EVALUATION OF THE CULLING VARIATE USED BY BREEDERS IN ACTUAL SELECTION

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ABSTRACT

The theoretical basis and computational procedures for estimating the culling variate utilized by breeders in actual selection are presented. The essential part of this procedure is to derive the unknown culling variate in terms of a linear combination of traits based on realized indirect selection differentials of those traits and phenotypic variances and covariances among traits in the population. Special emphasis is placed on the distribution of the variables involved. The accuracy of the culling variate is estimated by use of the biserial correlation with some modifications. Numerical illustrations are given for different types of selection.

IT is more common than exceptional to observe that the realized selection criterion differs to some extent from the intended one, irrespective of selection for a single trait or simultaneous selection for multiple objectives. Even in a well-designed selection experiment dealing with laboratory animals, it is common to observe that some individuals which are endowed with high predicted breeding value and were, therefore, singled out for reproduction were supplanted by inferior individuals owing to reproductive failure or early death or some other reason. On the other hand, breeders using an index including several traits often observe similar results. Also in practical breeding programs for multiple traits, some breeders prefer to use selection criteria based on experience and intuition rather than on theoretical considerations. In this case, there is no theoretical basis to predict, compare or interpret the effectiveness of selection, *i.e.*, whether or not the changes observed in the various traits are in accordance with existing quantitative genetic theory.

The description and evaluation of selection practiced on more than one trait have received little attention. To determine the relative importance of each trait and the role of an entire set of traits in selection, it is necessary to consider the interrelationships between these traits. The application of selection index principles for the examination in retrospect of selection on more than one trait was first used in swine by DICKERSON *et al.* (1954). Similar but more refined methods were presented by HARVEY and BEARDEN (1962), MAGEE (1965) and more recently by BERGER and HARVEY (1975) and KOCH, GREGORY and CUNDIFF (1974), under the assumption that all traits are normally distributed.

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Recently, YAMADA (1975) has pointed out that selection criteria in two-way selection for pupa weight in Tribolium could differ from each other by introducing unconscious secondary selection for pupation time. Accordingly, these selections resulted in asymmetrical heritabilities and genetic correlations. The same author also pointed out that the skewness of the distribution of a trait in two-way selection would result in different selection criteria, although the experimenter had intended to select only for a single trait.

The objectives of this paper are to extend the method used by DICKERSON *et al.* (1954) and others and to apply it to cases where the distributions among traits are not normal, as well as to provide a logical procedure to evaluate selection criteria used by breeders and experimenters, based on available information.

THEORETICAL CONSIDERATIONS

For simplicity, the description will first be presented in the case where two characters are bivariate normal. Let X_1 and X_2 represent the trait subjected to intended selection and the correlated trait, respectively. If selection is practiced only on X_1, the relationship of the selection differentials of X_1 and X_2 is given as

$$\Delta P_{2.1} = \Delta P_{1.1} \frac{\sigma_{X_{21}}}{\sigma^2_{X_1}} \tag{1a}$$

$$= \Delta P_{1.1}\, b_{2.1} \tag{1b}$$

where $\sigma^2_{X_1}$ and $\sigma_{X_{21}}$ represent the variance of X_1 and the covariance between X_1 and X_2, respectively, and $b_{2.1}$ is the regression coefficient of X_2 on X_1. $\Delta P_{i.j}$ is the selection differential of the first subscripted trait(i) when selection is intended for the second subscripted trait(j), as is illustrated in Figure 1. The notation which will appear in the following section is identical to that used previously except that G represents "genetic."

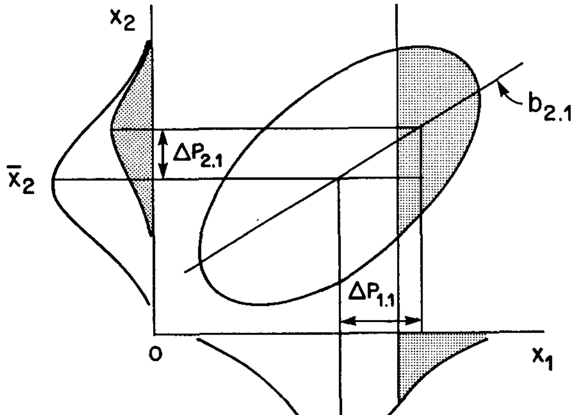

FIGURE 1.—The relationship between direct and indirect selection differentials.

The next example considers the case where selection was on X_1 and X_2. Thus, the criterion of selection is an index of the form of $I = b_1X_1 + b_2X_2$, in which the b_i's are unknown. The realized selection differentials in X_1 and X_2 will, therefore, be

$$\Delta P_{1.I} = \Delta P_{I.I} \frac{\sigma_{X_1.I}}{\sigma_I^2} = \frac{\Delta P_{I.I}}{\sigma_I^2} \mathrm{Cov}(X_1,I) \tag{2a}$$

$$= \frac{\Delta P_{I.I}}{\sigma_I^2} [b_1\, \sigma^2_{X_1} + b_2\, \sigma_{X_{12}}] \tag{2b}$$

$$\Delta P_{2.I} = \frac{\Delta P_{I.I}}{\sigma_I^2} [b_1\, \sigma_{X_{21}} + b_2\, \sigma^2_{X_2}] \tag{2c}$$

