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# Index Selection for Genetic Improvement of Quantitative Characters

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Summary. This paper reviews the basic theory and summarizes various modifications of the selection index. The limitations of selection index are discussed in four parts: (1) changes of parameters due to selection. (2) sampling errors of parameter estimation. (3) evaluation of relative economic weights and (4) internal deterrents to index selection.

Key words: Selection index — Index theory

## Introduction

Fisher's discriminant function (1936) was originally designed to differentiate species in taxonomy. Smith (1936) applied Fisher's concept of discriminant function to develop an index for the selection of plant lines. Hazel (1943) extended the index procedure for the selection of individuals in animal populations. The significant contributions of Hazel's 1943 paper were that he defined a method to estimate genetic variances and covariances which are required to derive the index and that he defined the aggregate genotype as a linear combination of genetic values, each weighted by the relative economic value. The unrestricted selection index will hereafter be designated as the *Smith-Hazel index* in this paper.

Hazel and Lush (1942) compared relative efficiency of tandem selection, independent culling levels and index selection when the traits involved are independent. They showed that index selection is the most efficient. Young (1961) evaluated relative efficiency when the traits are correlated and he concluded that index selection is at least as efficient as independent culling levels which in turn, is at least as efficient as tandem selection. He further found that relative efficiency depends upon number of traits selected, relative economic values of the traits, heritabilities, phenotypic and genetic correlations between traits, and selection intensity. A generalized treatment of Young's results (1961) was given by Finney (1962).

The theoretical evaluation of the relative efficiency of these three selection methods was confirmed experimentally by Sen and Robertson (1964) in Drosophila, Elgin et al. (1970) in alfalfa, Doolittle et al. (1972) in mice, and Eagles and Frey (1974) in oats, but not in Rasmuson's experimental situation with Drosophila (1964).

The objective of this paper is to review the basic theory, summarize various applications and discuss the limitations of the selection index for the genetic improvement of one or more quantitative characters.

## Review of Index Theory

The selection index and the aggregate genotype (or net merit) are defined as:

$$\text{Index: } I = \sum_{i=1}^{m} b_i x_i = \underline{x}'\underline{b}$$

$$\text{Aggregate genotype: } H = \sum_{i=1}^{n} a_i g_i = \underline{g}'\underline{a}$$

where

$\underline{x}' = (x_1 x_2 \ldots x_m)$ = a row vector of m known phenotypic values,

$\underline{g}' = (g_1 g_2 \ldots g_n)$ = a row vector of n unknown genetic values,

$\underline{a}' = (a_1 a_2 \ldots a_n)$ = a row vector of n known relative economic values, and

$\underline{b}' = (b_1 b_2 \ldots b_m)$ = a row vector of m index coefficients to be computed.

The following relationships exist from the above definitions:

$$\sigma_I^2 = \underline{b}'P\underline{b}$$

$$\sigma_H^2 = \underline{a}'F\underline{a}$$

$$\sigma_{IH} = \underline{b}'G\underline{a}$$

where    Var($\underline{x}$) = P, the phenotypic variance-covariance matrix (m x m),

Var($\underline{g}$) = F, the genetic variance-covariance matrix (n x n), and

Cov($\underline{x}$,$\underline{g}$) = G, the genetic covariance matrix (m x n) between the phenotypic values in I and the genotypic values in H.

If m = n, then G and F are identical. Note that m could be equal to, greater than or smaller than n.

The index coefficients, i.e. the vector $\underline{b}$, needed to construct the selection index, are derived such that the correlation between I and H is a maximum or that $\Sigma(H - I)^2$ is a minimum. The correlation between I and H is

$$r_{IH} = \frac{\underline{b}'G\underline{a}}{(\underline{b}'P\underline{b})^{1/2}(\underline{a}'F\underline{a})^{1/2}}$$

Maximizing $\log r_{IH}$ is equivalent to maximizing $r_{IH}$. Thus,

$$\log r_{IH} = \log(\underline{b}'G\underline{a}) - \tfrac{1}{2}\log(\underline{b}'P\underline{b}) - \tfrac{1}{2}\log(\underline{a}'F\underline{a}),$$

$$\frac{\partial \log r_{IH}}{\partial \underline{b}} = \frac{1}{\underline{b}'G\underline{a}}G\underline{a} - \tfrac{1}{2}\frac{1}{\underline{b}'P\underline{b}} \cdot 2P\underline{b} = 0 \text{ and}$$

$$P\underline{b} = G\underline{a} \cdot \frac{\underline{b}'P\underline{b}}{\underline{b}'G\underline{a}}$$

The scalar, $\underline{b}'P\underline{b}/\underline{b}'G\underline{a}$ can be dropped without affecting the proportionality of $b_i'$s. Therefore, $P\underline{b} = G\underline{a}$ are the index equations with solution $\underline{b} = P^{-1}G\underline{a}$.

