A further examination of the relative efficiency of three methods of selection for genetic gains under less-restricted conditions

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1. INTRODUCTION

In animal or plant breeding, three methods may be used for multi-character selection. These are tandem selection, independent culling levels and index selection (Fairfield Smith, 1936; Hazel & Lush, 1942; Hazel, 1943; Young & Weiler, 1960). Briefly tandem selection involves selection for several traits one at a time over a number of generations, while in the method of independent culling levels simultaneous but independent cullings are carried out on different traits. In index selection, each animal is given a score, which combines several traits, after weighting them according to their relative importance. Hazel & Lush (loc. cit.) compared the relative efficiency of these methods, in terms of genetic gain, when the traits under selection were independent and had equal heritability, economic weight and variance. They concluded that the index method was most efficient and tandem selection least, the efficiency of selection by independent culling levels being intermediate.

All the above methods have different applications in the field. Under some conditions, a method which is more efficient in terms of genetic gain may not be more efficient in terms of cost and labour. It is therefore important to know the amount by which one method is superior to another, in genetic gain, so that an optimal selection plan can be made. Since production traits in animals or plants are often correlated and have different values for heritability, variance and economic weight, it seems desirable to extend the comparisons of Hazel & Lush for more general conditions and to outline methods of comparing relative efficiency. The discussion has been confined to efficiency in terms of genetic gain in economic units, since problems of costs and labour will vary with circumstances.

As the three selection methods differ in principle, the relative efficiency of any two methods usually cannot be expressed in simple terms, and in the present work generalization has not always been possible. However, in all cases, numerical computations have been made to assess the extent to which changes in various pertinent factors affect relative efficiency. Comparisons involving the independent culling method, for correlated traits, are limited to the case of two characters, as the theory has not so far been extended to a greater number.

2. NOTATION

a_i Economic weight of the ith trait.

b_i Weighting coefficient for the ith trait in a selection index.

$bG_{j.i}$ Genetic regression coefficient of the jth trait on the ith trait $=\dfrac{G_{ij}}{G_{ii}}$.

C_{ij} Elements of the inverse phenotypic variance and covariance matrix.

G_i Genetic value of the ith trait.

G_{ij} Genetic covariance of the ith and the jth traits (for variance $i = j$).

ΔG_i Expected genetic change in the ith trait due to selection $= Ih_i^2\sqrt{(P_{ii})}$.

H_C Expected total genetic gain in value by using the independent culling levels method. It is written as H_C' when traits under selection are independent.

H_T Expected total genetic gain in value by using tandem selection. When traits are independent, H_T' is used.

H_X Expected total genetic gain in value by using index selection. When traits are independent, H_X' is used.

h_i^2 Heritability for the ith trait.

h_{12} $G_{12}/\sqrt{(P_{11}P_{22})}$.

I Total selection differential in standardized units.

i_j Selection differential for the jth trait in standardized units.

n Number of traits under consideration.

$[P]$ Phenotypic variance and covariance matrix.

P_{ij} Phenotypic covariance of the ith and jth trait (for variance $i = j$).

p The total proportion of animals saved.

q_i Proportion of animals saved with respect to the ith trait.

X_i The ith trait.

x_i Measurement of the ith trait.

z The ordinate of the standardized normal curve at the point of truncation.

$\left.\begin{array}{l}\alpha_i \\ \beta_i\end{array}\right\}$ Constants used in the independent culling levels methods.

$\left.\begin{array}{l}\eta \\ \xi\end{array}\right\}$ Total genetic change, in standardized units, in a trait, X_1 or X_2, due to simultaneous selection for both X_1 and X_2.

λ_i Relative importance of the ith trait, $= a_i h_i^2\sqrt{(P_{ii})}$.

ρ Phenotypic correlation coefficient.

ρ_G Genetic correlation coefficient.

3. METHOD OF COMPARISON

(a) *Genetic gains by three methods of selection*

To compare the efficiency of tandem, independent culling and index selection methods, the genetic gain expected from each must be calculated. For the present purpose, the generation length within each class of livestock can be regarded as constant and the expected genetic gains per generation can be compared. On this basis, the expected genetic gains by tandem selection are the gains achieved by

single trait selection, although, for convenience, this will be referred to as gains by tandem selection in the subsequent discussion.

When using tandem selection, the expected gain per generation (H_T) by selection of the trait X_i can be shown to be

$$H_T = \Delta G_i\left(a_i + \sum_{j \neq i}^{n} a_j b_{G_{j \cdot i}}\right)$$

$$= I h_i^2 \sqrt{(P_{ii})}\left(a_i + \sum_{j \neq i}^{n} a_j b_{G_{j \cdot i}}\right) \tag{1}$$

