Breeding Goals and Phenotyping Programs for Multi-Trait Improvement in the Genomics Era

J.C.M. Dekkers[1] and J.H.J van der Werf[2]
[1]Iowa State University, Ames, Iowa, USA, [2]University of New England, Armidale, New South Wales, Australia

ABSTRACT: Genomic information can enhance breeding programs by increasing the accuracy of estimated breeding values. In a multi-trait setting, genomic information also provides opportunities to remove limitations of traditional breeding programs with regard to genetic improvement of 'hard to measure' traits, in particular if they have unfavorable genetic correlations with 'easy to measure' traits. The objectives of this paper are to describe and discuss the impact of availability of genomic information on breeding goals and phenotyping programs for multi-trait improvement of selection programs towards an overall economic objective.
Keywords: Selection Index, Economic Values, Genomics

Introduction

The standard strategy for development of multi-trait selection criteria, as initially proposed by Hazel (1943) includes four steps: 1) Define the overall objective (e.g. profit per animal); 2) Develop a linear breeding goal (aggregate genotype, H) as a function of genetic traits that contribute to the overall objective; 3) Derive the economic value (v) for each trait in H, defined as the change in the overall objective per unit of change in the trait, keeping all other traits in H constant; 4) Derive a linear index (I) of information sources that maximizes the accuracy of the index with H. Selection index theory (Hazel, 1943) can be used to derive the optimal index in step 4) and to predict responses to multi-trait selection in the overall objective and in component traits. The latter is important to evaluate and compare alternate multi-trait selection criteria or breeding programs, as well as the value and impact of different sources of information on responses to selection. Results demonstrate how achieving improvement in the overall objective not only depends on genetic and economic parameters but also on what information (phenotypes, genomic data) is available, which is a crucial component of the design of breeding programs.

In principle, availability of genomic information does not affect the development of the first three steps above, although it could affect the sensitivity of step 4) to errors in economic values, which affects the importance of getting accurate results in step 3). Genomic predictions constitute additional sources of information that can enter the selection index and contribute to achieving multi-trait response toward the overall objective. Of particular interest in this regard is the extent to which genomic information can overcome the problems associated with multi-trait improvement for traits that are unfavorably correlated, i.e. for which the sign of the genetic correlation is opposite to the sign of the product of their economic values. The main objective of this paper is to discuss strategies to overcome these limitations, with emphasis on specific phenotype recording programs under genomic selection.

To set the stage, we will start with a brief description of the development of multi-trait selection criteria based on multi-trait estimated breeding values (EBV) and prediction of associated responses to selection and demonstrate how responses to selection depend on the variance-covariance matrix of the EBV. The latter matrix forms the connection between phenotype recording and multi-trait genetic improvement and drives the impact of targeted recording of phenotypes on multi-trait genetic improvement, both with and without genomic selection.

Multi-trait Selection Criteria

Consider the following aggregate genotype:

$$H = v_1g_1 + v_2g_2 \ldots v_ng_n = \mathbf{v'g} \quad [1]$$

where g_i and v_i are the additive genetic value and economic value of trait i, and the following multi-trait selection index:

$$I = b_1x_1 + b_2x_2 \ldots b_mx_m = \mathbf{b_x'x} \quad [2]$$

where x_j is the j^{th} source of information (an individual phenotypic record or the average of records) on the individual and/or its relatives on a trait in H or on a trait that is correlated to one or more traits in H. Following Hazel (1943), selection index weights that maximize the accuracy of I as a predictor of H can be derived as:

$$\mathbf{b_x} = \mathbf{P_x^{-1}G_xv} \quad [3]$$

where $\mathbf{P}_x$=var($\mathbf{x}$) is the mxm variance-covariance matrix of information sources in I and $\mathbf{G}_x$=cov($\mathbf{x}$,$\mathbf{g}$) is the mxn matrix with covariances between information sources in I and genetic traits in H. Also, define $\mathbf{C}$=var($\mathbf{g}$) as the nxn matrix of genetic variances and covariances between traits in H.

