Molecular Breeding Values for MAS or GS

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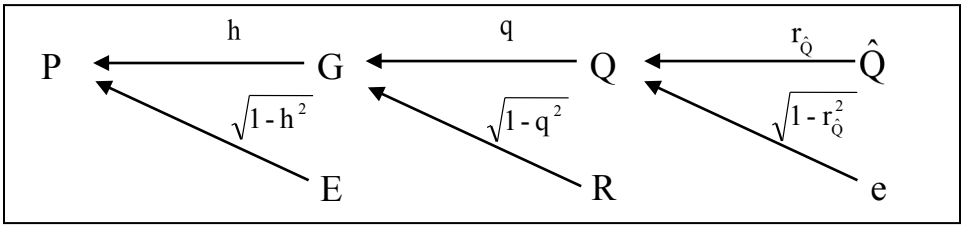
Incorporation MBV in Index Calculations of Total EBV (GEBV)



Lande and Thompson (1990, Genetics) index: $I_i = b_Q\hat{Q}_i + b_P P_i$

$\hat{Q}_i$ = MBV for individual i, = individual's EBV based on markers alone

P_i = individual's phenotype

$r_{MBV} = q\, r_{\hat{Q}}$ = accuracy of MBV as a predictor of total BV G

$q^2 = \sigma^2_Q / \sigma^2_G$ = proportion of genetic variance captured by markers (with inf. train size)

Assuming unbiased MBV (regression of G (or P) on MBV = 1; if not then divide MBV by $b_{P,MBV}$ to make it = 1)

- Variance of MBV = Var($\hat{Q}$) = $r^2_{MBV}\sigma^2_G$
- Cov($\hat{Q}$,P) = Cov($\hat{Q}$,G) = $r^2_{MBV}\sigma^2_G$

Table 1. Example calculation of MBV and index of phenotype and MBV with 3 SNPs with allele substitution effect estimates (allele A vs. B) of +10, +5, and –10 for for SNPs 1, 2, 3. The SNPs jointly explain 50% of the genetic variance for a trait with heritability 0.5. Resulting index weights on MBV and phenotype are $^2/_3$ and $^1/_3$, respectively.

	QTL 1		QTL 2		QTL 3				
Animal	Genotype	Value	Genotype	Value	Genotype	Value	MBV	Phenotype	Index value
1	AA	10	AA	5	AA	-10	5	35	15.0
2	AA	10	AA	5	BB	10	25	-10	13.3
3	AB	0	BB	-5	AB	0	-5	-15	-8.3
4	AB	0	BB	-5	AA	-10	-15	15	-5.0
5	BB	-10	AA	5	AB	0	-5	25	5.0

GEBV = $I_i = b_Q\hat{Q}_i + b_P P_i$ Derive optimal index weights by sel. index theory:

$$\begin{bmatrix} b_Q \\ b_P \end{bmatrix} = \mathbf{P}^{-1}\mathbf{G} = \begin{bmatrix} r^2_{MBV}\sigma^2_G & r^2_{MBV}\sigma^2_G \\ r^2_{MBV}\sigma^2_G & \sigma^2_P \end{bmatrix}^{-1} \begin{bmatrix} r^2_{MBV}\sigma^2_G \\ \sigma^2_G \end{bmatrix} = \begin{bmatrix} \dfrac{1-h^2}{1-r^2_{MBV}h^2} \\ \\ h^2\dfrac{(1-r^2_{MBV})}{1-r^2_{MBV}h^2} \end{bmatrix}$$

Thus, the relative weight on the MBV relative to phenotype is: $\dfrac{b_Q}{b_P} = \dfrac{{}^1\!/_{h^2} - 1}{1 - r^2_{MBV}}$

Table 2. Index weight on molecular score relative to phenotype (b_Q/b_P) for different heritabilities and accuracy of MBV.