When X_i is independent of other traits the expected genetic gain H'_T is

$$H'_T = a_i I h_i^2 \sqrt{(P_{ii})}.$$

When the method of independent culling levels is used, the expected genetic gain per generation by simultaneous culling of two correlated traits X_1 and X_2 is

$$H_C = \{a_1 \alpha_1 \sqrt{(P_{11})} + a_2 \beta_1 \sqrt{(P_{22})}\} i_1 + \{a_1 \alpha_2 \sqrt{(P_{11})} + a_2 \beta_2 \sqrt{(P_{22})}\} i_2$$
$$= V_1 i_1 + V_2 i_2 \qquad \text{(Young \& Weiler, loc. cit.)} \tag{2}$$

where i_1 and i_2 are the selection differentials of X_1 and X_2, when H_C is a maximum,

$$\alpha_1 = \frac{h_1^2 - \rho h_{12}}{1 - \rho^2}, \qquad \alpha_2 = \frac{h_{12} - \rho h_1^2}{1 - \rho^2},$$

$$\beta_1 = \frac{h_{12} - \rho h_2^2}{1 - \rho^2}, \qquad \beta_2 = \frac{h_2^2 - \rho h_{12}}{1 - \rho^2}.$$

When X_1, X_2 are independent, equation (2) reduces to

$$H'_C = a_1 h_1^2 \sqrt{(P_{11})} i_1 + a_2 h_2^2 \sqrt{(P_{22})} i_2, \tag{3}$$

which is identical to the formula presented by Hazel & Lush (loc. cit.), for in this case

$$\alpha_1 = h_1^2, \qquad \alpha_2 = 0,$$
$$\beta_1 = 0, \qquad \beta_2 = h_2^2.$$

Equation (3) can be expanded to n independent traits, and the expected gain due to selection for n traits is

$$H'_C = \sum_{i=1}^{n} a_i h_i^2 i_i \sqrt{(P_{ii})}, \tag{4}$$

where i_i may be written as $\dfrac{z_i}{q_i}$, where $\prod_{i=1}^{n} q_i = p$ the proportion of animals saved, and z_i is the ordinate of the normal curve corresponding to q_i.

Index selection was first used by Fairfield Smith (loc. cit.) for plants and later by Hazel (loc. cit.) in animal-breeding. The expected genetic gains by using the selection index may be written as (Fairfield Smith, loc. cit.; Morley, 1950)

$$H_X = I \sqrt{\left(\sum_{i=1}^{n} b_i^2 P_{ii} + 2 \sum_{i \neq j} b_i b_j P_{ij}\right)}. \tag{5}$$

When the traits under selection are independent the gain by index selection simplifies to

$$H'_X = I \sqrt{\left/ \left(\sum_{i=1}^{n} b_i^2 P_{ii} \right)\right.} \tag{6}$$

(b) Ratios of relative efficiencies

In comparing the relative efficiency of the selection index and other methods it is necessary to consider the ratios H_X/H_T, H_X/H_C and H_C/H_T, or, in the case of independent traits, H'_X/H'_T, H'_X/H'_C and H'_C/H'_T.

To simplify the above ratios, we now consider the relationships between the different genetic gains. In an index, when the traits under selection are independent,

$$P_{ij} = G_{ij} = 0 \ (i \neq j), \quad \text{so that} \quad b_i = a_i h_i^2.$$

If we write $\lambda_i = a_i h_i^2 \sqrt{(P_{ii})}$, then

$$H'_T = I\lambda_i, \tag{7}$$

$$H'_C = \sum_{i=1}^{n} i_i \lambda_i, \tag{8}$$

and

$$H'_X = I \sqrt{\left/ \left(\sum_{i=1}^{n} \lambda_i^2 \right)\right.}. \tag{9}$$

Using these relations, the ratio

$$\frac{H'_X}{H'_T} = \frac{I \sqrt{\left/ \left(\sum_{i=1}^{n} \lambda_i^2 \right)\right.}}{I\lambda_i} = \frac{\sqrt{\left(\sum_{i=1}^{n} \lambda_i^2 \right)}}{\lambda_i}, \tag{10}$$

which is independent of selection intensity (this is true also for H_X/H_T). The ratio

$$\frac{H'_X}{H'_C} = \frac{I \sqrt{\left/ \left(\sum_{i=1}^{n} \lambda_i^2 \right)\right.}}{\sum_{i=1}^{n} i_i \lambda_i} \tag{11}$$

is dependent on selection intensity and the number of traits under selection as well as the relative values of λ_i, as is also the ratio

$$\frac{H'_C}{H'_T} = \frac{\sum_{i=1}^{n} i_i \lambda_i}{I\lambda_i} \tag{12}$$

Hence, in comparing the relative efficiency of these selection methods, when the traits under selection are independent, changes in relative efficiency of selection methods are functions of selection intensity (p), number of traits under selection (n) as well the relative importance of the traits represented by the various λ values. An interesting point is that, when estimating the relative importance of any trait X_i, for a given set of parameters only the value of λ_i needs to be considered, as the components of λ_i (i.e. $a_i h_i^2$ and $\sqrt{(P_{ii})}$) have only the indirect importance of determining the size of λ_i.

When traits under selection are correlated, the relative efficiency is also affected by the levels of the phenotypic and genetic correlations (ρ and ρ_G). Therefore, in the following comparisons attempts have been made to relate changes in relative efficiency to changes in the five factors n, p, λ, ρ and ρ_G.

4. RESULTS

(a) *Effect of number of characters under selection and of selection intensity for equal λ-values*

The effects of number of traits under selection and selection intensity on the relative efficiency of selection methods have been investigated by Hazel & Lush (loc. cit.), and their formulae can be derived simply by the use of the ratios of genetic gains.