The accuracy of any linear index I defined in [2] (including the optimal index) can be derived as the correlation between H and I as:

$$r_{HI} = \sigma_{HI}/(\sigma_I\sigma_H) = \mathbf{b_x'G_xv}/(\sigma_I\sigma_H) \quad [4]$$

with

$$\sigma_{HI} = \mathrm{cov}(H,I) = \mathbf{b_x'G_xv} \quad [5]$$

$$\sigma_I^2 = \mathrm{var}(I) = \mathbf{b_x'P_xb_x} \quad [6]$$

$$\sigma_H^2 = \mathrm{var}(H) = \mathbf{v'Cv} \quad [7]$$

The vector of genetic superiorities of selected individuals for each of the traits in H, i.e. response to selection, per standard deviation of selection on the index (selection intensity = 1) is derived by regressing of I on $\mathbf{g}$:

$$\mathbf{S_g} = [S_{g_1}, \ldots, S_{g_n}] = \mathbf{b_x'G_x}/\sigma_I \quad [8]$$

Genetic superiority for the breeding goal is the sum of responses in traits, weighted by their economic values:

$$S_H = \mathbf{S_g v} \quad [9]$$

Note that equations [4] through [9] hold not only for the optimal weights derived using $\mathbf{b}=\mathbf{P^{-1}Gv}$, but for any arbitrary vector of index weights.

In modern breeding programs, information on traits is summarized in the form of EBV ($\hat{g}_i$) that are derived based on single or multi-trait BLUP genetic evaluation methods, using recorded phenotypes on all individuals in the population. In the genomics era, EBV also include genomic information, derived by blending direct genomic breeding values (DGVs) with standard BLUP EBV (Van Raden et al. 2009), or by joint analysis of phenotypes on genotyped or non-genotyped individuals, as in single-step BLUP (Misztal et al. 2009). The multi-trait selection criterion is then formulated as:

$$I = b_1 \hat{g}_1 + b_2 \hat{g}_2 + \ldots + b_m \hat{g}_m = \mathbf{b}_{EBV}' \hat{\mathbf{g}} \qquad [10]$$

When the EBV are derived using multi-trait BLUP and traits in *H* and *I* are the same, then, using properties of multi-trait BLUP EBV,

$$\mathbf{P}_{EBV} = \mathbf{G}_{EBV} = \text{var}(\hat{\mathbf{g}}) \qquad [11]$$

which is the variance-covariance matrix of EBV, and optimal index weights are equal to the economic values (Schneeberger et al. 1992):

$$\mathbf{b}_{EBV} = \mathbf{P}_{EBV}^{-1}\mathbf{G}_{EBV}\mathbf{v} = \mathbf{v} \qquad [12]$$

Thus, in this case, optimal index weights are independent of genetic parameters and the accuracy of the individual EBV because that information is already captured in the EBV. However, accuracy of the index and responses to selection do depend on the accuracy of the EBV because they are a direct function of the variance-covariance matrix of EBV, i.e.

$$r_{HI} = \sigma_{HI}/(\sigma_I\sigma_H) = \mathbf{b}_{EBV}'\mathbf{G}_{EBV}\mathbf{v}/(\sigma_I\sigma_H) \qquad [13]$$

and $$\mathbf{S}_g = \mathbf{b}_{EBV}'\mathbf{G}_{EBV}/\sigma_I \qquad [14]$$

with $$\sigma_I^2 = \mathbf{b}_{EBV}'\mathbf{G}_{EBV}\,\mathbf{b}_{EBV} \qquad [15]$$

and $$\mathbf{P}_{EBV} = \mathbf{G}_{EBV} = \mathbf{b}_{mt}\mathbf{P}_x\mathbf{b}_{mt} \qquad [16]$$

with $$\mathbf{b}_{mt} = \mathbf{P}_x^{-1}\mathbf{G}_x \qquad [17]$$

When traits in *H* and *I* are not the same, economic values on traits in *H* can be reparameterized to economic values on traits in *I* by the vector of genetic regressions of traits in *I* on traits in *H* (Schneeberger et al. 1992):