When the vector $\underline{b}$ arises from $\underline{b} = P^{-1}G\underline{a}$, the following equalities exist:

$$\sigma_{HI} = \sigma_I^2$$

$$b_{HI} = \sigma_{HI}/\sigma_I^2 = 1 \text{ and}$$

$$r_{HI} = \sigma_{HI}/\sigma_I\sigma_H = \sigma_I^2/\sigma_I\sigma_H = \sigma_I/\sigma_H$$

The statistical properties of the selection index were given by Henderson (1952), Williams (1962a) and Henderson (1963) in a 1961 symposium.

The traits comprising net merit are not necessarily included in the index, Binet (1965), for example, combined measurable traits into an index to seek genetic improvement in a correlated trait which itself was not included in the index. However, the Smith-Hazel index outlined above applies to derive the index coefficients. Such an index can be referred to as an *indirect selection index*.

## Heritability of an Index

The squared correlation between I and H has been misinterpreted by some researchers as the heritability of the selection index (Willham, 1965; Pirchner, 1969). Lin and Allaire (1977) showed that $r_{IH}^2$ has been misused when used as the heritability of an index and defined heritability of an index as the regression of genetic index (g*) on the selection index (I). The genetic index was obtained by substituting the genetic values of the index traits into the phenotypic values. Alternatively, heritability of an index can be estimated in the same manner as heritability of one trait by an analysis of covariance among relatives. The equality of these two estimation methods was shown by Lin (1976).

## Expected Gains

When selection is on I, the genetic gain in the aggregate genotype (H) is, as is well known:

$$\Delta H = b_{HI}(\bar{I}_s - \bar{I}_\mu) = \bar{i}\,\sigma_I \tag{1}$$

$$= r_{IH}\,\bar{i}\,\sigma_H$$

where $\bar{I}_\mu$ and $\bar{I}_s$ are the mean index values of the population and the selected individuals, respectively, and $\bar{i}$ is the selection intensity factor (i.e., $\bar{i} = (\bar{I}_s - \bar{I}_\mu)/\sigma_I$). The genetic gain in H is proportional to $r_{IH}$ which is a maximum when $\underline{b} = P^{-1}G\underline{a}$.

The genetic gain in the $i^{th}$ index trait due to selection on I is,

$$\Delta G_i = b_{G_iI}(\bar{I}_s - \bar{I}_\mu) = \underline{g}_i'\underline{b}\,(\bar{i}/\sigma_I)$$

where $\underline{g}_i$ is a row vector of genetic covariances between $i^{th}$ trait and each component trait incorporated in the index, i.e., the $i^{th}$ row of genetic variance-covariance matrix. In matrix notation,

$$\underline{\Delta} = G\underline{b}\,(\bar{i}/\sigma_I) \tag{2}$$

where $\underline{\Delta}$ is a column vector of genetic gains corresponding to each trait of the index.

Alternatively, $\Delta H$ can be expressed as,

$$\Delta H = b_{HI}(\bar{I}_s - \bar{I}_\mu) = \underline{a}'G\underline{b}\,(\bar{i}/\sigma_I) = \underline{a}'\underline{\Delta} = \Sigma\,a_i\Delta G_i$$

Hence, $\Delta H$ is a linear combination of the genetic gains in the index trait, each weighted by its relative economic weight.

After the formulation of the selection index, we may want to evaluate the effect on selection efficiency of dropping a trait in the index. If the trait contributes little to efficiency, we may delete the trait from the index even though it is an economically important trait. Since genetic gain in H due to index selection is directly proportional to

$r_{IH}$, the relative importance of one trait in the index can therefore be evaluated by the reduction in $r_{IH}$ when deleting that trait from the index. A formula for computing the percentage reduction in $\Delta H$ by dropping a trait from the index was given by Cunningham (1969).

## Various Applications of Selection Index

### Restricted Selection Index

Selection index can also be designed to change some traits while holding the response of other traits to zero. This is the restricted selection index of Kempthorne and Nordskog (1959). The biological validity of the restricted selection index has been experimentally confirmed by Abplanalp et al. (1963), Scheinberg et al. (1967), and Okada and Hardin (1967).

