

A BAYESIAN INTERPRETATION OF THE GENETIC SELECTION INDEX

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ABSTRACT

The general formulation proposed by Henderson (1963), of the genetic selection index model is shown to have a Bayesian interpretation in which the distribution associated with genetic values is treated as a prior distribution. A Bayes rule is constructed for the index in the case in which the expected values of records are unknown.

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In the usual formulation of the genetic selection index problem (see for example Comstock (1948)) one supposes that for each candidate for selection, observations  $Y_1, Y_2, \dots, Y_n$  are available on phenotypes corresponding to  $N$  traits of interest. It is further supposed that each phenotype is related to an unobservable genotype through the linear model  $Y_i = \mu_i + u_i + e_i$  where  $\mu_i$  is a constant,  $u_i$  is the genetic value corresponding to the genotype for the  $i^{\text{th}}$  trait and  $e_i$  is environmental "noise." That is  $\underline{Y} = \underline{\mu} + \underline{u} + \underline{e}$  where each component is an  $N$  dimensional column vector. Now if  $\underline{v} = (v_1, v_2, \dots, v_n)'$  is an  $N$ -vector of constants representing the relative economic values of the  $N$  traits, then one wishes to construct an index,  $I$ , (a function of  $\underline{Y}$ ) to use in selection for the "aggregate genetic value"  $T = \underline{v}'\underline{u}$ .

The usual approach is to assume that  $\underline{u}$  and  $\underline{e}$  are independent  $N$ -variate normal random variables, say  $\underline{u} \sim N(\underline{0}, \underline{G})$  independent of  $\underline{e} \sim N(\underline{0}, \underline{E})$  where  $\underline{G}$  and  $\underline{E}$  are positive definite and symmetric matrices of order  $N$ . Then one requires the index  $I$  to be a scalar valued linear function,  $I = \underline{b}'(\underline{Y} - \underline{\mu})$  and determines the vector  $\underline{b}$  to maximize the correlation between  $I$  and  $T$ . The result is  $I = \underline{v}'\underline{G}\underline{P}^{-1}(\underline{Y} - \underline{\mu})$ , where  $\underline{P} = \underline{G} + \underline{E}$ . This index has a number of desirable properties (see Henderson (1963)), and it will be here demonstrated that it also has a Bayesian interpretation.

In a Bayesian context, with distribution assumptions as above, the distribution for  $\underline{u} \sim N(\underline{0}, \underline{G})$  is viewed as the prior distribution, and then the likelihood (distribution of  $\underline{Y}$  given  $\underline{u}$ ) is  $N(\underline{\mu} + \underline{u}, \underline{E})$ . If we seek a Bayes rule,  $I$ , for  $T = \underline{v}'\underline{u}$  and are operating under quadratic loss,  $(I - T)^2$ , then the Bayes rule is the mean of the posterior distribution of  $T$  given  $\underline{Y}$ . i.e.,

$$I = E(T|\underline{Y}) = \underline{v}'E(\underline{u}|\underline{Y}) = \underline{v}'\underline{G}\underline{P}^{-1}(\underline{Y} - \underline{\mu})$$

as before. Note that for the Bayesian model, it is not necessary to assume that the index is linear.

A more general formulation of the problem (see Henderson (1963)) is to suppose that

$$\underline{Y} = \underline{X}\underline{\beta} + \underline{Z}\underline{u} + \underline{e}$$

where  $\underline{Y}$  is an (observable) N-variate random variable,  $\underline{X}$  is a known  $N \times p$  matrix of rank  $p \leq N$ ,  $\underline{\beta}$  is a p-vector of parameters,  $\underline{Z}$  is a known  $N \times r$  matrix of rank r,  $\underline{u}$  is an (unobservable) r-variate normal random variable with mean vector  $\underline{0}$  and positive definite covariance matrix  $\underline{G}$ ,  $\underline{e}$  is an N-variate normal random variable with mean vector  $\underline{0}$  and positive definite covariance matrix  $\underline{E}$ , and  $\underline{u}$  and  $\underline{e}$  are independent.