$$\boldsymbol{v}_I = \mathbf{b}'_{\mathbf{g}_H\mathbf{g}_I}\boldsymbol{v} \quad \text{with} \quad \mathbf{b}'_{\mathbf{g}_H\mathbf{g}_I} = \mathbf{C}_I^{-1}\mathbf{C}_{IH} \qquad [18]$$

where $\mathbf{C}_I$ is the genetic variance/covariance matrix among the traits in *I* and $\mathbf{C}_{IH}$ is the genetic covariance matrix between traits in *I* and traits in *H*. Accuracy of the index and responses in traits in *I* are derived following equations [13] and [14] but using the standard deviation of the full *H*. Responses for traits in *H* can be predicted by multiplying responses in traits in *I* obtained by the genetic regressions:

$$\mathbf{S}_{\mathbf{g}_H} = \mathbf{b}'_{\mathbf{g}_H\mathbf{g}_I}\,\mathbf{b}_{EBV}'\mathbf{G}_{EBV}/\sigma_I \qquad [19]$$

When EBV are single-trait, weights in $\mathbf{b}_{mt}$ from equation [17] must be replaced by single-trait index weights ($\mathbf{b}_{st}$), derived using trait-specific records for each trait EBV.

As demonstrated by equations [14] and [9], trait responses to selection on an index of multi-trait EBV are a direct function of the variance-covariance matrix of EBV ($\mathbf{P}_{EBV} = \mathbf{G}_{EBV}$), which quantifies the variance-covariance structure of the assumed multi-variate Normal distribution of EBV. Diagonal elements of $\mathbf{G}_{EBV}$ are equal to the square of accuracy of trait EBV and genetic variance, while off-diagonals depend on the information available and can result in correlations equal to 1 in extreme cases (i.e. when no trait-specific data is available for a trait). With full accuracy of EBV, $\mathbf{G}_{EBV}=\mathbf{C}$, the genetic variance-covariance matrix among traits. Figure 2 illustrates for a two-trait example for cases that will be discussed later, how adding information on traits affects both the magnitude and direction of responses in individual traits and thereby responses in the breeding goal, by expanding and tilting the ellipse of possible responses to selection. The response ellipse (Moav and Hill, 1966) provides all possible combinations of response in the two traits that can be achieved across the full range of relative economic values for the two traits, based on equation [14], given the assumed multi-normal distribution of trait EBV, as quantified by matrix $\mathbf{G}_{EBV}$.

Incorporating Genomic Information in Multi-trait Selection Criteria

Methods to incorporate marker or genomic information into single and multi-trait selection criteria using selection index theory were described by Lande and Thompson (1980) for marker information and by Dekkers (2007) for genomic prediction information. Briefly, genetic evaluations based on marker genotypes (Direct Genomic Values, DGV) can be included in selection index equations as separate information sources for the genetic traits in *I* or *H*, or by defining each DGV as a new correlated trait with heritability equal to 1, genetic variance equal to the variance of DGV = $r_{DGV}^2\sigma_g^2$, where r_{DGV} is the accuracy of the DGV, and a genetic correlation with the corresponding phenotype-based trait equal to r_{DGV} (Dekkers, 2007). If genomic information is used to obtain DGV with BLUP properties, which is the aim of genomic prediction, then variances and covariances involving the DGV are derived using properties of BLUP EBV and accuracies of the DGV. Assuming environmental covariances are zero, covariances of the DGV of individual *i* on trait *k* with a phenotype information source in *I* or with the genetic value of relative *j* on trait *l* are equal to a_{ij} $r_{g_{kl}}r_{DGV_{ik}}^2\sigma_{g_k}\sigma_{g_l}$, where a_{ij} is the pedigree relationship between individuals *i* and *j* and $r_{g_{kl}}$ is the genetic correlation between traits *k* and *l*. Derivation of covariances with other sources of information requires the approximation that phenotypes used for training are on different individuals than phenotypes that contribute to pedigree-based EBV. This may often not be the case and could lead to overestimation of the benefit of adding genomic information.

Accuracy of genomic EBV depends on the size of the training population, heritability of the phenotypes used for training, historical effective population size, and relationships of individuals in training and selection

candidates, and can be derived empirically or analytically (e.g., Goddard et al. 2011).