Heritability	Squared accuracy of MBV (r^2_{MBV})				
(h^2)	0.10	0.25	0.50	0.75	1.00
0.10	10	12	18	36	Total weight
0.25	3.33	4	6	12	Total weight
0.50	1.11	1.33	2	4	Total weight
0.75	0.37	0.44	0.67	1.33	Total weight
1.00	0	0	0	0	Either

The Lande and Thompson (1990) formulation of the index can be extended to situations where phenotypes of relatives are used:

$$\text{GEBV} = I = \mathbf{b'X} = \begin{bmatrix}\mathbf{b}'_{\mathbf{Q}}, \mathbf{b}'_{\mathbf{P}}\end{bmatrix}\begin{bmatrix}\mathbf{X_Q} \\ \mathbf{X_P}\end{bmatrix}$$

$\mathbf{X}_Q$ = vector with marker-based EBV on the individual itself and/or its relatives

$\mathbf{X}_P$ = vector with phenotypic records on the individual itself and/or its relatives

$$\mathbf{b} = \begin{bmatrix}\mathbf{b}_Q \\ \mathbf{b}_P\end{bmatrix} = \mathbf{P}^{-1}\mathbf{G} = \begin{bmatrix}\text{Var}(\mathbf{X}_Q) & \text{Cov}(\mathbf{X}_Q, \mathbf{X}'_P) \\ \text{Cov}(\mathbf{X}_P, \mathbf{X}'_Q) & \text{Var}(\mathbf{X}_P)\end{bmatrix}^{-1}\begin{bmatrix}\text{Cov}(\mathbf{X}_Q, G) \\ \text{Cov}(\mathbf{X}_P, G)\end{bmatrix}$$

Elements ij of all matrices and vectors that involve $\mathbf{X}_Q = a_{ij}\ r^2_{MBV}\ \sigma^2_G$ $\quad a_{ij}$ = genetic relationship

These methods can also be extended to include data on multiple traits and multiple trait breeding goals (see Lande and Thompson 1990).

$$\textbf{Accuracy of GEBV} = \mathbf{r_{GEBV}} = \sqrt{\frac{\mathbf{b'G}}{\sigma^2_{\mathbf{G}}}}$$

It is useful to note that the index GEBV = $I_i = b_Q\hat{Q}_i + b_P P_i$ can be reparameterized into an equivalent index of MBV and the **phenotype adjusted for the MBV** as follows:

$$\text{GEBV} = I'_i = b'_Q\,\hat{Q}_i + b'_P P'_i \qquad \text{with} \qquad P'_i = P_i - \hat{Q}_i$$

Residual heritability = heritability of phenotype adjusted for the MBV:

$$h^2_{P'} = \frac{\sigma^2_G - r^2_{MBV}\sigma^2_G}{\sigma^2_P - r^2_{MBV}\sigma^2_G} = \frac{h^2(1 - r^2_{MBV})}{1 - r^2_{MBV}h^2}$$

$$\begin{bmatrix}b'_Q \\ b'_P\end{bmatrix} = \mathbf{P}^{-1}\mathbf{G} = \begin{bmatrix}r^2_{MBV}\sigma^2_G & 0 \\ 0 & \sigma^2_P - r^2_{MBV}\sigma^2_G\end{bmatrix}^{-1}\begin{bmatrix}r^2_{MBV}\sigma^2_G \\ \sigma^2_G - r^2_{MBV}\sigma^2_G\end{bmatrix} = \begin{bmatrix}1 \\ h^2_{P'}\end{bmatrix}$$

Thus, the resulting index is: $I'_i = \hat{G}_i = \hat{Q}_i + h^2_{P'}P'_i$

Advantage of index $I^{'}$ over index I is that its index weights remain constant over generations as the variance of MBV changes (with changing marker frequencies)

Note: $h^2_{P'}P^{'}_i$ = individual's EBV for polygenes, $\hat{Q}_i$, based on own phenotype adjusted for the QTL.

This index can be expanded to BLUP EBV from a model that includes QTL or markers as a fixed or random effect.
Such models result in estimates of molecular scores, $\hat{Q}_i$, and EBV for residual genetic effects, $\hat{R}_i$, with accuracy $\mathrm{r}_{\hat{R}}$.