Tallis (1962) extended Kempthorne and Nordskog's methodology by setting the response of some traits by a fixed amount while genetic gains in others should be maximum. This method was called the *optimum selection index*. Cunningham et al. (1970) worked out a simpler solution to the restricted selection index than that originally developed by Kempthorne and Nordskog. Morley (1955) and Abplanalp et al. (1963) developed a backward solution to the restricted selection index for a special case when a breeder wants to improve one trait and hold another constant.

An extreme case of Tallis' optimum selection index is to control the relative gains in all traits incorporated in the index. Suppose that three traits ($x_1$, $x_2$ and $x_3$) are used to construct an index, and a breeder wishes to increase $x_1$ by 2.5 units for each .1 unit decrease in $x_2$ and hold $x_3$ constant (i.e., $\Delta G_1 : \Delta G_2 : \Delta G_3 = 2.5: -.1 : 0$). Then the index coefficients for this index can be derived from expression (2). That is

$$\underline{b} = G^{-1} \underline{\Delta}$$

since $\bar{1}/\sigma_I$ is a scalar which can be dropped and $\underline{\Delta}' = (2.5: -.1 : 0)$. In doing so, an index can be derived which bypasses the problems of estimating the relative economic values and phenotypic variance-covariance parameters. However, the genetic change in each trait can be regulated according to its relative economic value by simply substituting $\underline{a}$ for $\underline{\Delta}$ in the above expression.

Therefore, the restricted selection index provides a way to manipulate genetic changes in component traits, whereas the Smith-Hazel index deals with the aggregate genotype as a single trait and provides no control over its components. A similar approach has been used to achieve genetic gains in each index trait at a prechosen rate by Pesek and Baker (1969) and Casey (1970).

James (1968) worked out a general formula to cover

Kempthorne and Nordskog's restricted selection index, Tallis' optimum selection index and Binet's indirect selection index in one computational scheme. A general treatment of restricted indexes was also given by Harville et al. (1972).

### Weight-free Selection Index

Elston (1963) developed a selection index without going through the Smith-Hazel index procedures. The index he used was,

$$I = (x_1 - k_1)(x_2 - k_2) .... (x_n - k_n)$$

where $k_i$ is a minimum value set by a breeder for trait $x_i$. Any individual which fails to meet the minimum standard for any one trait will be culled. This index also sidestepped the problems of estimating relative economic weights, phenotypic and genetic parameters. In practice, this is an algorithm for the method of independent culling levels. Baker (1974) recommended the use of this index when the index traits have equal importance. However, the Smith-Hazel index should be preferred if the relative economic values differ a great deal.

### Non-linear Index Selection

Theoretically, a selection index can be a linear or non-linear function of observable traits. However, it has almost always been assumed that the net merit of an individual was a linear combination of genetic values, each weighted by relative economic value. Some composite traits in farm animals such as litter weight or feed efficiency, are the products or ratios of component traits. Smith (1967) transformed the composite traits to a logarithmic scale so that the effect of the component traits becomes linear. The usual index procedure then can be applied to the transformed variables to derive the index. In this case, the phenotypic and genetic parameters would have to be estimated on a logarithmic scale. A similar approach was taken by Bohren (1970) to derive a linear index by making a logarithmic transformation.

Smith (1936) has pointed out that the precision of the selection function might be increased by considering higher powers and products of the variates. However, his concept has lain essentially unrecognized. Kempthorne and Nordskog (1959) suggested that we can define the squared traits as a new variable to handle the non-linear situation of net merit. By this reasoning, the quadratic, cubic or higher-order index can be dealt with in the same manner as the linear index. Nevertheless, the problem is how to assign relative economic weight for the newly defined variables. Wilton et al. (1968) developed an index for net

merit which included squares and cross products of the traits. This has been called the *quadratic index*.

## Family Index

Information on relatives can be utilized to increase the accuracy of selection. The biometric relations between relatives were explored by Wright (1921a, b) and first applied by Lush (1931, 1935 and 1944) to predict individual breeding value. Lush (1947) used the family mean to aid the individual records in making the selection. This is the *family index*. Legates and Lush (1954) constructed an index to improve fat production in dairy cattle by combining information on fat yield of the cow, her dam, her daughters, her maternal and paternal sisters. Osborne (1957) showed that maximum efficiency of selection can be obtained by combining individual, full-sib family and half-sib family information in poultry. With sib test data, when the trait under consideration is measured only in females, an index can be constructed by combining full-sib and half-sib family information.

Henderson (1963) has generalized the procedure for combining information on the individual itself and all relatives in a selection program. This is the *best index* of Henderson.