Impact of Genomics on Formulation of Breeding Goals

Formulation of breeding objectives and breeding goals should be driven by the economics of the production system or market that is the target of genetic improvement and by the genetic traits that drive differences in the overall breeding objective (e.g. profit per animal) in that production system or market. Thus, formulation of breeding objectives and breeding goals is in principle independent of the design of the breeding program or of information collected to effect genetic improvement, including genomic information. However, availability of genomic information can affect the impact that uncertainty about estimates of parameters that contribute to development of breeding goals has on responses to selection, in particular uncertainty of economic values.

Methods for derivation of economic values were summarized by Knap (2014). Most theory and methods for derivation of economic values was developed prior to the 1990's. Since that time, development of breeding goals and estimation of economic values has received limited attention in the literature. There may be several reasons for this, including: i) adequate methods for estimation of economic values are available; ii) several studies have shown that response in the overall breeding objective is rather robust to inaccuracies in estimates of economic values (VandePitte and Hazel, 1970; Smith, 1983); iii) with the increasing prevalence of corporate breeding programs, development of breeding objectives has moved outside the public domain; iv) increasing competition among breeding programs has increased emphasis on market position and marketability when making multi-trait selection decisions.

Robustness of responses to multi-trait selection to uncertainty about economic values is driven by non-zero genetic and phenotypic correlations between traits and limited accuracy of EBV of some traits, which results in response in those traits to primarily result from correlated responses in the more accurately evaluated correlated traits, regardless of their economic value. However, genomics allows more accurate EBV to be obtained for in principle all traits. To investigate the impact of this on robustness of responses to uncertainty in economic values, figure 1 shows the response in H with two traits with true economic values equal to 1 but when a wrong economic value is used for one of the traits, resulting in a suboptimal index and suboptimal responses to selection. Comparing responses in H resulting from the suboptimal to the optimal index shows that lost response from using improper estimates of economic values generally is larger when accuracies of EBV are increased by genomic selection. Thus, the importance of deriving proper economic values and weights for multi-trait selection criteria is more important in the era of genomics than it may have been previously. Similar arguments apply when evaluating the impact of modified index weights or desired gains indexes to address market considerations (e.g. Dekkers and Gibson, 1998) on responses to selection. In addition, decisions on investment into genomics require correct estimates of the economic impact of genetic improvement.

Impact of Genomics on Phenotype Recording Programs

Phenotype recording is a crucial component of animal breeding programs. As demonstrated earlier (equation [14]), for multi-trait selection on EBV, the magnitude and direction of response to selection in breeding goal traits is proportional to the variance covariance matrix of EBV, $\mathbf{G}_{EBV}$, which depends on the information that is used to estimate EBV and, therefore, on the sources of information that are available. Although the use of molecular information in theory reduces the importance of phenotypic records, the large training data that are required for accurate genomic prediction (Goddard et al. 2011) and the need for retraining (Wolc et al. 2011) requires continuous emphasis on phenotype recording programs. However, the design of phenotype recording programs may require substantial change with the advent of genomic selection. For example, König and Swalve (2009) showed that specialized test herds for potential bull dams in dairy cattle lose their benefits with genomic selection and suggested that these facilities or investments are better used to collect data that contribute to development of genomic predictions. Genomic selection also allows phenotype recording investments to be made in specific traits to overcome limitations of traditional programs.

With traditional phenotype-based selection, the accuracy of EBV at the time of selection is determined by genetic parameters and the number or records available on the individual and its close relatives on traits that are included in the multi-trait index. Design of traditional breeding programs, therefore, includes decisions on family structure and about which traits to record on which individuals and when within that family structure. For a given population capacity, family structure is primarily driven by the number of sires and dams used for breeding, which also determines selection intensities and rates of inbreeding. Trait characteristics also impose limitations on which traits records can be recorded on the individual and/or it's close relatives, at what age of selection candidates those records are available, and whether the traits can be recorded on animals within the nucleus breeding population. Categories of traits that do not meet these criteria, which we will refer to as hard to measure (htm) traits, in contrast to easy to measure (etm) traits, include sex-limited traits, traits that require animals to be sacrificed (e.g. meat quality traits), traits that are not available at a young age, traits that are expensive or difficult to measure, traits that require keeping animals in non-nucleus environments (e.g. disease traits), and traits measured on crossbred animals. Improving accuracy of EBV for htm traits requires records to be collected on sibs or progeny. These limitations reduce the accuracy of EBV that can be obtained on htm traits or increases generation intervals and/or increases rates of inbreeding because of extensive use of family information. This limits opportunities to select for htm traits and limits genetic