If traits under selection are uncorrelated and have equal λ-values,

$$\frac{H_X'}{H_T'} = \frac{\lambda_i \sqrt{n}}{\lambda_i} = \sqrt{n}, \tag{13}$$

$$\frac{H_X'}{H_C'} = \frac{I\lambda_i \sqrt{n}}{ni\lambda_i} = \frac{I}{i\sqrt{n}}, \tag{14}$$

$$\frac{H_C'}{H_T'} = \frac{ni\lambda_i}{I\lambda_i} = \frac{ni}{I}. \tag{15}$$

Hazel & Lush (loc. cit.) concluded that:

(i) The index is more efficient than tandem selection, the relative efficiency of the former increasing with n.

(ii) The index is more efficient than independent culling, its superiority rising with increasing n but falling with increasing selection intensity.

(iii) The independent culling method is more efficient than tandem selection, the superiority of the former rising both with increasing n and increasing selection intensity.

(b) *Effect of unequal λ-values*

When traits under selection have different λ-values, the ratios of genetic gains for uncorrelated traits cannot be reduced to simpler forms. To simplify computations, we now consider situations where n is fixed, since the effects of changes in n on the relative efficiency of various comparisons have been discussed earlier. It is also understood that in carrying out tandem selection, the trait with the largest λ-value is selected and the following calculations are based on this condition.

(i) *Index and tandem selection*

The relative efficiencies of the index and tandem selection for $n = 2$ and $n = 3$ are calculated according to (10). The results are shown in Table 1.

The relative efficiency varies with changes in relative importance of the traits. The superiority of the index method is at a maximum when the traits under selection have equal values of λ. This superiority decreases appreciably when λ-values are different. Thus, when $n = 2$, the index is 41% more efficient when $\lambda_1 = \lambda_2$, but

Table 1. *The relative efficiency of tandem and index selection*
for uncorrelated traits of unequal importance

Two traits			Three traits							
λ_1*	λ_2	H'_X/H'_T†	λ_1	λ_2	λ_3	H'_X/H'_T	λ_1	λ_2	λ_3	H'_X/H'_T
1	1	1·41	1	1	1	1·73	2	2	1	1·50
2	1	1·12	2	1	1	1·22	3	2	1	1·25
3	1	1·05	3	1	1	1·11	3	3	1	1·45
4	1	1·03	4	1	1	1·06	4	3	1	1·28
5	1	1·02	5	1	1	1·04	5	3	1	1·18
6	1	1·01	6	1	1	1·03	6	4	1	1·21

* λ_i = relative importance of the ith trait = $a_i h_i^2 \sqrt{(P_{ii})}$.

† H'_X/H'_T = relative efficiency of index over tandem selection.

only 5% more efficient when $\lambda_1 = 3\lambda_2$. The decline in relative superiority of the index is appreciable from the point $\lambda_1 = \lambda_2$ to $\lambda_1 = 2\lambda_2$, but with further increase in the difference between λ-values the decline is slow.

The same general pattern occurs when $n = 3$. It can be seen from Table 1 that if the λ_i are not all equal, the index has the greatest superiority when they are nearest to equality, that is, when their values are $2:2:1$ or $3:3:1$. The overall superiority of the index method is higher when $n = 3$ than when $n = 2$. This is not surprising because, as has been shown earlier, the relative efficiency of the index over the tandem method increases with increasing values of n.

(ii) *Index and independent culling levels*

Before (11) can be calculated, it is necessary to estimate the expected genetic gains by each method. The calculation of H'_X, the genetic gains by index selection, is reasonably simple as is indicated by equation (6), but calculation of H'_C, the genetic gains by using the culling method, involves the maximization of H'_C for a number of combinations of p- and λ-values. The results of maximization, giving various q-values for each p at which H'_C is a maximum, for two independent traits under selection are shown in Table 2. Table 2, which is an extension of a table presented

Table 2. *The appropriate proportion saved for two traits of*
unequal importance, for maximal genetic gains

λ_1*	λ_2	$p = 0.8$†		$p = 0.5$		$p = 0.2$		$p = 0.1$		$p = 0.05$	
		q_1‡	q_2	q_1	q_2	q_1	q_2	q_1	q_2	q_1	q_2
1	1	0·89	0·89	0·71	0·71	0·45	0·45	0·32	0·32	0·22	0·22
2	1	0·81	0·99	0·53	0·94	0·24	0·82	0·14	0·71	0·09	0·56
3	1	0·80	1·00	0·51	0·99	0·22	0·91	0·11	0·91	0·06	0·83
4	1	0·80	1·00	0·50	1·00	0·20	1·00	0·10	1·00	0·06	0·91
5	1	0·80	1·00	0·50	1·00	0·20	1·00	0·10	1·00	0·05	1·00
6	1	0·80	1·00	0·50	1·00	0·20	1·00	0·10	1·00	0·05	1·00

* λ_i = relative importance of the ith trait = $a_i h_i^2 \sqrt{(P_{ii})}$.

† p = total proportion of animals saved.

‡ q_i = proportion saved from the ith trait.