In the matrix notation, these equations can be expressed as

$$\begin{bmatrix} \Delta P_{1.I} \\ \\ \Delta P_{2.I} \end{bmatrix} = \frac{\Delta P_{I.I}}{\sigma_I^2} \begin{bmatrix} \sigma^2_{X_1} & \sigma_{X_{12}} \\ \\ \sigma_{X_{21}} & \sigma_{X_2} \end{bmatrix} \begin{bmatrix} b_1 \\ \\ b_2 \end{bmatrix} \tag{3a}$$

which yields a solution of b_i's as

$$\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} = \begin{bmatrix} \sigma^2_{X_1} & \sigma_{X_{12}} \\ \sigma_{X_{21}} & \sigma^2_{X_2} \end{bmatrix}^{-1} \begin{bmatrix} \Delta P_{1.I} \\ \Delta P_{2.I} \end{bmatrix} \tag{3b}$$

by imposing the condition of

$$\sigma_I^2 \,/\, \Delta P_{I.I} = 1 \;. \tag{3c}$$

In the above, $\Delta P_{1.I}$ and $\Delta P_{2.I}$ are the realized selection differentials in X_1 and X_2, which are expressed as the deviation of the mean of selected individuals, $\bar{X}_{i(S)}$, from the population mean, $\bar{X}_{i(0)}$, of the trait considered, *i.e.*,

$$\begin{bmatrix} \Delta P_{1.I} \\ \Delta P_{2.I} \end{bmatrix} = \begin{bmatrix} \bar{X}_{1(S)} \\ \bar{X}_{2(S)} \end{bmatrix} - \begin{bmatrix} \bar{X}_{1(0)} \\ \bar{X}_{2(0)} \end{bmatrix} \tag{4}$$

The equations (3a) are identical to the ones obtained by HARVEY and BEARDEN (1962) and MAGEE (1965), except that in those studies the variables were standardized.

The variances and covariances of equations (3a,b) can also be expressed in terms of direct and indirect selection differentials based on paper selection for X_1 or X_2, assuming that the intensity of selection expressed in terms of standard deviation units, i, is the same whether selection is solely on X_1 or solely on X_2, *i.e.*, $\Delta P_{1.1}/\sigma_{X_1} = \Delta P_{2.2}/\sigma_{X_2}$. The value of i can be obtained from BECKER (1975). Thus, we have

$$\sigma^2_{X_i} = \sigma_{X_{i.i}} = \Delta P^2_{i.i} \,/\, i^2 \text{ and } \sigma_{X_{i.j}} = \Delta P_{i.j}\, \Delta P_{j.j} \,/\, i^2 \;. \tag{5}$$

It is worthwhile to note here that regression and correlation coefficients may also be expressed in terms of selection differentials as

$$\frac{\Delta P_{1.2}}{\Delta P_{2.2}} = \frac{\Delta P_{1.2}\Delta P_{2.2}}{\Delta P^2_{2.2}} = \frac{\sigma_{X_{1.2}}}{\sigma_{X_{2.2}}} = b_{1.2} \tag{6a}$$

$$\frac{\Delta P_{2.1}}{\Delta P_{1.1}} = \frac{\Delta P_{2.1}\Delta P_{1.1}}{\Delta P^2_{1.1}} = \frac{\sigma_{X_{2.1}}}{\sigma_{X_{1.1}}} = b_{2.1} \tag{6b}$$

$$\frac{\Delta P_{1.2}}{\Delta P_{1.1}} = \frac{\Delta P_{1.2}\Delta P_{2.2}}{\Delta P_{1.1}\Delta P_{2.2}} = \frac{\sigma_{X_{1.2}}}{\sqrt{\sigma_{X_{1.1}}\sigma_{X_{2.2}}}} = r_{1.2} \quad \text{(by definition)} \tag{6c}$$

$$\frac{\Delta P_{2.1}}{\Delta P_{2.2}} = \frac{\Delta P_{2.1}\Delta P_{1.1}}{\Delta P_{1.1}\Delta P_{2.2}} = \frac{\sigma_{X_{2.1}}}{\sqrt{\sigma_{X_{1.1}}\sigma_{X_{2.2}}}} = r_{2.1} \quad \text{(by definition)} \tag{6d}$$

and

$$\begin{aligned} b_{1.2}b_{2.1} = r_{1.2}r_{2.1} &= \frac{\sigma_{X_{1.2}}\sigma_{X_{2.1}}}{\sigma_{X_{1.1}}\sigma_{X_{2.2}}} \\ &= \frac{\sigma^2_{X_{12}}}{\sigma^2_{X_1}\sigma^2_{X_2}} \quad \text{(assuming bivariate normality)} \\ &= r^2_{12} \end{aligned} \tag{6e}$$

The quantities $\sigma_{X_{i.i}}$ and $\sigma_{X_{i.j}}$ appearing in equations (5) to (6e) are defined as the directional variance and covariance, respectively.

These two directional covariances, as well as the variances of the same trait obtained by truncating either the higher or lower tail of the distribution should be equal to each other under the assumption of a bivariate normal distribution.

The substitution of (5) into (3a) will yield

$$\begin{bmatrix} \Delta P_{1.I} \\ \Delta P_{2.I} \end{bmatrix} = \frac{\Delta P_{I.I}}{\sigma^2_I\, i^2} \begin{bmatrix} \Delta P_{1.1} & \Delta P_{1.2} \\ \Delta P_{2.1} & \Delta P_{2.2} \end{bmatrix} \begin{bmatrix} \Delta P_{1.1} & 0 \\ 0 & \Delta P_{2.2} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} \tag{7}$$

in which I is the realized selection index or culling variate in the actual selection.

