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Heritability of a Linear Combination of Traits*

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Summary. The heritability, h_I^2, of a linear combination of phenotypes, I, when defined as the ratio of the variance of the genetic index, σ_{g*}^2, to the variance of the index, σ_I^2, is shown to be different from the square of the correlation, r_{HI}^2, between the index and an arbitrary linear combination of genetic effects, H. The gain in H for selection on I is shown to be proportional to $h_I^2 \cdot b_{Hg*}$ for any index.

Key words: Selection Index - Heritability

Introduction

Smith (1936) applied Fisher's concept of the discriminant function (1936) to develop an index procedure for the selection of plant lines. Hazel (1943) extended the index procedure for the selection of individuals in animal populations by defining an aggregate genotype as a linear combination of genetic values, each weighted by the relative economic values. The selection index has been widely advocated for improvement in one or a series of quantitative traits. The squared correlation between the selection index and the aggregate genotype has been interpreted by some researchers as the heritability of the index. The purposes of this note are to define the heritability of an index, h_I^2, i.e. a linear combination of phenotypes and to show the relationship between h_I^2, b_{HI} and r_{HI}^2.

Selection Index Theory

Selection index theory is briefly outlined where the resulting index and aggregate genotype (or net merit) are defined as follows:

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

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

where $\underline{p}' = (p_1, p_2, \ldots p_m)$ = a row vector (the transpose of column vector $\underline{p}$) of m known phenotypic values,

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

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

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

Equations for $\underline{b}$, which arise from maximizing the correlation between H and I, are given by Henderson (1963) as

$$\underline{b} = P^{-1}G\underline{a} ,$$

where P is the phenotypic variance-covariance matrix (m × m) and G is the genetic covariance matrix (m × n). The following equalities exist:

$$\sigma_{HI} = \underline{b}'G\underline{a} = \underline{b}'P\underline{b} = \sigma_I^2 ,$$

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

and $$r_{HI} = \sigma_{HI}/\sigma_H\sigma_I = \sigma_I/\sigma_H .$$

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Heritability of Single Trait in Relation to the Heritability of an Index

A usual model for partitioning the phenotypic value for a single trait (p) on an animal into additve genetic effects (g) and residual effects (e) is

$$p = \mu + g + e$$

where $E(g) = E(e) = E(ge) = 0$, μ is common mean, and variance of p in the population is

$$\sigma_p^2 = \sigma_g^2 + \sigma_e^2 .$$

Heritability of one trait, in the narrow sense, may be defined as the regression of g on p and given as

$$h^2 = \frac{\sigma_g^2}{\sigma_p^2} .$$

Under this model the regression of g on p is equal to the squared correlation,

$$r_{gp}^2 = \frac{(\sigma_{gp})^2}{\sigma_g^2 \sigma_p^2} = \frac{(\sigma_g^2)^2}{\sigma_g^2 \sigma_p^2} = \frac{\sigma_g^2}{\sigma_p^2} .$$

Heritability of an index may be defined from a model where each phenotype in a linear combination of phenotypes is partitioned as for a single trait:

$$I = \sum_i^m b_i p_i = \sum_i^m b_i(\mu + g_i + e_i)$$

$$= \mu^* + g^* + e^* ,$$

where $\mu^* = \sum_i b_i \mu_i$, $g^* = \sum_i b_i g_i$, and $e^* = \sum_i b_i e_i$. When e^* is uncorrelated with g^*, the variance of I is $\sigma_I^2 = \sigma_{g*}^2 + \sigma_{e*}^2$.

The subscripts $i = 1, \dots, m$ denote the traits included in the index, I. The concept of a gentic index is introduced and defined as the linear combination of the genetic component of each phenotype weighted by the respective index coefficients (b_i). The genetic index, in contrast with the aggregate genotype, weights each additive genetic value, g_i, with the corresponding selection index coefficient, b_i, reflecting the relative selection pressure applied to each additive value while in the later the weights reflect relative economic values. The variances and covariances obtained from the above definitions are

$$\sigma_{g*}^2 = \underline{b}'G\underline{b} ,$$

$$\sigma_{g*I} = \underline{b}'G\underline{b} = \sigma_{g*}^2,$$

and $\sigma_{g*H} = \underline{b}'G\underline{a}$.

The heritability of the index, h_I^2, when defined as the ratio of genetic variance to the total variance of the index, is

$$h_I^2 = \sigma_{g*}^2/\sigma_I^2 = \underline{b}'G\underline{b}/\underline{b}'P\underline{b} .$$

The heritability can be calculated from the genetic and phenotypic parameters of the phenotypes in the index. The genetic index as a generalization of the concept for the genetic value of one trait appears to be reasonable and consistent with the definition for genetic effects in one trait. When the number of traits in the index is reduced to one trait, $h_I^2 = h^2$ for the single trait.

While it may seem to be a reasonable extension from the case of one trait where $h^2 = r_{gp}^2$, the heritability for an index is not r_{HI}^2. The squared multiple correlation coefficient r_{HI}^2 measures the association between I and H and is not equal to the ratio of the variance of the genetic index to the total variance of the index. Use of r_{HI}^2 as the heritability of an index would be inconsistent with the historical definition given by Lush (1945).

The regression of H on I is equal to unity and is fixed as a condition of the development of a selection index (Henderson 1963). Setting $b_{HI} = 1$ equalizes the interpretative value of differences on the index scale and on the aggregate genotypic value scale. Heritability for an index makes more sense when it varies as a function of genetic parameters. Therefore, it is wrong to say heritability of index is unity in terms of regression or to say heritability of index is a square of the correlation between I and H.

Expected Gains in H from Selection on I

The genetic gains in aggregate genotype (H) need to be distinguished from gains in the genetic index (g^*).

When selection is on I, the genetic gain in H is

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

$$= \bar{i}\,\sigma_I$$

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 of the index or the selection differential for population with variance equal to 1. When selection is on I, the genetic gain in g* is

$$\Delta g^* = b_{g^*I}(\bar{I}_s - \bar{I}_\mu)$$

$$= h_I^2\,\bar{i}\,\sigma_I \ .$$

Therefore, the former deals with genetic progress in selection goal (H), while the latter deals with genetic advance in the selection criterion (I). Genetic advance in the selection criterion is of little significance in the analysis of selection for gain in H using the best index. The topic is pursued for the clarification of the relationship between I, H and g^*. Any linear function of $\underline{p}$ can be utilized as a selection criterion without explicitly defining H to develop the index. Analysis of selection for an arbitrary index would then likely focus on gain in the genetic basis of the selection criterion. The correlated response in H in terms of g* is

$$\Delta H = b_{Hg^*}(\Delta g^*)$$

$$= b_{Hg^*}h_I^2\,\bar{i}\,\sigma_I \ .$$

The expression reduces to $\bar{i}\,\sigma_I$ when the selection index weights satisfy $P\underline{b} = G\underline{a}$, which leads to $\sigma_{Hg^*} = \sigma_{HI} = \sigma_I^2$. This formulation shows that the product of h_I^2 and b_{Hg^*} is proportional to the expected change in H from selection on I. Gains in H from arbitrary indexes are dependent on nonzero h_I^2 and b_{Hg^*}.

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