improvement in the breeding goal, even if the htm traits have high economic importance. For htm traits that have unfavorable genetic correlations with etm traits that typically have higher accuracy of EBV, response to selection can even be unfavorable, despite their economic importance. Many traits related to disease resistance and robustness fall in this category (Rauw et al. 1998).

Gibson (1989) recognized the impact that the design of breeding programs can have on the direction of selection trait responses for a given breeding goal, which he termed 'artificial evolution'. He proposed investigating the impact of alternative designs on the ratio of response between traits i and j: $R_{ij} = S_i/S_j$, with S_i predicted as in equation [8] and showed how alternative designs and economic weights could change this ratio of trait responses.

To overcome the limitations of traditional breeding programs for genetic improvement of htm traits, several strategies have been developed and proposed, including sib- or progeny-testing and combined pure-bred and cross-bred breeding programs that utilize data collected in the field (Wei and van der Werf, 1994). These, however, require substantial investments, have complicated logistics, for example by requiring pedigree to be tracked in order for phenotype records to be linked back to the selection candidates, and can lead to increased rates of inbreeding.

Genomic prediction reduces the importance of having records on selection candidates themselves and/or their close relatives, although it is well known that accuracy of genomic EBV is higher for selection candidates that have close relatives in the training data (Habier et al. 2007). One of the features of genomic prediction is that it capitalizes on the contributions that distant relatives can make to the EBV of selection candidates, through their genomic relationships across the genome and/or at specific regions of the genome, depending on the method used for genomic prediction. This removes many of the restrictions on accuracy of EBV for htm traits and also increases the value of each individual phenotypic record because the information from each record is leveraged across a larger number of individuals, both in the current generation and in future generations.

Genomic selection also allows for greater flexibility in investments in phenotyping, for example for investments to be directed at specific htm traits. Although in principle, all traits can benefit from genomic prediction, optimization of data collection designs may include prioritization of which traits should be emphasized in the creation of a training data set. While the aim of building training data should be to collect as many traits as possible on the individuals that are genotyped, some traits (e.g. disease challenge traits) may require specialized facilities that may prevent recording these animals for other traits.

As an example of determining priorities for trait recording, table 1 demonstrates that in a multi-trait selection setting, as expected, availability of a genomic prediction of a given accuracy (0.75 in the example) for a trait that has low accuracy in the traditional program leads to a greater relative improvement in the breeding goal than availability of a genomic prediction for the trait that has higher accuracy under traditional selection. However, this difference is greater, in relative terms, when the two traits have an unfavorable genetic relationship. The table also shows that the low accuracy trait requires a lower accuracy of the genomic EBV to obtain the same improvement in response in the breeding goal than the high accuracy trait, especially if the traits have an antagonistic relationship.

Figure 2 shows the response ellipses for the scenarios with positive and negative correlations for the scenario of table 2. The shape of the response ellipses is driven by the variance-covariance structure among the EBV, i.e. matrix $\mathbf{G}_{EBV}$, which depends on the underlying genetic parameters and the information that is available on each trait. Optimal directions of selection are driven by the shape of the response ellipse within the space of the overall objective, *H*, which is visualized by the iso-profit contours. The optimal direction of selection is the point on the ellipse that reaches the highest iso-profit contour. Results clearly show the impact of both the underlying genetic parameters (favorable versus unfavorable trait correlations relative to trait economic values) and the information that is available on each trait on optimal responses in *H* and individual traits. When the trait correlation is unfavorable, improvement in the trait with low accuracy (trait 2) is problematic, and even in the wrong direction. Increasing the accuracy for trait 2 expands the response ellipse in the dimension of variation for trait 2 and allows greater improvements to be made in trait 2 and, therefore, in *H*. Thus, prioritization of trait recording to maximize response in the breeding goal is driven by the economic parameters and how changes in accuracy of EBV for individual traits modify the variance-covariance structure of EBV towards the underlying genetic constraints, i.e. variance-covariance matrix **C**.