The solution of b_i's can be obtained with the same condition of (3c) as

$$\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} = i^2 \begin{bmatrix} \Delta P_{1.1} & \Delta P_{1.2} \\ \Delta P_{2.1} & \Delta P_{2.2} \end{bmatrix} \begin{bmatrix} \Delta P_{1.1} & 0 \\ 0 & \Delta P_{2.2} \end{bmatrix}^{-1} \begin{bmatrix} \Delta P_{1.I} \\ \Delta P_{2.I} \end{bmatrix} \tag{8a}$$

or $\mathbf{b} = i^2\, [\Delta\mathbf{P}_{i.j}\ \mathrm{diag}\ \Delta\mathbf{P}_{j.j}]^{-1}\, \Delta\mathbf{P}_{i.I}$

where $\mathbf{b}$, $\Delta\mathbf{P}_{i.j}$, diag $\Delta\mathbf{P}_{j.j}$ and $\Delta\mathbf{P}_{i.I}$ represent corresponding column vectors or matrices shown in (8a).

One can extend the theory to the evaluation of the index for k traits as follows:

$$\begin{bmatrix} b_1 \\ b_2 \\ \cdot \\ \cdot \\ b_k \end{bmatrix} = i^2 \begin{bmatrix} \Delta P_{1.1} & \Delta P_{1.2} & \cdots & \Delta P_{1.k} \\ \Delta P_{2.1} & \Delta P_{2.2} & \cdots & \Delta P_{2.k} \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ \Delta P_{k.1} & \Delta P_{k.2} & \cdots & \Delta P_{k.k} \end{bmatrix} \begin{bmatrix} \Delta P_{1.1} & & & \mathbf{0} \\ & \Delta P_{2.2} & & \\ & & \cdot & \\ \mathbf{0} & & & \cdot \\ & & & \Delta P_{k.k} \end{bmatrix}^{-1} \begin{bmatrix} \Delta P_{1.I} \\ \Delta P_{2.I} \\ \cdot \\ \cdot \\ \Delta P_{k.I} \end{bmatrix} \qquad (9a)$$

or $\mathbf{b} = i^2\,[\Delta \mathbf{P}_{i.j}\ \mathrm{diag}\ \Delta \mathbf{P}_{j.j}]^{-1}\,\Delta \mathbf{P}_{i.I}$. (9b)

The constant i^2 can be removed from (8a,b) and (9a,b) to derive the index, since rankings of individuals are required rather than absolute values.

To express the weights, b_i's, relative to the maximum ($b_{\max}$), one simply divides each b_i by $b_{\max}$, *i.e.*, $b_i^* = b_i/b_{\max}$.

In the case where simultaneous selection for multiple traits by means of the intended selection index, $I_E = w_1X_1 + w_2X_2 + \ldots + w_nX_n$, is used as a reference, the realized selection index, I, can be evaluated as accurately as before.

Once the values of b_i's in the realized index are determined, the corresponding genetic gains of the component traits can be obtained as follows:

$$\Delta G_{i.I} = \frac{\Delta P_{I.I}}{\sigma_I^2}\,\mathrm{Cov}_G(X_i,I)$$

$$= \mathrm{Cov}_G(X_i,I) \qquad (10)$$

since $\Delta P_{I.I}/\sigma_I^2 = 1$ from (3c), which yields

$$\begin{bmatrix} \Delta G_{1.I} \\ \Delta G_{2.I} \end{bmatrix} = \begin{bmatrix} \sigma_{G_1}^2 & \sigma_{G_{12}} \\ \sigma_{G_{21}} & \sigma_{G_2}^2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} \qquad (11)$$

Genetic components of variances and covariances in (11) as well as those of phenotypic in (3b) should be estimated from ordinary variance component analysis.

The genetic variances and covariances in (11) can be expressed as follows:

$$\sigma_{G_1}^2 = \sigma_{G_{1.1}} = \Delta G_{1.1}\,\Delta P_{1.1} / i^2 \qquad (12a)$$

$$\sigma_{G_2}^2 = \sigma_{G_{2.2}} = \Delta G_{2.2}\,\Delta P_{2.2} / i^2 \qquad (12b)$$

$$\sigma_{G_{12}} = \sigma_{G_{1.2}} = \Delta G_{1.2}\,\Delta P_{2.2} / i^2 \qquad (12c)$$

$$\sigma_{G_{21}} = \sigma_{G_{2.1}} = \Delta G_{2.1}\,\Delta P_{1.1} / i^2 \qquad (12d)$$

The $\Delta P_{i.j}$'s and $\Delta G_{i.j}$'s can be evaluated by applying the same selection intensity, say Q, actually given to the population under consideration, from the techniques of linear heritability and genetic correlation, first given by Abplanalp (1961) and later Yamada (1972), after some modifications suggested by Arthur and Abplanalp (1975) as follows:

Assuming a one-way linear mathematical model for X as an example,

$$X_{kl} = \mu_X + B_{X_k} + W_{X_{kl}},\ \ k = 1,2,\ldots,a;\ \ 1 = 1,2,\ldots,n \qquad (13)$$

where B_{X_k} is the effect of the k^{th} genetic group, and $W_{X_{kl}}$ is the within-group random deviation of the l^{th} individual belonging to the k^{th} genetic group.