## Further Use of an Index

Young and Tallis (1961) extended the index to select for lifetime production. This has been called a *performance index*. This is different from the Smith-Hazel index only in terms of predicting producing abilities instead of breeding values. James (1961) constructed a selection index to maximize genetic gains over all environments when genotype and environment interaction exists. Henderson (1963) further extended index selection to cover selection among lines and lines crosses. Van Vleck (1970) expanded the index procedure to select for traits each having direct and maternal genetic effects. Van Vleck (1976) further extended the procedure to take into account direct, maternal and grandmaternal effects.

The selection theory has been derived with the assumption that interaction among genotypes does not exist within groups. Griffing (1967) showed that selection for individuals with the greatest genotypic values could result in a decrease in the progeny mean when the 'direct additive effect' and 'associate additive effect' were negatively correlated. Griffing (1969) developed an index which incorporated the direct and associated phenotypic values to yield maximum response.

In poultry, Morris (1963) and Gowe and Strain (1963) reported that part-record selection may improve the part

record at the expense of the residual record such that the total annual egg production will show no change at all. Therefore, an index can be constructed to maximize annual egg production by treating part record and residual record as two separate traits. Young (1964) presented a multi-stage index selection procedure for one or more traits available at each of several stages in an individual's lifetime.

## Index in Retrospect

The selection index actually practiced as determined in retrospect is called the index in retrospect (Dickerson et al. 1954). The various indexes described above are derived before selection begins, whereas the index in retrospect is obtained after the conclusion of selection.

Allaire and Henderson (1966) presented the computation of the retrospective index in matrix notation. The index in retrospect can be easily obtained from expression (2).

$$\underline{b}* = G^{-1} \underline{\Delta}$$

where $\underline{b}*$ is the vector of the retrospective index weights, and $G^{-1}$ and $\underline{\Delta}$ were defined as before. Note that $1/\sigma_I$ in expression (2) was dropped since it is a scalar to the set of equations. Alternatively, the retrospective index weights can be obtained as,

$$\underline{b}* = P^{-1} \underline{\Delta}*$$

where $\underline{\Delta}*$ is a column vector of phenotypic gains in each index trait. With the retrospective index determined, the aggregate genotype in retrospect can be determined subsequently as,

$$\underline{\Delta}* = P\underline{b}* = G\underline{a}*$$

Hence, $\underline{a}* = G^{-1} \underline{\Delta}* = G^{-1} P\underline{b}*$ where $\underline{a}*$ is a vector of the relative economic values in retrospect (Van Vleck 1974).

## Limitations of Selection Index

From the literature reviewed earlier, the use of a selection index would be expected to lead to maximum genetic gain. Although index selection has been used extensively in plant or animal breeding research, there are some potential problems frequently associated with it. They will be discussed below.

## Changes of Parameters due to Selection

The effect of truncation selection upon parameters in the selected groups was mathematically described by Cochran

(1951). In this section, the effect of selection on parameters of the offspring population rather than the selected group itself will be discussed. Selection response arises from the existence of genetic variability. The more efficient the selection index, the faster the percent reduction in the genetic variance can be expected in subsequent generations. Index selection would not only reduce the genetic variance of the index traits and genetic covariances between these traits but also change the phenotypic variances and covariances. The changes of the parameter estimates due to selection may justify the reconstruction of the index (Lin 1976). Therefore, the selection index should be a dynamic index and not a static one. Animal breeders often assume that the changes of parameters are negligible. Subsequently, the same selection index has almost always been used throughout a given selection experiment. Inevitably, this could lead to misleading results and interpretation.

Theoretically, selection may increase or decrease the genetic variance, depending upon initial gene frequencies. However, selection should decrease the genetic parameters in the long run. This was confirmed by experimental findings (Yamada et al. 1958; Friars et al. 1962; Festing and Nordskog 1967) and by most computer simulation studies (Parker et al. 1969; McMillan et al. 1973; Bruns and Harvey 1976). No genetic gain is possible without some change in genetic variability. It is doubtful that the analysis of covariance between relatives is sensitive enough to detect small changes in genetic variability. No significant decrease in heritability estimates due to selection doesn't provide proof that changes in genetic variance does not take place. Sampling errors of estimation alone could overshadow small reductions in genetic variability. In simulation studies, the genotype of each individual is assumed to be known. The genetic variances and covariances can thus be computed directly without the use of the analysis of covariance among relatives. Therefore, it appears that analysis of gene-effect simulation models would be effective in demonstrating changes in genetic parameters.