Index weights for combining these two estimates, realizing that the variance of Residual EBV is equal to $r^2_{\hat{R}}\sigma^2_R$, where $\sigma^2_R = h^2_{P'}(\sigma^2_P - r^2_{MBV}\sigma^2_G)$ is the polygenic variance, can be derived as:

$$\begin{bmatrix} b^{'}_Q \\ b^{'}_P \end{bmatrix} = \mathbf{P}^{-1}\mathbf{G} = \begin{bmatrix} r^2_{MBV}\sigma^2_G & 0 \\ 0 & \mathrm{r}^2_{\hat{R}}\sigma^2_R \end{bmatrix}^{-1} \begin{bmatrix} r^2_{MBV}\sigma^2_G \\ \mathrm{r}^2_{\hat{R}}\sigma^2_R \end{bmatrix} = \begin{bmatrix} 1 \\ 1 \end{bmatrix}$$

Thus the GEBV is: $I^{'}_i = \hat{G}_i = \hat{Q}_i + \hat{R}_i$

Ad hoc blending: Harris BL, Johnson DL: Genomic predictions for New Zealand dairy bulls and integration with national genetic evaluation. J Dairy Sci 2010, 93:1243-1252.

Or use single step

Predicting Response to Marker-Assisted or Genomic Selection

Standard selection index theory can be used to predict responses to selection on GEBV, assuming multi-variate normality.

Consider the previously derived selection index of MBV and own phenotype:

$$\text{GEBV} = I_i = b_Q \hat{Q}_i + b_P P_i$$

$$\begin{bmatrix} b_Q \\ b_P \end{bmatrix} = \mathbf{P}^{-1}\mathbf{G} = \begin{bmatrix} r^2_{MBV}\sigma^2_G & r^2_{MBV}\sigma^2_G \\ r^2_{MBV}\sigma^2_G & \sigma^2_P \end{bmatrix}^{-1} \begin{bmatrix} r^2_{MBV}\sigma^2_G \\ \sigma^2_G \end{bmatrix} = \begin{bmatrix} \dfrac{1-h^2}{1-r^2_{MBV}h^2} \\ \\ h^2\dfrac{(1-r^2_{MBV})}{1-r^2_{MBV}h^2} \end{bmatrix}$$

The accuracy of this index and response to selection can be derived by standard selection index theory as:

$$r_{GEBV} = \sqrt{\frac{\mathbf{b'G}}{\sigma^2_\mathbf{G}}} = \sqrt{\begin{bmatrix} \dfrac{1-h^2}{1-r^2_{MBV}h^2} & h^2\dfrac{(1-r^2_{MBV})}{1-r^2_{MBV}h^2} \end{bmatrix}\begin{bmatrix} r^2_{MBV} \\ 1 \end{bmatrix}}$$

$$= \sqrt{\frac{r^2_{MBV} - 2r^2_{MBV}h^2 + h^2}{1-r^2_{MBV}h^2}} = \sqrt{r^2_{MBV} + h^2\frac{(1-r^2_{MBV})^2}{1-r^2_{MBV}h^2}}$$

Similarly for the alternate index parameterization:

$$\text{GEBV'} = I'_i = b'_Q \hat{Q}_i + b'_P P'_i$$

and

$$r_{GEBV'} = \sqrt{\frac{\mathbf{b'G}}{\sigma^2_\mathbf{G}}} = \sqrt{\begin{bmatrix} 1 & h^2_{P'} \end{bmatrix}\begin{bmatrix} r^2_{MBV} \\ 1-r^2_{MBV} \end{bmatrix}} = \sqrt{r^2_{MBV} + h^2_{P'}(1-r^2_{MBV})}$$

Using $h^2_{P'} = \dfrac{h^2(1-r^2_{MBV})}{1-r^2_{MBV}h^2}$ it can be shown that $r_{GEBV'}=r_{GEBV}$, i.e. the two indexes are equivalent

Assuming equal selection in males and females, with selection intensity i, response to selection can be predicted as: $R_{\text{MAS}} = i\, r_{GEBV}\, \sigma_g$