Now, calculate the following quantities by selecting the top q individuals for X' with selection intensity, Q.

$$\Delta B_{X.X'} = \frac{a}{a-1} [\Delta P_{B_{X.X'}}] - \frac{n}{n-1} [\Delta P_{W_{X.X'}} / n] \tag{14a}$$

$$\Delta W_{X.X'} = \frac{n}{n-1} [\Delta P_{W_{X.X'}}] \tag{14b}$$

in which

$$\Delta P_{B_{X.X'}} = \frac{1}{q} \sum_{i.j} (\bar{X}_{k.} - \bar{X}_{..}) \, \delta_{kl} \tag{15a}$$

$$\Delta P_{W_{X.X'}} = \frac{1}{q} \sum_{i.j} (X_{kl} - \bar{X}_{k.}) \, \delta_{kl} \ . \tag{15b}$$

Equations (15a) and (15b) are defined as between-group and within-group selection differentials, respectively, and $\delta_{kl} = 1$ for all selected individuals based on the primary selection criterion X', and $\delta_{kl} = 0$ otherwise.

The interpretation of $\Delta B_{X.X'}$ and $\Delta W_{X.X'}$ are as follows:

$$\Delta G_{X.X'} = \frac{1}{r^G} \Delta B_{X.X'} \tag{16a}$$

$$\Delta E_{X.X'} = \Delta W_{X.X'} - (1 - r^G) \, \Delta G_{X.X'} \tag{16b}$$

and

$$\Delta T_{X.X'} = \Delta G_{X.X'} + \Delta E_{X.X'} \tag{16c}$$

where r^G is Wright's coefficient of relationship between the member of the same genetic group, and $\Delta G_{X.X'}$ and $\Delta E_{X.X'}$ are defined as the genetic and environmental selection differentials, respectively. $\Delta T_{X.X'}$ is the estimator of $\Delta P_{X.X'}$, similar to the case of variance component analysis, *i.e.*, $\sigma^2_T = \sigma^2_G + \sigma^2_E$.

In the above from (14a) to (16c), X and X' are mutually exchangeable, *i.e.*, $X = X'$ in the case of direct selection and $X \neq X'$ in the case of indirect selection.

Heritability and genetic correlation can be obtained from

$$h^2_X = \frac{\Delta G_{X.X}}{\Delta T_{X.X}}$$

$$r_{G_{X.X'}} = \frac{\Delta G_{X.X'}}{\Delta T_{X.X'}} \left[\frac{\Delta G_{X.X} \, \Delta G_{X'.X'}}{\Delta T_{X.X} \, \Delta T_{X'.X'}} \right]^{-1/2}$$

Substituting (12 a~d) into (11), we have

$$\begin{bmatrix} \Delta G_{1.I} \\ \Delta G_{2.I} \end{bmatrix} = \frac{1}{i^2} \begin{bmatrix} \Delta G_{1.1} & \Delta G_{1.2} \\ \Delta G_{2.1} & \Delta G_{2.2} \end{bmatrix} \begin{bmatrix} \Delta P_{1.1} & 0 \\ 0 & \Delta P_{2.2} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$

or

$$\Delta \mathbf{G}_{i.I} = \Delta \mathbf{G}_{i.j} \, \mathrm{diag} \, \Delta \mathbf{P}_{j.j} \, \mathbf{b}_i \, / \, i^2$$

The application of the above derivation to k traits is a straightforward procedure and is omitted.

How well the derived index fits the actual selection can be evaluated by using biserial correlation, under the assumption that the derived index and the underlying variate of the actual selection are distributed as the bivariate normal and the index is continuous while the underlying variate takes either a 1 or 0 value.

The estimator of the correlation is

$$r_b = \frac{\bar{I}_{(S)} - \bar{I}}{\sigma_I} \, \frac{Q}{z} = \frac{\bar{I}_{(S)} - \bar{I}}{\bar{I}_{(Q)} - \bar{I}} \tag{20}$$

since $$\frac{z}{Q} = \frac{\bar{I}_{(Q)} - \bar{I}}{\sigma_I}$$

where $\bar{I}_{(Q)}$, $\bar{I}_{(S)}$ and $\bar{I}$ represent the average of the derived index values of the top q individuals selected by truncation, the average index value of actually selected individuals, and the average index value of the whole population, respectively. σ_I is the square root of the variance of the derived index, Q is the proportion of selected individuals in relation to the whole population, and z is the height of the ordinate of the normal distribution at the point of truncation above which the proportion of the selected to the whole population is equal to Q.

The selection index in retrospect mentioned above can also apply to the case where within- and between-family selection or combination of these were practiced in a lowly heritable trait but with individual selection in other traits. If such is known *a priori*, the indirect selection differentials in (3a,b) should be partitioned into their components and the variance-covariance matrix should be calculated accordingly, *i.e.*,

$$\Delta\mathbf{P}'_{i.I} = [\Delta P_{W_{X_1}.I} \quad \Delta P_{B_{X_1}.I} \quad \Delta P_{X_2.I}] \tag{21}$$

$$[\sigma_{X_{ij}}] = \begin{bmatrix} \sigma^2_{W_{X_1}B} & \sigma_{W_{X_1}B_{X_1}} & \sigma_{W_{X_1}X_2} \\ \sigma_{B_{X_1}W_{X_1}} & \sigma^2_{B_{X_1}} & \sigma_{B_{X_1}X_2} \\ \sigma_{X_2\,W_{X_1}} & \sigma_{X_2\,B_{X_1}} & \sigma^2_{X_2} \end{bmatrix} \tag{22}$$

where the subscripts W_{X_i}, B_{X_i} and X_j of the elements of the vector or matrix are within- and between-family effects of the i^{th} trait and individual records of the j^{th} trait, respectively, and the prime of a vector indicates a row vector. It must be noticed that the covariance between within-family and between-family effects is zero for all i and j.