Following the artificial evolution concept of Gibson (1989), Amer (2012) investigated the impact of implementing genomic selection on the ratio of response in robustness versus production: $R_{Rob,Prod} = S_{Rob}/S_{Prod}$. Using dairy cattle as an example, results showed that, depending on the genetic parameters, large training data sets and priority on recording robustness phenotypes would be needed for genomic selection to result in an increase in $R_{Rob,Prod}$ compared to progeny testing; for small training data sets, and assuming even less training data is available for robustness than production, genomic selection resulted in a reduction of $R_{Rob,Prod}$, i.e. reducing the relative response for robustness.

As an example of the development of specialized data sets for genetic improvement, Banks et al. (2006) described the development of a specialized information nucleus for the collection of records on htm traits in sheep. Van der Werf et al. (2010) described criteria and algorithms for the choice of sires whose progeny should be included in an information nucleus for the purpose of maximizing information for estimation of quantitative genetic parameters for new traits, conduct whole-genome

association studies, and enhance estimation of breeding values of selection candidates by phenotype-based or genomic prediction. Criteria included i) trait diversity, aiming for high diversity of EBV among contributing sires across the multi-trait space of EBV expressed in economic units, ii) orthogonality, which aims to orthogonalize genetic and phenotypic differences among contributing sires by increasing diversity (based on pedigree-relationships) among individuals with similar multi-trait EBV, and iii) genetic diversity, by minimizing relationships among contributing sires. If sires have genomic data, van der Werf et al. (2010) suggested use of haplotype diversity across the genome as an additional criterion for choice of contributing sires. Massault et al. (2013) described an algorithm to optimize the choice of individuals to phenotype within a pedigree to maximize accuracy of EBV of selection candidates. Similar criteria could also be used to identify individuals that should be genotyped and phenotyped for the purpose of building multi-trait training data sets for genomic prediction. When the focus is on choice of individuals for genotyping based on existing information, the accuracy of EBV should also be included in order to maximize available information on genotyped individuals. Implications for long-term rates of inbreeding should also be considered, since individuals with accurate EBV are more likely to be selected. Optimal allocation of resources also depends on the cost of phenotyping versus genotyping. To maximize use of data collected in the information nucleus, van Grevenhof et al. (2012) showed that individuals in the nucleus rather than their parents should be genotyped. Investments in genotyping should also be compared to the alternative of directing these investments to additional phenotyping in a traditional program (e.g. Tribout et al. 2012).

Conclusions

Availability of genomic information does not affect the development of breeding goals and economic values but can affect the sensitivity of the outcome of breeding programs to errors in economic values or the use of suboptimal economic values. In a multi-trait setting, the magnitude and direction of responses to selection on EBV is driven by, besides selection intensities, the variance-covariance structure of EBV among selection candidates, which depends on the information available to derive EBV, along with underlying genetic parameters. Selection index theory provides convenient methodology to explore the limitations of breeding programs and the impact of availability of additional phenotypic or genomic information on individual traits. Availability of genomic information impacts the outcome of multi-trait breeding programs in terms of the magnitude and direction of responses in individual traits and in the overall objective by changing the variance-covariance structure of EBV among selection candidates. Genomic information provides opportunities to prioritize phenotype recording to overcome limitations of traditional phenotype-based programs for multi-trait genetic improvement. Additional research is needed on strategies and tactical approaches to optimize genotyping and phenotyping to maximize the benefit of genomic information in multi-trait breeding programs.

Figure 1: Lost response from uncertainty about economic values with traditional (TS) and genomic (GS) selection, depending on the genetic correlation between traits (r_g=r_p). True economic values = 1 for both traits. Accuracy of EBV equal to 0.64 and 0.43 for traits 1 and 2 under TS and equal to 0.9 for both traits under GS.