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by Hazel & Lush (loc. cit.), is not only useful for subsequent discussions here, but may be of value in practice when λ-values of the traits are known.

The expected genetic gains of H'_C and H'_X and the ratios of relative efficiency are shown in Table 3. The superiority of the index over independent culling levels is

Table 3. *The relative efficiency of index and independent culling levels for uncorrelated traits*

λ_1*	λ_2	†$p = 0{\cdot}8$ H'_X/H'_C‡	$p = 0{\cdot}5$ H'_X/H'_C	$p = 0{\cdot}2$ H'_X/H'_C	$p = 0{\cdot}1$ H'_X/H'_C	$p = 0{\cdot}05$ H'_X/H'_C
1	1	1·19	1·18	1·12	1·10	1·09
2	1	1·11	1·09	1·08	1·07	1·07
3	1	1·05	1·05	1·05	1·05	1·05
4	1	1·03	1·03	1·03	1·03	1·03
5	1	1·02	1·02	1·02	1·02	1·02
6	1	1·01	1·01	1·01	1·01	1·01

* λ_i = the relative importance of the ith trait.
† p = proportion of animals saved.
‡ H'_X/H'_C = the relative efficiency of the index and independent culling levels.

again at a maximum when $\lambda_1 = \lambda_2$, and there is a steady decline in its superiority as the ratio λ_1/λ_2 increases. Thus when $\lambda_1 = 4\lambda_2$ the difference in relative efficiency is only small, irrespective of selection intensity. If the λ-values are fixed the index method is more efficient when selection intensity is low; this is consistent with results shown earlier. An interesting point is that the efficiency of the index relative to independent culling and to tandem selection is the same when $\lambda_1 = 3\lambda_2$ (Tables 1 and 3), because, in this situation, H'_C is a maximum when culling is done entirely on the more important trait, thus reducing the independent culling method to that of single character selection. An exception is that when p is small (0·05) some attention may be paid to the less important trait but the additional genetic gain through this is negligible.

(iii) *Tandem selection and independent culling levels*

The ratios of relative efficiency using values of H'_T and H'_C calculated earlier are shown in Table 4. The superiority of independent culling levels over the tandem

Table 4. *The relative efficiency of tandem selection and independent culling levels for uncorrelated traits*

λ_1*	λ_2	†$p = 0{\cdot}8$ H'_C/H'_T‡	$p = 0{\cdot}5$ H'_C/H'_T	$p = 0{\cdot}2$ H'_C/H'_T	$p = 0{\cdot}1$ H'_C/H'_T	$p = 0{\cdot}05$ H'_C/H'_T
1	1	1·20	1·21	1·26	1·28	1·30
2	1	1·00	1·02	1·04	1·04	1·05
3	1	1·00	1·00	1·00	1·01	1·01
4	1	1·00	1·00	1·00	1·00	1·00
5	1	1·00	1·00	1·00	1·00	1·00
6	1	1·00	1·00	1·00	1·00	1·00

* λ_i = the relative importance of the ith trait.
† p = proportion of animals saved.
‡ H'_C/H'_T = relative efficiency of independent culling levels and tandem selection.

method is again at a maximum when $\lambda_1 = \lambda_2$ and, as in previous cases, there is a sudden decrease in relative efficiency of the superior method when $\lambda_1 > \lambda_2$. When $\lambda_1 = 3\lambda_2$ the two methods have identical efficiency at lower selection intensity; at very high intensity the independent culling level method is very slightly more efficient. The overall efficiency of independent culling levels is higher when selection is more intense, which is consistent with the results shown earlier.

(c) *Effect of correlation between traits*

The relative efficiency of selection methods can also be affected by the changes in both phenotypic (ρ) and genetic correlations (ρ_G) between traits under selection, since changes in correlations affect genetic gains. In the following consideration the number of traits under selection is limited to two, as only bivariate distributions have so far been considered.

(i) *Index and tandem selection*

$$\frac{H_X}{H_T} = \frac{I \sqrt{(b_1^2 P_{11} + b_2^2 P_{22} + 2b_1 b_2 P_{12})}}{\Delta G_1 (a_1 + a_2 b_{G2.1})}.$$

Consider a case when $P_{11} = P_{22} = a_1 = a_2 = 1$, $h_1^2 = h_2^2$, so that $\lambda_1 = \lambda_2$.
It can be shown that

$$b_1 = a_1(C_{11} G_{11} + C_{12} G_{21}) + a_2(C_{11} G_{12} + C_{12} G_{22}),$$
$$b_2 = a_1(C_{21} G_{11} + C_{22} G_{21}) + a_2(C_{21} G_{12} + C_{22} G_{22}),$$

where C_{ij} are the elements of the inverse phenotypic variance and covariance matrix $[P]^{-1}$. Under this condition $C_{11} = C_{22}$, $G_{11} = G_{22}$, so that $b_1 = b_2$ independent of changes in P_{12} and G_{12}, the phenotypic and genetic covariances. We have, therefore,

$$H_X = I \sqrt{(2b_1^2 + 2b_1^2 P_{12})}$$
$$= I b_1 \sqrt{\{2(1 + P_{12})\}}. \tag{16}$$