The variances and covariances in (22) can be replaced by direct and indirect selection differentials as given in (5). Namely,

$$\begin{aligned} &\sigma^2_{W_{X_i}} = \Delta W_{i.i}\, \Delta P_{i.i}/i^2, \quad \sigma_{W_{X_i}W_{X_j}} = \Delta W_{i.j}\, \Delta P_{j.j}/\, i^2, \\ &\sigma_{B_{X_i}B_{X_i}} = \Delta B_{i.j}\, \Delta P_{j.j}/\, i^2, \quad \sigma_{W_{X_i}X_j} = \sigma_{W_{X_i}W_{X_j}}, \\ &\sigma_{B_{X_i}X_j} = \sigma_{B_{X_i}B_{X_j}}, \quad \sigma^2_{B_{X_i}} = \Delta B_{i.i}\, \Delta P_{i.i}/i^2; \text{ etc.} \end{aligned} \tag{23}$$

In the above $\Delta P_{i.j}$ and $\Delta P_{j.j}$ should be replaced by $\Delta T_{i.j}$ and $\Delta T_{j.j}$, respectively, for computational purpose.

The resulting index is therefore

$$I = b_1(X_{1_{kl}} - \bar{X}_{1_{k.}}) + b_2(\bar{X}_{1_{k.}} - \bar{X}_{1_{..}}) + b_3(X_{2_{kl}} - \bar{X}_{2_{..}})$$

The last comment is on independent culling level selection. One may argue that the breeder may have applied independent culling levels rather than a linear combination of traits. If this view was strongly suggested, the following selection index can be evaluated:

$$I = X_1^{b_1} X_2^{b_2} X_3^{b_3}$$

The solution of b_i's can be obtained by ln transformation. Index contours will consist of hyperbolas that slice the population as is shown in Figure 2. It is questionable, however, if the use of such a multiplicative index is more advantageous than a linear one, because (1) the selection index in retrospect is definitely an approximation of actual selection in terms of linear form, and (2) such a multiplicative index will give a new complication for the interpretation of the consequence of selection.

NUMERICAL ILLUSTRATIONS

A set of hypothetical data of 25 individuals which belong to 5 genetic groups sampled randomly from a base population and measured on three traits is presented in Table 1. For simplicity, r^G is assumed to be unity, although it is unrealistic.

Suppose that 8 individuals were selected by a breeder without describing his selection criteria. The selection intensity actually applied was $Q = 8/25 = 30\%$. One would like to know the breeder's culling variates in terms of the selection index in retrospect, based on available information.

The variance-covariance matrix and other important statistics obtained from the data are as follows:

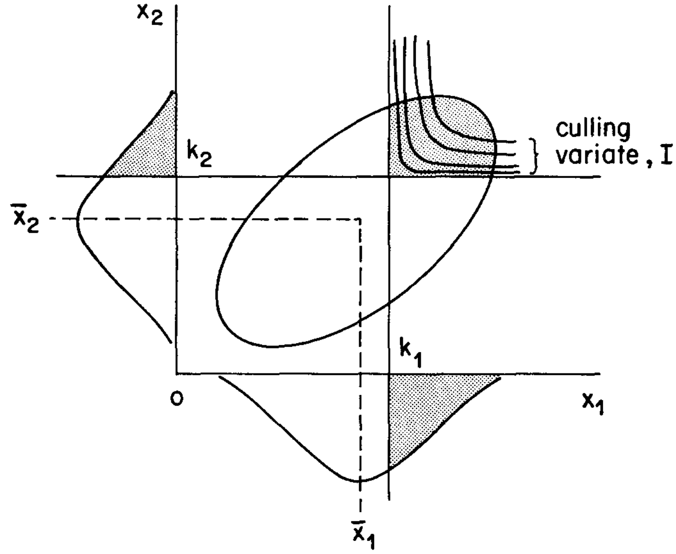

FIGURE 2.—Multiplicative index, $I = X_1^{b_1} X_2^{b_2}$, is applied to independent culling level selection. k_1 and k_2 are truncated points on X_1 and X_2.

TABLE 1

Data of 25 individuals

Genetic groups	No. of individuals	Traits X_1	X_2	X_3	Selected or not Case 1	Case 2	Case 3	Case 4
1	1	20	20	28				
1	2	16	24	20				
1	3	24	16	36				
1	4	32	22	32				
1	5	28	18	24				
2	6	24	24	16			1	
2	7	20	$\underline{28}$	24				
2	8	28	20	28				
2	9	$\underline{36}$*	$\underline{26}$	32	1	1		
2	10	32	22	20	1	1	1	
3	11	26	22	32				
3	12	22	$\underline{26}$	$\underline{40}$				
3	13	30	18	$\underline{48}$				1
3	14	$\underline{38}$	24	$\underline{44}$				1
3	15	$\underline{34}$	20	36	1	1		1
4	16	28	$\underline{32}$	24			1	
4	17	24	$\underline{28}$	32				
4	18	32	24	$\underline{40}$				1
4	19	$\underline{40}$	$\underline{30}$	$\underline{36}$	1	1	1	1
4	20	$\underline{36}$	26	28	1	1	1	
5	21	32	26	28	1	1	1	
5	22	28	$\underline{30}$	$\underline{36}$				1
5	23	$\underline{36}$	$\underline{22}$	$\underline{44}$				1
5	24	$\underline{44}$	$\underline{28}$	$\underline{40}$	1	1	1	1
5	25	$\underline{40}$	24	32	1	1	1	
	Average	30	24	32				

* The individuals whose measurements of each trait are underlined were used to calculate direct selection differentials of three traits for estimating LINEAR parameters.