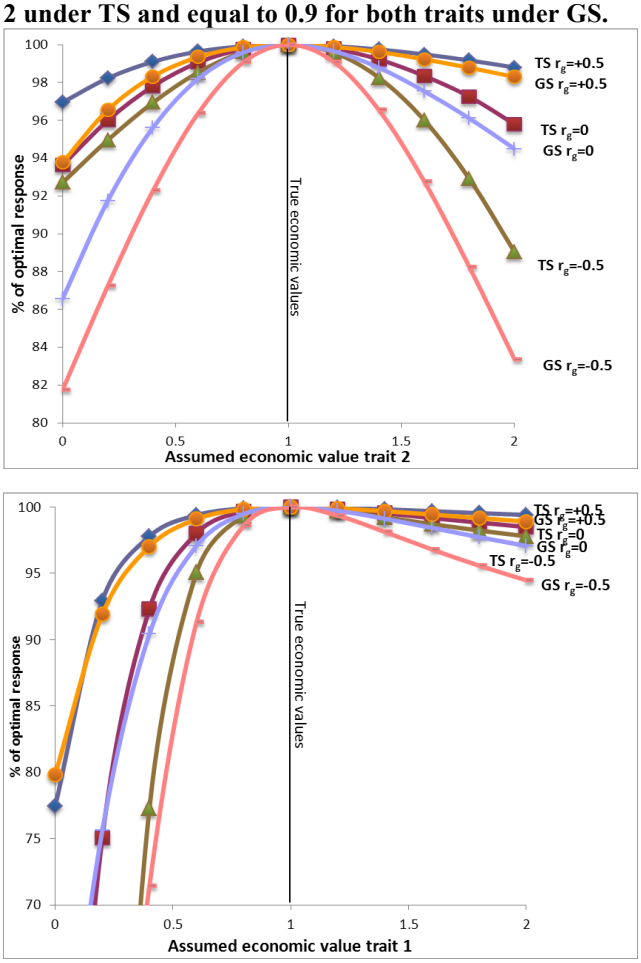

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Table 1: Optimal responses to selection for two traits with equal economic values and genetic standard deviations (=1), genetic and phenotypic correlations equal to +0.5, 0, or -0.5, and EBV based on own phenotype (h^2 = 0.3 and 0.05 for traits 1 and 2) or genomics (GS) with accuracy 0.75 for both traits.

Availability and accuracy of GEBV		r_g = r_p	Responses to selection			% increase in H
trait 1	trait 2		trait 1	trait 2	H	
-	-	0.5	0.564	0.261	0.826	
0.75	-		0.742	0.374	1.116	35.1
-	0.75		0.579	0.705	1.284	55.4
0.75	0.75		0.690	0.683	1.372	66.1
-	0.60[1]		0.563	0.552	1.115	35.1
-	-	0	0.507	0.085	0.592	
0.75	-		0.712	0.064	0.777	31.3
-	0.75		0.322	0.61	0.932	57.4
0.75	0.75		0.522	0.537	1.059	78.9
	0.55[1]		0.386	0.392	0.778	31.3
-	-	-0.5	0.513	-0.12	0.397	
0.75	-		0.681	-0.23	0.451	13.6
-	0.75		0.148	0.428	0.577	45.3
0.75	0.75		0.345	0.331	0.676	70.3
-	0.43[1]		0.384	0.067	0.451	13.6

[1] Accuracy of genomic EBV for trait 2 to achieve the same improvement in response as having a genomic EBV for trait 1 with accuracy 0.75.

Figure 2: Response ellipses and optimal directions of response (arrows) for index selection for two traits with equal economic values and genetic standard deviations (=1), genetic and phenotypic correlations equal to +0.5 (top graph) or -0.5 (bottom graph) and EBV based on own phenotype (h^2 = 0.3 and 0.05 for traits 1 and 2) or genomics (GS) with accuracy 0.75 for both traits. Black ellipse = selection on true breeding values; blue = selection on EBV based on own phenotype; purple = +GS for trait 1 only; green = +GS for trait 2 only; orange = +GS for both traits. Broken lines are iso-profit contours, specifying combinations of responses that result in equal response in the breeding goal. Optimal response is achieved at the tangent between the response ellipse and iso-profit contours.