Now $b_1 = (C_{11} + C_{12})(G_{11} + G_{12})$. (Since $a_1 = a_2 = 1$, $G_{11} = G_{22}$, $G_{12} = G_{21}$.) In the matrix $[P]^{-1}$ the elements C_{ij} are

$$C_{11} = \frac{P_{22}}{P_{11} P_{22} - P_{12}^2}, \qquad C_{22} = \frac{P_{11}}{P_{11} P_{22} - P_{12}^2}, \qquad C_{12} = \frac{-P_{12}}{P_{11} P_{22} - P_{12}^2},$$

and b_1 therefore may be written as

$$b_1 = \frac{(1 - \rho)(G_{11} + G_{22})}{1 - \rho^2} = \frac{G_{11} + G_{12}}{1 + \rho} \quad (\text{since } P_{11} = P_{22} = 1), \tag{17}$$

and, from equation (16),

$$H_X = \frac{I(G_{11} + G_{12}) \sqrt{(2(1 + \rho))}}{1 + \rho}$$
$$= I(G_{11} + G_{12}) \sqrt{\frac{2}{1 + \rho}} \tag{18}$$

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Now, under the same condition, the gain by tandem selection

$$H_T = I\left(a_1 \frac{G_{11}}{\sqrt{(P_{11})}} + a_2 \frac{G_{11}}{\sqrt{(P_{11})}} \cdot \frac{G_{12}}{G_{11}}\right)$$

$$= I(G_{11} + G_{12}), \quad \text{since } a_1 = a_2 = 1, P_{11} = P_{22} = 1. \tag{19}$$

We have, therefore,

$$\frac{H_X}{H_T} = \sqrt{\frac{2}{1+\rho}} \tag{20}$$

The relative efficiency of these two methods under this special condition is a function of the phenotypic correlation, independent of changes in the genetic correlation. Thus, when $\rho = 0.5$ the index is about 15% more efficient, when $\rho = 0.3$ the index is about 23% more efficient, and when $\rho = -0.5$ the index is 100% more efficient. The reason for this is intuitively clear because in the calculation of the expected gain by single character selection the phenotypic correlation makes no contribution. When $\rho = 0$, then the index is $\sqrt{2}$ times more efficient, as was shown earlier. The superiority of the index thus increases with decreasing levels of phenotypic correlation.

Table 5. *The relative efficiency of tandem and index selection for two correlated traits for different values of various parameters, but with one trait twice as important as the other*

Case	Phenotypic correlation	Genetic correlation	H_X/H_T†
*(A) $a_1 = a_2 = 1$ $h_1^2 = 2h_2^2 = 0.6$ $\sqrt{(P_{11})} = \sqrt{(P_{22})} = 1$	0.5	-0.4	1·02
		-0.2	1·00
		0·2	1·00
		0·4	1·00
	0.3	-0.2	1·00
		-0.1	1·01
		0·1	1·03
		0·2	1·04
‡(B) or (C) $a_1 = 2a_2 = 2$ $h_1^2 = h_2^2 = 0.6$ $\sqrt{(P_{11})} = \sqrt{(P_{22})} = 1$	0.5	-0.4	1·09
		-0.2	1·02
		0·2	1·01
		0·4	1·04
	0.3	-0.2	1·00
		-0.1	1·01
		0·1	1.04
		0·2	1·06

* a_i = economic weight of the ith trait.
  h_i^2 = heritability of the ith trait.
  $\sqrt{(P_{ii})}$ = standard deviation of the ith trait.
† H_X/H_T = relative efficiency of the index method over the method of independent culling levels.
‡ The same results may be obtained by putting
     $a_1 = a_2 = 1, \quad h_1^2 = h_2^2 = 0.6, \quad \sqrt{(P_{11})} = 2\sqrt{(P_{22})} = 2 \quad$ (Case C).

Equation (20) could no longer hold if there were changes in relevant parameters. For example, consider the following situations:

(A) $a_1 = a_2 = P_{11} = P_{22} = 1$, $h_1^2 = 2h_2^2 = 0\cdot6$ so that $\lambda_1 = 2\lambda_2$,

(B) $a_1 = 2a_2 = 2$, $P_{11} = P_{22} = 1$, $h_1^2 = h_2^2 = 0\cdot6$ and $\lambda_1 = 2\lambda_2$,

(C) $a_1 = a_2 = 1$, $P_{11} = 4P_{22} = 4$, $h_1^2 = h_2^2 = 0\cdot6$ and $\lambda_1 = 2\lambda_2$.

The relative efficiencies of index and tandem selection, for various levels of genetic and phenotypic correlations, are shown in Table 5. From the examples shown in Table 5, it is seen that the relative efficiency changes with changes in both phenotypic and genetic correlations. However, in the situation defined above (i.e. $\lambda_1 = 2\lambda_2$), the effects of changes in either phenotypic or genetic correlations are relatively small, except perhaps in one case, where a difference of 9% in relative efficiency has resulted when a large positive phenotypic correlation is accompanied by a large negative genetic correlation. The overall superiority of the index in the present cases, as compared with that when $\lambda_1 = \lambda_2$, has decreased considerably, which is consistent with the earlier findings. Results in Table 5 also show that the effects of changes in levels of genetic correlation vary with the changes in other parameters, thus generalization on its effect when traits are of unequal importance does not seem possible.