I. *Basic statistics.*

A. Phenotypic and genetic variance and covariance components estimated by ANOVA-ANOCOVA, based on the model (13). $\sigma^2_{T_i} = \sigma^2_{G_i} + \sigma^2_{E_i}$ and $\sigma_{T_{ij}} = \sigma_{G_{ij}} + \sigma_{E_{ij}}$.

$$[\sigma_{T_{ij}}] = \begin{bmatrix} 52.00 & 6.84 & 28.16 \\ 6.84 & 18.00 & -2.80 \\ 28.16 & -2.80 & 72.00 \end{bmatrix}$$

$$[\sigma_{G_{ij}}] = \begin{bmatrix} 12.00 & 12.04 & 12.96 \\ 12.04 & 8.00 & 3.20 \\ 12.96 & 3.20 & 32.00 \end{bmatrix}$$

$$[\ h^2\ ]' = [\ 0.2308 \quad 0.4444 \quad 0.4444]$$

B. Phenotypic and genetic selection differentials computed from (16a~c). $\Delta P_{i.j}$'s were estimated by $\Delta T_{j.j}$'s and thus $\Delta T_{i.j} = \Delta G_{i.j} + \Delta E_{i.j}$.

$$[\Delta T_{i.j}] = \begin{bmatrix} 8.6250 & 0.6875 & 4.4375 \\ 1.3125 & 4.9375 & 1.5000 \\ 5.1250 & 1.0000 & 10.1250 \end{bmatrix}$$

$$[\Delta G_{i.j}] = \begin{bmatrix} 1.7500 & 2.5625 & 3.1875 \\ 1.6250 & 1.5000 & 1.1875 \\ 2.6250 & -0.2500 & 4.5000 \end{bmatrix}$$

Phenotypic and genetic variance-covariance matrices computed from the above, giving $i = 1.081$ after Table 2 of BECKER (1975).

$$[\sigma_{T_{i.j}}] = \Delta\mathbf{T}_{i.j} \text{ diag } \Delta\mathbf{T}_{j.j}/i^2 = \begin{bmatrix} 63.6600 & 2.9049 & 38.4487 \\ 9.6874 & 20.8623 & 12.9968 \\ 37.8270 & 4.2253 & 87.7281 \end{bmatrix}$$

$$[\sigma_{G_{i.j}}] = \Delta\mathbf{G}_{i.j} \text{ diag } \Delta\mathbf{T}_{j.j}/i^2 = \begin{bmatrix} 12.9165 & 10.8273 & 27.6181 \\ 11.9939 & 6.3379 & 10.2891 \\ 19.3748 & -1.0563 & 38.9903 \end{bmatrix}$$

$$[\ h^2\ ]' = [\ 0.2029 \quad 0.3038 \quad 0.4444\ ]$$

II. *Case study 1.*

The culling variate is obtained from the first two traits by intentionally ignoring the third trait to compare the efficiency with three-trait selection. Observed selection differentials in the first two traits are:

$$\Delta\mathbf{P}'_{i.I} = [\ 6.75 \quad 1.25\ ]$$

A. With the parameters taken from I.A (ANOVA-ANOCOVA estimates).

$$\mathbf{b} = \begin{bmatrix} 52.00 & 6.84 \\ 6.84 & 18.00 \end{bmatrix}^{-1} \begin{bmatrix} 6.75 \\ 1.25 \end{bmatrix} = \begin{bmatrix} 0.1270 \\ 0.0212 \end{bmatrix} \qquad \text{from (3b)}$$

$$I = 0.1270\mathrm{X}_1 + 0.0212\mathrm{X}_2$$

$$r_b = \frac{0.8829}{1.0363} = 0.8520 \qquad \text{from (20)}$$

$$\Delta\mathbf{G}_{i.I} = \begin{bmatrix} 12.00 & 12.04 \\ 12.04 & 8.00 \end{bmatrix} \begin{bmatrix} 0.1270 \\ 0.0212 \end{bmatrix} = \begin{bmatrix} 1.7792 \\ 1.6987 \end{bmatrix} \qquad \text{from (11)}$$

B. With the parameters taken from I.B (LINEAR estimates).

$$\mathbf{b} = \begin{bmatrix} 63.6600 & 2.9049 \\ 9.6874 & 20.8623 \end{bmatrix}^{-1} \begin{bmatrix} 6.75 \\ 1.25 \end{bmatrix} = \begin{bmatrix} 0.1055 \\ 0.0109 \end{bmatrix} \qquad \text{from (8a)}$$

$$I = 0.1055X_1 + 0.0109X_2$$

$$r_b = \frac{0.7258}{0.8549} = 0.8489$$

$$\Delta \mathbf{G}_{i.I} = \begin{bmatrix} 12.9165 & 10.8273 \\ 11.9939 & 6.3379 \end{bmatrix} \begin{bmatrix} 0.1055 \\ 0.0109 \end{bmatrix} = \begin{bmatrix} 1.4807 \\ 1.3344 \end{bmatrix} \quad \text{from (11)}$$