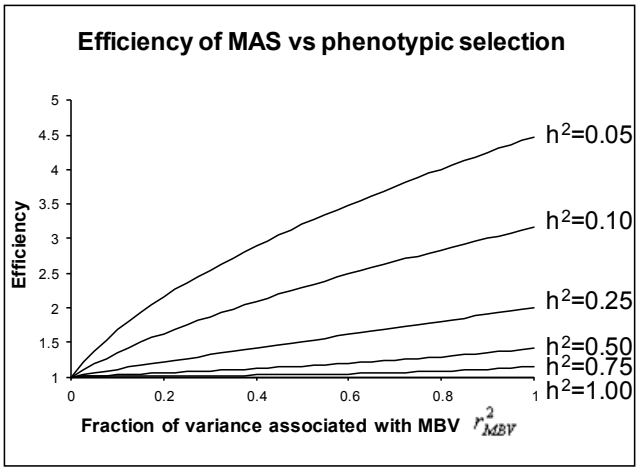
Response to phenotypic selection without QTL information is: $R_{\text{P}} = i\, h\, \sigma_g$

Thus, the efficiency of selection using marker information, defined as response to MAS relative to response without marker information, is given by:

$$E = \frac{R_{\text{MAS}}}{R_{\text{P}}} = \frac{r_{GEBV}}{h} = \sqrt{\frac{r^2_{MBV}}{h^2} + \frac{(1-r^2_{MBV})^2}{1-r^2_{MBV}h^2}}$$

An equivalent equation can be derived using the alternate index I':

$$E = \frac{R_{\text{MAS}}}{R_{\text{P}}} = \frac{r_{GEBV'}}{h} = \frac{1}{h}\sqrt{r^2_{MBV} + h^2_{P'}(1-r^2_{MBV})}$$



Modelling MBV as a Correlated Trait

After Dekkers (2007, JABG 124); Schrooten et al. (2005, JABG 123)

When based on multiple regions/markers, marker-based EBV behave as a Mendelian inherited polygenic trait with heritability =1:

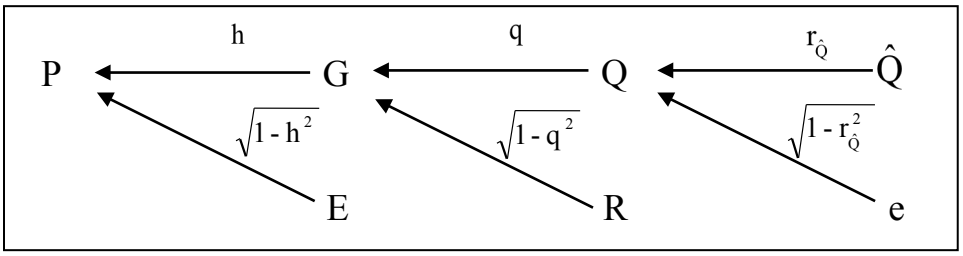
$$\text{MBV} = \hat{Q} = \sum_j (\hat{g}_j^{pat} + \hat{g}_j^{mat})$$

$\hat{g}_j^{pat}$ and $\hat{g}_j^{mat}$ = BLUP estimate of the effects of the paternal and maternal marker allele or haplotype for interval j.

$$\hat{Q}_{progeny} = \tfrac{1}{2}\hat{Q}_{sire} + \tfrac{1}{2}\hat{Q}_{dam} + (\sum_j \hat{g}_{ij}^{pat} - \tfrac{1}{2}\hat{Q}_{sire}) + (\sum_j \hat{g}_{ij}^{mat} - \tfrac{1}{2}\hat{Q}_{dam})$$

➔ marker-based EBV represent estimates that can be viewed and modeled as a genetic trait that can be observed on individuals without error ➔ heritability =1.

This allows standard selection index software to be used to model genomic selection (e.g. SelAction), including modelling the Bulmer effect and methods for prediction of inbreeding.



Marker-based EBV, $\hat{Q}$, are estimates of genetic effects Q.

$Q = \hat{Q} + e$ e = prediction error

$r_{\hat{Q}}$ = accuracy of $\hat{Q}$ as a predictor Q, = correlation between Q and $\hat{Q}$.

Then, the correlation of $\hat{Q}$ with G, i.e. the accuracy of the MBV is equal to $r_{MBV} = q\, r_{\hat{Q}}$

= accuracy of the marker-based EBV as a predictor of the total genetic value G

Define marker-based EBV, $\hat{Q}$, as a correlated trait with $h^2 = 1$, along with the regular trait.
Correlations required for selection index calculations (e.g., based on path diagram):

Genetic correlation between traits: $r_{G\hat{Q}} = q r_{\hat{Q}} = r_{MBV}$

Phenotypic correlation between traits: $r_{P\hat{Q}} = hq r_{\hat{Q}} = h\, r_{MBV}$

Phenotypic and genetic st.dev of MBV $= r_{MBV}\, \sigma_G$

Use of these parameters results in variances and covariances that are identical to the elements in matrix **P** and vector **G** of the Lande & Thompson (1990) index.