(ii) *Index and independent culling levels*

$$\frac{H_X}{H_C} = \frac{I \sqrt{(b_1^2 P_{11} + b_2^2 P_{22} + 2b_1 b_2 P_{12})}}{V_1 i_1 + V_2 i_2},$$

where

$$V_1 = \{a_1 \alpha_1 \sqrt{(P_{11})} + a_2 \beta_1 \sqrt{(P_{22})}\},$$

$$V_2 = \{a_1 \alpha_2 \sqrt{(P_{11})} + a_2 \beta_2 \sqrt{(P_{22})}\}.$$

Consider the special case used previously; when $P_{11} = P_{22} = a_1 = a_2 = 1, h_1^2 = h_2^2$ so that $\lambda_1 = \lambda_2$ and $b_1 = b_2$ as has been shown earlier. Then

$$V_1 = \alpha_1 + \beta_1,$$

$$V_2 = \alpha_2 + \beta_2.$$

Since

$$h_{12} = \frac{G_{12}}{\sqrt{(P_{11} P_{22})}},$$

we have

$$h_{12} = G_{12},$$

so that

$$\alpha_1 = \beta_2, \quad \alpha_2 = \beta_1 \quad \text{and} \quad V_1 = V_2.$$

Also

$$V_1 = (\alpha_1 + \beta_1)$$

$$= \frac{G_{11} + G_{12}}{1 + \rho}. \tag{21}$$

From equations (17) and (21) we find that, under this special condition, $V_1 = V_2 = b_1 = b_2$, so that

$$\frac{H_X}{H_C} = \frac{I \sqrt{\{2(1+\rho)\}}}{i_1 + i_2}, \tag{22}$$

again independent of genetic correlations. The relative efficiency depends on the phenotypic correlation and the selection intensity. In cases where $V_1 = V_2$, the value of H_C is a maximum when $i_1 = i_2$, thus, when $\rho = 0$, equation (22) is reduced to (14) for $n = 2$.

Equation (22) could no longer hold if there are changes in relative values of P_{ij}, h_i^2, a_i, etc. Where all these parameters differ, the expression for H_X/H_C remains complex. Some computations were made, however, using a series of values for the parameters, and the results are presented in Table 6. Four cases were considered:

(A) $P_{11} = P_{22} = 1$, $h_1^2 = h_2^2 = 0.6$, $a_1 = a_2 = 1$ so that $\lambda_1 = \lambda_2$
with varying levels of phenotypic correlation.

(B) $P_{11} = P_{22} = 1$, $h_1^2 = 2h_2^2 = 0.6$, $a_1 = a_2 = 1$ so that $\lambda_1 = 2\lambda_2$
with varying levels of phenotypic and genetic correlations.

(C) $P_{11} = P_{22} = 1$, $h_1^2 = h_2^2 = 0.6$, $a_1 = 2a_2 = 2$ so that $\lambda_1 = 2\lambda_2$.

(D) $P_{11} = 4P_{22} = 4$, $h_1^2 = h_2^2 = 0.6$, $a_1 = a_2 = 1$ so that $\lambda_1 = 2\lambda_2$.

Table 6. *The relative efficiency of the index and independent culling levels methods of selection for two correlated traits*

Case	Phenotypic correlation	Genetic correlation	H_X/H_C†	
			$p = 0.1$	$p = 0.5$
*(A)	0.5	any value	1.03	1.05
$a_1 = a_2 = 1$	0.3	any value	1.07	1.09
$h_1^2 = h_2^2 = 0.6$				
$\sqrt{(P_{11})} = \sqrt{(P_{22})} = 1$	−0.5	any value	1.22	1.43
	0.5	−0.4	1.01	1.02
		−0.2	1.00	1.00
(B)		0.2	1.00	1.00
$a_1 = a_2 = 1$		0.4	1.00	1.00
$h_1^2 = 2h_2^2 = 0.6$	0.3	−0.2	1.00	1.00
$\sqrt{(P_{11})} = \sqrt{(P_{22})} = 1$		−0.1	1.01	1.01
		0.1	1.03	1.03
		0.2	1.04	1.04
	0.5	−0.4	1.09	1.09
		−0.2	1.02	1.02
(C)‡ or (D)		0.2	1.01	1.01
$a_1 = 2a_2 = 2$		0.4	1.02	1.03
$h_1^2 = h_2^2 = 0.6$	0.3	−0.2	1.00	1.00
$\sqrt{(P_{11})} = \sqrt{(P_{22})} = 1$		−0.1	1.01	1.00
		0.1	1.04	1.04
		0.2	1.05	1.06

* a_i = economic weight of the ith trait.
h_i^2 = heritability of the ith trait.
$\sqrt{(P_{ii})}$ = standard deviation of the ith trait.
† H_X/H_C = relative efficiency of the index method over the method of independent culling levels.
‡ The same results may be obtained by putting
$$a_1 = a_2 = 1, \quad h_1^2 = h_2^2 = 0.6, \quad \sqrt{(P_{11})} = 2\sqrt{(P_{22})} = 2 \quad \text{(Case D)}.$$

The superiority of the index increases with decreasing value of phenotypic correlation when $\lambda_1 = \lambda_2$. The index is also more efficient when the selection intensity is low, which is, of course, expected from earlier discussions. The superiority of the index is only relatively small when $\lambda_1 = 2\lambda_2$. In this case the effect of the genetic correlation again changes with changes in other parameters, and generalization of its effect on relative efficiency does not seem possible. The relative efficiency for some cases in Table 6 is similar to that shown in Table 5 for the comparison of the index with tandem selection. This is because the values of V_1 in all cases are several times larger than V_2. When this is so, H_C is a maximum when only the more important trait is selected, and the method of independent culling levels becomes equivalent to single character selection.