III. *Case study 2.*

The culling variate is obtained from all three traits, providing

$$\Delta \mathbf{P}'_{i.I} = [\ 6.75 \quad 1.25 \quad -0.50\ ]$$

A. Based on ANOVA-ANOCOVA estimates.

$$\mathbf{b} = \begin{bmatrix} 52.00 & 6.84 & 28.16 \\ 6.84 & 18.00 & -2.80 \\ 28.16 & -2.80 & 72.00 \end{bmatrix}^{-1} \begin{bmatrix} 6.75 \\ 1.25 \\ -0.50 \end{bmatrix} = \begin{bmatrix} 0.1708 \\ -0.0070 \\ -0.0740 \end{bmatrix}$$

$$I = 0.1708X_1 - 0.0070X_2 - 0.0740X_3$$

$$r_b = \frac{1.1812}{1.2638} = 0.9346$$

$$\Delta \mathbf{G}_{i.I} = \begin{bmatrix} 12.00 & 12.04 & 12.96 \\ 12.04 & 8.00 & 3.20 \\ 12.96 & 3.20 & 32.00 \end{bmatrix} \begin{bmatrix} 0.1708 \\ -0.0070 \\ -0.0740 \end{bmatrix} = \begin{bmatrix} 1.0064 \\ 1.7639 \\ -0.1773 \end{bmatrix}$$

B. Based on LINEAR estimates.

$$\mathbf{b} = \begin{bmatrix} 63.6600 & 2.9049 & 38.4487 \\ 9.6874 & 20.8623 & 12.9968 \\ 37.8270 & 4.2253 & 87.7281 \end{bmatrix}^{-1} \begin{bmatrix} 6.75 \\ 1.25 \\ -0.50 \end{bmatrix} = \begin{bmatrix} 0.1472 \\ 0.0357 \\ -0.0709 \end{bmatrix}$$

$$I = 0.1572X_1 + 0.0357X_2 - 0.0709X_3$$

$$r_b = \frac{1.0757}{1.1252} = 0.9583$$

$$\Delta \mathbf{G}_{i.I} = \begin{bmatrix} 12.9165 & 10.8273 & 27.6181 \\ 11.9939 & 6.3379 & 10.2891 \\ 19.3748 & -1.0563 & 38.9903 \end{bmatrix} \begin{bmatrix} 0.1472 \\ 0.0357 \\ -0.0709 \end{bmatrix} = \begin{bmatrix} 0.3297 \\ 1.2623 \\ 0.0498 \end{bmatrix}$$

IV. *Case study 3.*

In this particular example, eight individuals were chosen *a priori*, based on the following index.

$$I_E = (X_{1_{kl}} - \overline{X}_{1_{k.}}) + 2(\overline{X}_{1_{k.}} - \overline{X}_{1_{..}}) + (X_{2_{kl}} - \overline{X}_{2_{..}}) - (X_{3_{kl}} - \overline{X}_{3_{..}})$$

From Table 1, we compute

$$\Delta \mathbf{P}'_{i.I} = [\Delta P_{W_{X_1}.I} \quad \Delta P_{B_{X_1}.I} \quad \Delta P_{X_2.I} \quad \Delta P_{X_3.I}]$$
$$= [2.00 \quad 2.50 \quad 2.50 \quad -4.00]$$

A. Variance-covariance matrix appropriate for the analysis is obtained from I.A., based on (23), *i.e.*, $\sigma^2_{W_{X_1}} = \sigma^2_{X_1} - \sigma^2_{B_{X_1}}$, etc.

$$[\sigma_{T_{i.j}}] = \begin{bmatrix} \sigma_{W_{X_1}} & 0 & \sigma_{W_{X_1}W_{X_2}} & \sigma_{W_{X_1}W_{X_3}} \\ 0 & \sigma^2_{B_{X_1}} & \sigma_{B_{X_1}B_{X_2}} & \sigma_{B_{X_1}B_{X_3}} \\ \sigma_{W_{X_2}W_{X_1}} & \sigma_{B_{X_2}B_{X_1}} & \sigma^2_{X_2} & \sigma_{X_2X_3} \\ \sigma_{W_{X_3}W_{X_1}} & \sigma_{B_{X_3}B_{X_1}} & \sigma_{X_3X_2} & \sigma^2_{X_3} \end{bmatrix} = \begin{bmatrix} 40.00 & 0 & -5.20 & 15.20 \\ 0 & 12.00 & 12.04 & 12.96 \\ -5.20 & 12.04 & 18.00 & -2.80 \\ 15.20 & 12.96 & -2.80 & 72.00 \end{bmatrix}$$

$$\mathbf{b}' = ([\sigma_{T_{ij}}]^{-1}\,[\Delta P_{i.I}])' = [0.0723 \;\; 1.7660 \; -1.0886 \; -0.4311]$$

$$r_b = \frac{3.5625}{5.6478} = 0.6308$$

B. Similarly from I.B. (23), *i.e.*, $\sigma_{W_{X_1}}\sigma_{W_{X_2}} = \sigma_{X_{1.2}} - \sigma_{B_{X_{1.2}}} = 63.6600 - 12.9165 = 50.7435$ and $\sigma_{W_{X_1}X_2} = \sigma_{W_{X_1}W_{X_2}} = \sigma_{X_{1.2}} - \sigma_{B_{X_{1.2}}} = 2.9049 - 10.8273 = -7.9224$.

$$[\sigma_{T_{i.j}}] = \begin{bmatrix} 50.7435 & 0 & -7.9224 & 10.8306 \\ 0 & 12.9165 & 10.8273 & 27.6181 \\ -2.3065 & 11.9939 & 20.8623 & 12.9968 \\ 18.4522 & 19.3748 & 4.2253 & 87.7281 \end{bmatrix}$$

$$\mathbf{b}' = [\; 0.5170 \quad 0.9805 \quad -0.2764 \quad -0.2597 \;]$$

$$r_b = \frac{2.9028}{3.5019} = 0.8289$$

When within- and between-family selections were not taken into consideration, the index obtained by ANOVA estimates is

$$I = 0.1341X_1 + 0.0716X_2 - 0.1052X_3, \text{ with } r_b = 0.9877.$$

V. *Case study 4.*

Actual selection was independent culling levels for X_1 and X_3. $X_1 \geq 28$ and $X_2 \geq 36$, ignoring X_2. We would like to compare the efficiency of additive and multiplicative indices.