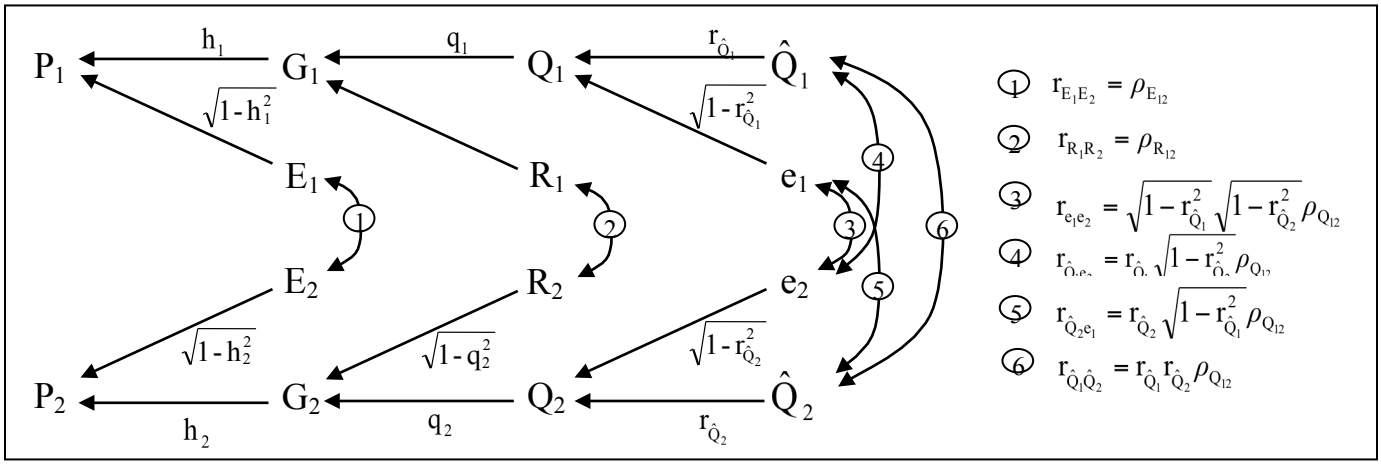
E.g.: $\text{Cov}(\hat{Q}_i, P_j) = \text{Cov}(\hat{Q}_i, G_j) = a_{ij}\text{Cov}(\hat{Q}, G) = a_{ij} r_{G\hat{Q}} \sigma_G r_{MBV} \sigma_G = a_{ij}\, r_{MBV}^2\, \sigma_G^2$

Extension to multiple traits

$\rho_{G_{12}}$, $\rho_{R_{12}}$, and $\rho_{Q_{12}}$ = genetic correlations traits 1 and 2 for the genetic components G, R, Q.

$$r_{G_i\hat{Q}_j} = q_i r_{\hat{Q}_i} r_{\hat{Q}_i\hat{Q}_j} + q_i\sqrt{1-r^2_{\hat{Q}_i}}\, r_{\hat{Q}_j e_i} = q_i r_{\hat{Q}_i} r_{\hat{Q}_i} r_{\hat{Q}_j}\rho_{Q_{12}} + q_i\sqrt{1-r^2_{\hat{Q}_i}}\, r_{\hat{Q}_j}\sqrt{1-r^2_{\hat{Q}_i}}\,\rho_{Q_{12}} = q_i r_{\hat{Q}_j}\rho_{Q_{12}}$$

$$r_{P_i\hat{Q}_j} = h_i r_{G_i\hat{Q}_j} = h_i q_i r_{\hat{Q}_j}\rho_{Q_{12}}$$



With random allocation of markers (GS) $E(q_1^2) = E(q_2^2) = q^2$ and $E(\rho_{R_{12}}) = E(\rho_{Q_{12}}) = \rho_{G_{12}}$