Thus, here, the N phenotypes depend on N linear functions of r genetic values. This model reduces to that described above if we let  $r = N$ ,  $\underline{X}\underline{\beta} = \underline{\mu}$  and  $\underline{Z} = \underline{I}_N$ , the identity matrix of order N. Again, if we seek an index to select for  $T = \underline{v}'\underline{u}$  (where now  $\underline{v}$  is an r-vector) the usual result has a Bayesian interpretation. Thus the prior distribution for  $\underline{u}$  is r-variate  $N(\underline{0}, \underline{G})$  and the likelihood of  $\underline{Y}$  given  $\underline{u}$  is N-variate  $N(\underline{X}\underline{\beta} + \underline{Z}\underline{u}, \underline{E})$  so that with quadratic loss, the Bayes rule is

$$I = E(T|\underline{Y}) = \underline{v}'E(\underline{u}|\underline{Y}) = \underline{v}'\underline{G}\underline{Z}'\underline{A}^{-1}(\underline{Y} - \underline{X}\underline{\beta}),$$

where  $\underline{A} = \underline{Z}\underline{G}\underline{Z}' + \underline{E}$  is the marginal covariance matrix of  $\underline{Y}$ . Again linearity obtains for the Bayes rule but is assumed in the usual approach. Note that the economic weighting  $T = \underline{v}'\underline{u}$  is not the only way to make use of the genetic values. We may calculate a Bayes rule,  $\hat{\underline{u}}$ , for the whole vector,  $\underline{u}$ . If the loss function is  $(\hat{\underline{u}} - \underline{u})'K(\hat{\underline{u}} - \underline{u})$  for any positive definite matrix  $\underline{K}$  of order r, then the result is simply

$$\hat{\underline{u}} = E(\underline{u}'\underline{Y}) = \underline{GZ}'\underline{A}^{-1}(\underline{Y} - \underline{X}\underline{\beta}), \quad (1)$$

and does not depend on  $\underline{K}$ .

If all candidates for selection provide the same information, i.e., values of the same random variable  $\underline{Y}$ , above, and selection is based on ranking by the index, then this ranking does not depend on the value of  $\underline{\beta}$ . That is, the difference in values of the index when applied to two individuals does not depend on  $\underline{\beta}$ . Thus, in this case,  $\underline{\beta}$  need not be known. If however,  $\underline{\beta}$  must be estimated, Henderson (1963) replaces  $\underline{\beta}$  in the index, by its maximum likelihood estimator  $\hat{\underline{\beta}} = (\underline{X}'\underline{A}^{-1}\underline{X})^{-1}\underline{X}'\underline{A}^{-1}\underline{Y}$ . Notice that this can lead to difficulties for some pathological models. That is, with  $\underline{\beta}$  replaced by  $\hat{\underline{\beta}}$ , the index becomes

$$\underline{GZ}'\underline{A}^{-1}(\underline{Y} - \hat{\underline{X}}\hat{\underline{\beta}}) = \underline{GZ}'\underline{A}^{-1}\left[\underline{I}_N - \underline{X}(\underline{X}'\underline{A}^{-1}\underline{X})^{-1}\underline{X}'\underline{A}^{-1}\right]\underline{Y},$$

and if the model happens to have  $\underline{Z}' = \underline{B}\underline{X}'$  for some  $r \times p$  matrix  $\underline{B}$ , then the index is zero for all  $\underline{Y}$ .

Now, if  $\underline{\beta}$  is unknown, then to be consistent with the Bayesian approach, one is required to have a prior distribution for  $\underline{\beta}$ . Thus, with  $\underline{\theta}' \equiv (\underline{\beta}' \ \underline{u}')$  and  $\underline{W} \equiv (\underline{X} \ \underline{Z})$ , we have  $\underline{Y} = \underline{W}\underline{\theta} + \underline{e}$ , where as before,  $\underline{e} \sim N(\underline{0}, \underline{E})$ , independent of  $\underline{\theta}$ . The prior distribution for  $\underline{\theta}$  is taken to be  $(p+r)$ -variate normal with mean vector  $\underline{\theta}_0 = (\underline{\beta}_0' \ \underline{0}')$  and positive definite covariance matrix

$$\underline{G}^* = \begin{bmatrix} \underline{G} & \underline{G}\underline{\beta}_0 \\ \underline{G}' & \underline{G}\underline{\beta}_0' \\ \underline{G}\underline{\beta}_0 & \underline{G} \\ \underline{G}\underline{\beta}_0' & \underline{G} \end{bmatrix}.$$