(iii) *Independent culling levels and tandem selection*

From equations (19) and (21), when $a_1 = a_2 = 1$, $P_{11} = P_{22} = 1$, $h_1^2 = h_2^2$, and $i_1 = i_2$,

$$\frac{H_C}{H_T} = \frac{2i_1}{I(1+\rho)} \tag{23}$$

When $\rho = 0$, equation (23) is reduced readily to equation (15) for uncorrelated traits. The relative efficiency in this case is again independent of genetic correlation, but is affected by changes in phenotypic correlation and selection intensity. Thus when $p = 0\cdot1$ and $\rho = 0\cdot5$ the culling method is 12% more efficient; for the same p-values, if $\rho = 0\cdot3$ the culling method is 16% more efficient, and if $\rho = -0\cdot5$ it is 64% more efficient. Hence, the superiority of the culling method increases with decreasing values of ρ. The overall efficiency of the culling method is slightly lower when there is a reduction in selection intensity. When $\lambda_1 = 2\lambda_2$, the efficiencies of the two selection methods are similar, as discussed earlier.

5. DISCUSSION

In estimating the relative efficiency of selection methods the ideal way, of course, would be to calculate the expected genetic gains by each selection method, following the steps described earlier. In most cases, however, it is possible to reach some conclusion from the results presented above, without carrying out tedious computations. Thus, for example, when two negatively correlated traits of equal importance are under selection, the index method is the choice when selection intensity is low. If the selection intensity is high, then independent culling levels may be more appropriate because of the relative simplicity of operation. Again, if one trait is three times more important than another, then tandem selection is probably the choice and other factors, such as correlations and selection intensity, have but minor effects on relative efficiency. It follows, therefore, that the question of relative efficiency is only important when the traits have about equal importance, and a simple computation of λ-values for each trait would often give sufficient ground for the rejection of more sophisticated methods of selection for genetic gains.

In addition to considering maximum gains in economic terms, it is necessary in animal breeding to estimate the changes in means of various important traits in future generations, since if traits are correlated genetically any changes in one might be accompanied by a deterioration of others. Continued application of a single scheme of selection might, therefore, not be desirable. For example, use of an index for selecting fleece weight and crimps based on parameters given by Morley (1955) and economic weights by Dunlop & Young (1960) would lead to an expected decrease in crimp number in future generations. If long-term decreases in crimps are undesirable in some circumstances, then it is important to alter the selection method or to select for fleece weight while at the same time controlling crimp number.

The method of selecting for one trait while keeping the other trait constant, using a specially constructed index, has been described by Morley (1955). However, it is worth noting that independent culling levels can also be applied in this way. From equations shown by Young & Weiler (loc. cit.), the genetic gains by the culling method for two correlated traits are

$$H_C = a_1 \sqrt{(P_{11})}\, \xi + a_2 \sqrt{(P_{22})}\, \eta,$$

where ξ and η are the expected genetic changes in traits X_1 and X_2 respectively. If we wish to keep $\eta = 0$, we have

$$\beta_1 i_1 + \beta_2 i_2 = 0,$$

$$i_2 = \frac{-\beta_1}{\beta_2} i_1 \tag{24}$$

For any given proportion of animals saved we can obtain a combination of i_1 and i_2 which satisfies (24). Again we have a choice of two methods of selection.

On the other hand, if it is desirable to make as much progress on one particular trait as possible, then a selection index can be used. Thus if X_1 and X_2 are two correlated traits, the aim is to construct an index in order to improve X_1 while at the same time using X_2 for correcting the environmental effects on X_1. This particular application of the index has been suggested by Hazel (loc. cit.) and a special case has been discussed by Rendel (1954), who found that the phenotypic regression coefficient of X_1 on X_2 might be used to advantage if the genetic correlation between X_1 and X_2 were smaller than the phenotypic correlation. However, in cases where the estimate of genetic correlation is available, it seems appropriate to apply an index which can account for the genetic covariance.

