heritabilities. In our model studies it was found that the reduction in the total genetic gain was of the order of 25 to 37 percent in case of loose linkage and 43 to 57 per cent in case of tight linkage. In addition, a reduction of about 25 per cent in case of loose linkage and 50 per cent in case of tight linkage in the Harmonieziffer was observed, indicating an asymmetrical development in the individual characters.

Relative weights, depending on the economic significance, are assigned to each character incorporated in an index (Smith, 1936; Hazel, 1943; and Henderson, 1963). These weights, therefore, affect the total gain as well as the expected gain in the individual traits. It was, therefore, essential to study the consequences of the differential economic weights assigned to the characters. In all those cases where equal weights were assigned to the characters, the genetic gains were higher than in the cases where the characters were weighted differently. It was, however, observed that the value of Harmonieziffer was higher in the later case as compared to those obtained in case of equal economic weights. This means, by assigning more weights to the characters with low heritabilities, desired rate of improvement may be achieved. The results are in full agreement with those reported by Singh (1969) on rye.

It is evident from the above discussion that while constructing selection indices, one has to take into account the linkage conditions in the population. Besides, at the time of the selection, emphasis should be given on those characters which have high but approximately equal heritabilities. Assignment of economic weights to the characters should be made with extra care. One should try to keep the differences among the weights of different traits as small as possible. Only in those cases where the character is very important but has very low heritability, high economic weights may be assigned to the character, because such differential assignment of weights reduces the total genetic gain very drastically. However, additional informations need to be collected before making any definite recommendation about it.

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Received October 16, 1972

Communicated by W. Seyffert

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