The likelihood is then N-variate normal,  $N(\underline{W}\underline{\theta}, \underline{E})$ , and the Bayes rule for  $\underline{\theta}$  with respect to the quadratic loss  $(\tilde{\underline{\theta}} - \underline{\theta})' \underline{K} (\tilde{\underline{\theta}} - \underline{\theta})$  (where  $\underline{K}$  is any positive definite matrix of order  $p+r$ ) is the posterior mean of  $\underline{\theta}$ . That is, the Bayes rule is

$$\tilde{\underline{\theta}}(\underline{Y}) = E(\underline{\theta} | \underline{Y}) = \underline{\theta}_0 + \underline{G}^* \underline{W}' (\underline{W} \underline{G}^* \underline{W}' + \underline{E})^{-1} (\underline{Y} - \underline{W} \underline{\theta}_0).$$

(Note that the  $(p+r) \times N$  matrix of covariances between components of  $\underline{\theta}$  and  $\underline{Y}$  is  $\underline{G}^* \underline{W}'$ .)

Our interest is only in the last  $r$  rows of  $\tilde{\underline{\theta}}(\underline{Y})$ , namely

$$\tilde{\underline{u}}(\underline{Y}) = (\underline{G}'_{\underline{\beta u}} \underline{X}' + \underline{G}'_{\underline{u}} \underline{Z}') (\underline{W} \underline{G}^* \underline{W}' + \underline{E})^{-1} (\underline{Y} - \underline{X} \underline{\beta}_0).$$

If  $(\underline{Z} \underline{G}'_{\underline{\beta u}} \underline{X}' + \underline{A})$  is non-singular, where  $\underline{A} = \underline{Z} \underline{G}'_{\underline{u}} \underline{Z}' + \underline{E}$  as above, this can be written

$$\tilde{\underline{u}}(\underline{Y}) = (\underline{G}'_{\underline{\beta u}} \underline{X}' + \underline{G}'_{\underline{u}} \underline{Z}') (\underline{Z} \underline{G}'_{\underline{\beta u}} \underline{X}' + \underline{A})^{-1} (\underline{Y} - \underline{X} \tilde{\underline{\beta}})$$

where  $\tilde{\underline{\beta}}$  is the Bayes rule for  $\underline{\beta}$ , i.e., the first  $p$  rows of  $\tilde{\underline{\theta}}(\underline{Y})$ .

If  $\underline{\beta}$  and  $\underline{u}$  are a-priori independent so that  $\underline{G}_{\underline{\beta u}} = \underline{0}$ , (and thus  $(\underline{Z} \underline{G}'_{\underline{\beta u}} + \underline{A}) = \underline{A}$  is non-singular), then the Bayes rule for  $\underline{u}$  reduces to

$$\tilde{\underline{u}}_{\underline{I}}(\underline{Y}) = \underline{G}'_{\underline{u}} \underline{Z}' \underline{A}^{-1} (\underline{Y} - \underline{X} \tilde{\underline{\beta}}), \quad (2)$$

and

$$\tilde{\underline{X}} \underline{\beta} = \left[ \underline{X} \underline{G}'_{\underline{\beta}} \underline{X}' (\underline{X} \underline{G}'_{\underline{\beta}} \underline{X}' + \underline{A})^{-1} \right] \underline{Y} + \left[ \underline{I}_{\underline{N}} - \underline{X} \underline{G}'_{\underline{\beta}} \underline{X}' (\underline{X} \underline{G}'_{\underline{\beta}} \underline{X}' + \underline{A})^{-1} \right] (\underline{X} \underline{\beta}_0),$$

is a matrix weighted average of the observation,  $\underline{Y}$  and the a-priori mean  $\underline{X}\underline{\beta}_0$ .

Thus if under the prior distribution,  $\underline{\beta}$  and  $\underline{u}$  are independent, the Bayes rule (2) for  $\underline{u}$  is the usual index (1) with  $\underline{\beta}$  replaced by its Bayes rule  $\tilde{\underline{\beta}}$  rather than its maximum likelihood estimator  $\hat{\underline{\beta}}$ .

#### REFERENCES

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