The variance-covariance matrix based on ANOVA estimates for X_1 and X_3, after coding the variables, $x_i = (X_i+1) - (\text{smallest } X_i \text{ value})$ and ln transformation, is

$$[\sigma_{X_{ij}}] = \begin{bmatrix} 0.5257 & 0.2374 \\ 0.2374 & 0.5901 \end{bmatrix}$$

Observed indirect selection differentials in ln units are

$\Delta\mathbf{P}'_{i.I} = [\; 0.4382 \quad 0.5732 \;]$

$\mathbf{b}' = [\; 0.4825 \quad 0.7772 \;]$

$I = 0.4825 \ln X_1 + 0.7772 \ln X_3$ or $I = X_1^{0.4825} X_3^{0.7772}$

$r_b = 0.9719$

Conventional additive index computed from $\Delta\mathbf{P}'_{i.I} = [5.25 \quad 8.50]$ is

$\mathbf{b}' = [\; 0.04700 \quad 0.1002 \;]$, $r_b = 0.9777$.

The above results indicate that the linear index is at least as efficient as the multiplicative index. However, little reliance can be placed on these results with such a small amount of data.

DISCUSSION

A characteristic feature of this study is to provide a technique which enables one to evaluate objectively the realized selection as actually practiced by a breeder without knowing his selection criteria, provided that the data on all traits that contributed to the selection criteria are available. Few investigators have attempted to quantify such data. This study describes a useful technique designed to evaluate the results of long-term selection in plants and animals.

For assessing the effectiveness of long-term selection in animals and poultry, such as described by DEMPSTER, LERNER and LOWRY (1952), YAMADA, BOHREN and CRITTENDEN (1958) and GOWE, LENTZ and STRAIN (1973), it has been established that realized heritability can be expressed as the ratio of actual gain to cumulative selection differential of the trait under selection. It is equally important to check if intended selection criteria remain the same throughout the period of experimentation in the case of actual selection. If the criteria which were practiced in the case of realized selection were different from those used in the intended selection, the above mentioned ratio should rather follow the pattern of realized "coheritability" as defined by YAMADA (1968) than that of "heritability."

Another feature of the present study emphasized the use of equations (8) instead of (3b). One should mention, however, that the variances and covariances in (3b) are obtained from the static analysis of the population using the whole range of the distribution with the assumption of normality. Such an ideal situation of normal distributions of those variables is not generally met in biological situations. Furthermore, it is frequently observed that the distribution of a variable under selection tends to be skewed as selection advances, although the original distribution was merely normal (YAMADA, unpublished data in Tribolium, mice and chickens). In the case the distribution of the trait under consideration is not normal, such as a longer tail toward the negative direction of the distribution, then the selection differentials for both negative(—) and positive(+) directions will not be the same when one uses the same selection intensity, *i.e.*, $\Delta P_{1.1(-)} > \Delta P_{1.1(+)}$. No mathematical solution is available as far as the problem related to deviation from normality is concerned. Thus, it would seem appropriate, for the time being, to consider the selection differentials or responses as being caused by asymmetrical effective variances or heritabilities for different directions of selection with the same selection intensity. This in turn is equivalent to saying that $\Delta P_{1.1(-)} = i\ \sigma_{X_{1(-)}} > \Delta P_{1.1(+)} = i\ \sigma_{X_{1(+)}}$, rather than $\Delta P_{1.1(-)} = i_{(-)}\ \sigma_{X_1} > \Delta P_{1.1(+)} = i_{(+)}\ \sigma_{X_1}$. The same argument can be extended to cover differential variances and covariances of two traits when the joint distribution deviates from normality. Therefore, $\Delta P^2{}_{1.1}/\Delta P^2{}_{2.2} = \sigma_{X_{1.1}}/\sigma_{X_{2.2}}$ and $\Delta P_{1.2}\,\Delta P_{2.2}/\Delta P_{2.1}\,\Delta P_{1.1} = \sigma_{X_{1.2}}/\sigma_{X_{2.1}}$, for the same selection intensity in both X_1 and X_2. Such interpretations of differential variances and covariances seem to be particularly useful to understand asymmetry in realized heritabilities and genetic correlations observed in two-way selection for a single trait or selection for different traits (Falconer 1969; Yamada and Bell 1969).

The variances and covariances obtained from (5) and (12a ~ d) should therefore represent actual situations for the distributions, if those parameters were estimated by paper selection along with the directions of selection which actually took place in each component trait. In this sense, the realized selection index derived from (8) would be more useful and practical than that from (3) when the distributions of the variables are not normal.

It must be pointed out, as did Abplanalp (1961), that the use of LINEAR estimates of genetic parameters requires a large population and intense selection in order for the results to be very reliable.

As to the efficiency of the realized selection index, Allaire and Henderson (1966) have presented two estimators. However, it is questionable if these estimators answer the question concerning the fit of the derived index to the actual selection.

If the estimate of the biserial correlation deviates substantially from unity, one should suspect first that some additional information which had been utilized by the breeder is still missing in the evaluation of the realized index or actual selection. One should look for this information to improve the validity of the retrospective selection index. This, in turn, improves the prediction of genetic gains in component traits. Secondly, one should check the distribution of the derived index jointly with the variables included in the index as curvilinear relationships may decrease the efficiency.

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