Suppose X, Y, Z are three traits in an animal and we wish to maximize the genetic changes in X. If we take one pair of traits, X, Y, or X, Z, at a time and denote X by X_1 and Y or Z by X_2, then an index

$$S = b_1 X_1 + b_2 X_2$$

can be formed. Now if we put $b_1 = 1$ and give no economic weight to X_2,

$$b_2 = \frac{P_{11} G_{21} - P_{12} G_{11}}{P_{22} G_{11} - P_{12} G_{21}}. \tag{25}$$

The expected genetic change in X_1 by using an index has been shown by Fairfield Smith (loc. cit.) and Morley (1950) to be

$$\Delta G'_X = I \frac{\sum_j b_j G_{ij}}{\sigma_S},$$

where σ_S is the standard deviation of the selection index. When $b_1 = 1$,

$$\Delta G'_X = I \frac{G_{11}}{\sqrt{(P_{11})}} \left(\frac{1 + b_2 \dfrac{G_{12}}{G_{11}}}{\sqrt{\left(1 + b_2^2 \dfrac{P_{22}}{P_{11}} + 2b_2 \dfrac{P_{12}}{P_{11}}\right)}} \right) \tag{26}$$

Remembering that the genetic change in X_1 by single character selection is

$$\Delta G = I \frac{G_{11}}{\sqrt{(P_{11})}},$$

equation (26) may be written as

$$\Delta G'_X = \Delta G \left(\frac{1 + b_2 \dfrac{G_{12}}{G_{11}}}{\sqrt{\left(1 + b_2^2 \dfrac{P_{22}}{P_{11}} + 2b_2 \dfrac{P_{12}}{P_{11}}\right)}} \right)$$

$$= \Delta G . K \text{ (say).} \tag{27}$$

The value of K gives information about the additional gain in X_1, in terms of percentages, when such an index is used. For example, a value of $1 \cdot 20$ for K indicates that 20% more gain can be expected by using such an index. It follows that the size of K indicates whether the index approach is worthwhile.

If the genetic covariance is zero,

$$b_2 = -\frac{P_{12}}{P_{22}} \tag{28}$$

and

$$\Delta G'_X = \Delta G . \frac{1}{\sqrt{(1 - \rho^2)}}.$$

Since ρ cannot be greater than unity, $\Delta G'_X \geqslant \Delta G$ ($\rho < 1$) and the index is more efficient when ρ is large. In these circumstances, the method suggested by Rendel (loc. cit.) has the same efficiency as the index. Now if the K value obtained by using Y as environmental correction for X is greater than that when Z is used, then, of course, Y should be chosen for this purpose. Following the same principle, an index can also be constructed using both Y and Z as environmental corrections for X, but the computations become tedious and the additional advantage is probably small.

Independent culling levels can also be used to this end by putting the economic weight of Y (or Z) equal to zero. Then we have

$$\Delta G'_X = \{\sqrt{(P_{11})}\,\alpha_1\} i_1 + \{\sqrt{(P_{11})}\,\alpha_2\} i_2$$

$$= T'_1 i_1 + T'_2 i_2 \text{ (say),} \tag{29}$$

and $\Delta G'_X$ can be maximized accordingly. Here two alternative methods for increasing the genetic progress in a single trait, beyond that which may be achieved by single character selection, are available. The relative merit of these methods for the present purpose depends on the relative sizes of $\Delta G'_X$ which may be attained by each method, and numerical calculation in each case is necessary.

The relative efficiency of selection methods therefore may be affected by some special applications of these methods, apart from the various factors (n, p, etc.) discussed earlier. These special applications are often useful in animal-breeding work, and the two cases outlined above show some of the possibilities. However, the relative efficiency of any special applications of selection methods can probably be compared by the same principle used in this work, i.e. by comparing the relative genetic gains.

However, it seems appropriate to reiterate that the relative efficiency of selection methods in terms of genetic gains in economic value is but one of the several factors in determining an optimum method of selection. Factors such as practicability, costs, and the consequences due to the use of any method could all have significant bearing in choosing an optimum method.

It should be pointed out that the comparisons discussed in this work have been limited to linear cases: i.e. all the regressions involved are assumed to be linear. When this condition is altered, the relative efficiency of selection methods may be quite different.

SUMMARY

The relative efficiency of three methods of selection (index, independent culling levels and tandem) is compared in terms of genetic gains in economic units. The comparison covers cases where variances, heritabilities and economic weights are unequal, while the case of two correlated characters is also examined. Various factors may influence the relative efficiency, including selection intensity, the number of traits under selection, the relative importance of those traits (in terms of a factor λ, which is the product of economic weight, heritability and phenotypic standard deviation), and the correlations between them.

The conclusions are:

(i) In all circumstances the index is never less efficient than independent culling levels, though in some cases it is no more efficient. Independent culling is, in turn, never less, but in some cases no more efficient than tandem selection.

(ii) The superiority of the index over other methods increases with an increasing number of traits under selection, but decreases with increasing differences in relative importance, its superiority being at a maximum when the traits are of equal importance. The superiority of the index over independent culling levels decreases with increasing selection intensity, but its superiority over tandem selection is independent of intensity.

(iii) The superiority of independent culling over tandem selection increases with increasing selection intensity or an increasing number of traits under selection, but decreases with increasing differences in relative importance.

(iv) The relative efficiency of the index over other methods is much affected by the phenotypic correlation between traits when the traits are of equal importance, the relative efficiency of the index being higher when the phenotypic correlation is low or negative. The effect of genetic correlation is only apparent when the traits are of unequal importance and its influence on relative efficiency changes with changes in other parameters.

(v) The relative efficiency of selection methods may be changed by their use for special purposes.

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