*Sampling Errors of Parameter Estimation*

Phenotypic and genetic parameters are required for the computation of a selection index. Williams (1962b) labeled the Smith–Hazel index as an *estimated index* since phenotypic and genetic parameters are never known and thus the index has to be derived by use of sample estimates. Sampling errors associated with estimation from a small data set could affect the reliability of the index. Brim et al. (1959) pointed out that inaccurate estimation of population parameters could bias estimates of theoretical gains. They suggested an alternative index such

that each trait is weighted according to its relative economic value. Williams (1962b) called this the *base index*. This base index is virtually equivalent to Panse's 'straight selection' (1946). Panse compared the expected genetic gain of the discriminant function (i.e., selection index) with straight selection and found that the discriminant function was more efficient than straight selection.

The index coefficients of the Smith-Hazel index will be equal to the relative economic weights if the phenotypic variance-covariance matrix (P) is equivalent to the genetic variance-covariance matrix (G). Under this circumstance, the Smith-Hazel index and the base index are identical. Generally, the main difference between the Smith-Hazel index and the base index is that the Smith-Hazel index maximizes the correlation between H and I, whereas the base index maximized the correlation between H and g*, where g* was defined as earlier. Subsequently, regression of H on the Smith-Hazel index is unity, while regression of H on the base index is less than unity, which illustrates why the estimated index should be more efficient than the base index unless estimation error is large enough to reverse this theoretical expectation.

The influence of errors of parameter estimation on the accuracy of the selection index has been investigated by Heidhues (1961), Williams (1962b), Harris (1964), and Pease et al. (1967). The general conclusions by these researchers were that errors of parameter estimation would affect the accuracy of the selection index. Williams (1962b) pointed out that the base index is superior to the estimated index unless a large amount of data are available for the estimation of the parameters. If the parameter estimates deviate only slightly from the underlying parameters, the use of the estimated index is justified. Harris (1964) supported this conclusion from his simulation study. Pease et al. (1967) reported that estimation error of the genetic correlation has a larger effect than estimation error of heritability on the efficiency of index selection.

Experimentally, the base index was found to be as efficient as the Smith-Hazel index when based on poor estimation of parameters (Elgin 1970). Eagles and Frey (1974) confirmed, theoretically and experimentally, that the Smith-Hazel index was only slightly more efficient than the base index. However, the base index has certain advantages because of its simplicity and its freedom from errors of parameter estimation or when population parameter estimates are not available.

The effect of errors of parameter estimation on selection efficiency depends upon many factors: e.g., the number of traits selected, the relative economic weights, levels of genetic and phenotypic parameters, and selection intensity. Further research is needed to clarify the importance of these factors. Furthermore, given a fixed number of observations for estimation, the sampling errors of the

parameter estimates depend upon the method of estimation, experimental set up and the true parameters of the traits.

## Evaluation of Relative Economic Weights

Relative economic weights have been derived in two ways: direct economic analysis of a production system (Hogsett and Nordskog 1958) or by multiple regression analysis by regressing estimates of profit on phenotypic traits (Andrus and McGilliard 1975). The dilemma with the former approach is that some traits are hard to define objectively, and subsequently difficult to assign an economic value to. The difficulty with the latter approach is that relative economic weights would vary with how profit is defined, the number of traits considered in the multiple regression equation and sampling variability.

The correlation between the index and net merit ($r_{IH}$) is always maximized for any given set of economic values. Given any phenotypic and genetic variance-covariance matrix, different indexes corresponding to different sets of economic values could be derived. Theoretically, there are unlimited sets of economic values. However, it is possible that a certain degree of variation in relative economic weights will not change expected response very much. Under this circumstance, different indexes derived from different sets of economic values will have the same genetic implication in the selection program. Brim et al. (1959) found that expected genetic gain was little affected by changes in price ratios under conditions existing in their study.

Furthermore, economic values may change from time to time or vary from one location to another, suggesting the necessity of reconstructing the index to handle the economic changes. Changes in economic values signify a change in net merit, the selection goal, thereby reducing the overall selection gains, which is a major external deterrent to genetic progress from index selection.

## Internal Deterrents to Index Selection

As with single trait selection, response to index selection would become impossible if the heritability of the index reduces to zero. A negative genetic correlation may arise after a period of selection for positively correlated traits (Lerner 1958) or two genetically uncorrelated traits (Hogsett and Nordskog 1958). The induction of negative correlations among favorable traits will reduce genetic progress.

A plateau or zero genetic change may occur in index selection when gains in some component traits are balanced by losses in others, thereby leading to zero change in net merit. This can occur since the unrestricted selec-

tion index deals with the change in net merit and has no control over the relative changes in its component traits. A selection limit may appear with index selection even though the genetic variances of the component traits are not exhausted. Under this circumstance, how to utilize the residual genetic variances of the component traits merits further research.

## Acknowledgement

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