$$\rightarrow\ r_{\hat{Q}_1\hat{Q}_2} = \frac{\mathrm{Cov}(\hat{Q}_1,\hat{Q}_2)}{\sqrt{\mathrm{Var}(\hat{Q}_1)\mathrm{Var}(\hat{Q}_2)}} = \frac{r^2_{\hat{Q}_1} r^2_{\hat{Q}_2}\rho_{Q_{12}}}{r_{\hat{Q}_1} r_{\hat{Q}_2}} = r_{\hat{Q}_1} r_{\hat{Q}_2}\rho_{Q_{12}} = r_{\hat{Q}_1} r_{\hat{Q}_2}\rho_{G_{12}}$$

Table 1. Genetic parameters[1] for 4 traits considered for derivation of selection criteria: phenotype for trait (P_1) and trait 2 (P_2), and MBV for trait 1 ($\hat{Q}_1$) and trait 2 ($\hat{Q}_2$).

	P_1	P_2	$\hat{Q}_1$	$\hat{Q}_2$
P_1	h_1^2	$\rho_{P_{12}}$	$h_1 q_1 r_{\hat{Q}_1} =^2 h_1 r_{MBV_1}$	$h_1 q_1 r_{\hat{Q}_2}\rho_{Q_{12}} = h_1 r_{MBV_2}\rho_{G_{12}}$
P_2	$\rho_{G_{12}}$	h_2^2	$h_2 q_2 r_{\hat{Q}_1}\rho_{Q_{12}} = h_2 r_{MBV_1}\rho_{G_{12}}$	$h_2 q_2 r_{\hat{Q}_2} = h_2 r_{MBV2}$
$\hat{Q}_1$	$q_1 r_{\hat{Q}_1} = r_{MBV_1}$	$q_2 r_{\hat{Q}_1}\rho_{Q_{12}} = r_{MBV_1}\rho_{G_{12}}$	1	$r_{\hat{Q}_1} r_{\hat{Q}_2}\rho_{Q_{12}} = r_{\hat{Q}_1} r_{\hat{Q}_2}\rho_{G_{12}}$
$\hat{Q}_2$	$q_1 r_{\hat{Q}_2}\rho_{Q_{12}} = r_{MBV_2}\rho_{G_{12}}$	$q_2 r_{\hat{Q}_2} = r_{MBV_2}$	$r_{\hat{Q}_1} r_{\hat{Q}_2}\rho_{Q_{12}} = r_{\hat{Q}_1} r_{\hat{Q}_2}\rho_{G_{12}}$	1

[1] h_i^2 = heritability of phenotype for trait i

q_i^2 = proportion of genetic variance associated with markers for trait i

$r_{\hat{Q}_i}$ = accuracy of $\hat{Q}_i$ as a predictor of marker-associated genetic effects, Q_i.

r_{MBV_i} = accuracy of $\hat{Q}_i$ as a predictor of the total genetic value, G_i

$\rho_{G_{12}}$ = genetic correlation between traits 1 and 2

ρ_{P12} = phenotypic correlation between traits 1 and 2

$\rho_{Q_{12}}$ = correlation between Q_1 and Q_2

$\rho_{R_{12}}$ = correlation between residual genetic effects for traits 1 (R_1) and 2 (R_2)

[2] Results after the equality signs assume q_1=q_2 and $\rho_{G_{12}} = \rho_{Q_{12}} = \rho_{R_{12}}$, and use $q_i r_{\hat{Q}_i} = r_{MBV_i}$

$$\rho_{G_{12}} = q_1 q_2\rho_{Q_{12}} + \sqrt{1-q_1^2}\sqrt{1-q_2^2}\rho_{R_{12}} \qquad \rho_{P_{12}} = h_1 h_2\left(q_1 q_2\rho_{Q_{12}} + \sqrt{1-q_1^2}\sqrt{1-q_2^2}\rho_{R_{12}}\right)$$

Examples of Modelling MAS/GS using SelAction by Modelling MBV as Correlated Traits

(Dekkers, 2007, JABG 124)

Each generation, 20 males were selected. Each male was mated to three selected females, which each producing eight offspring (four male, four female). Heritability of the trait was 0.1 or 0.4 and selection was on BLUP EBV based on phenotypic and/or marker data.

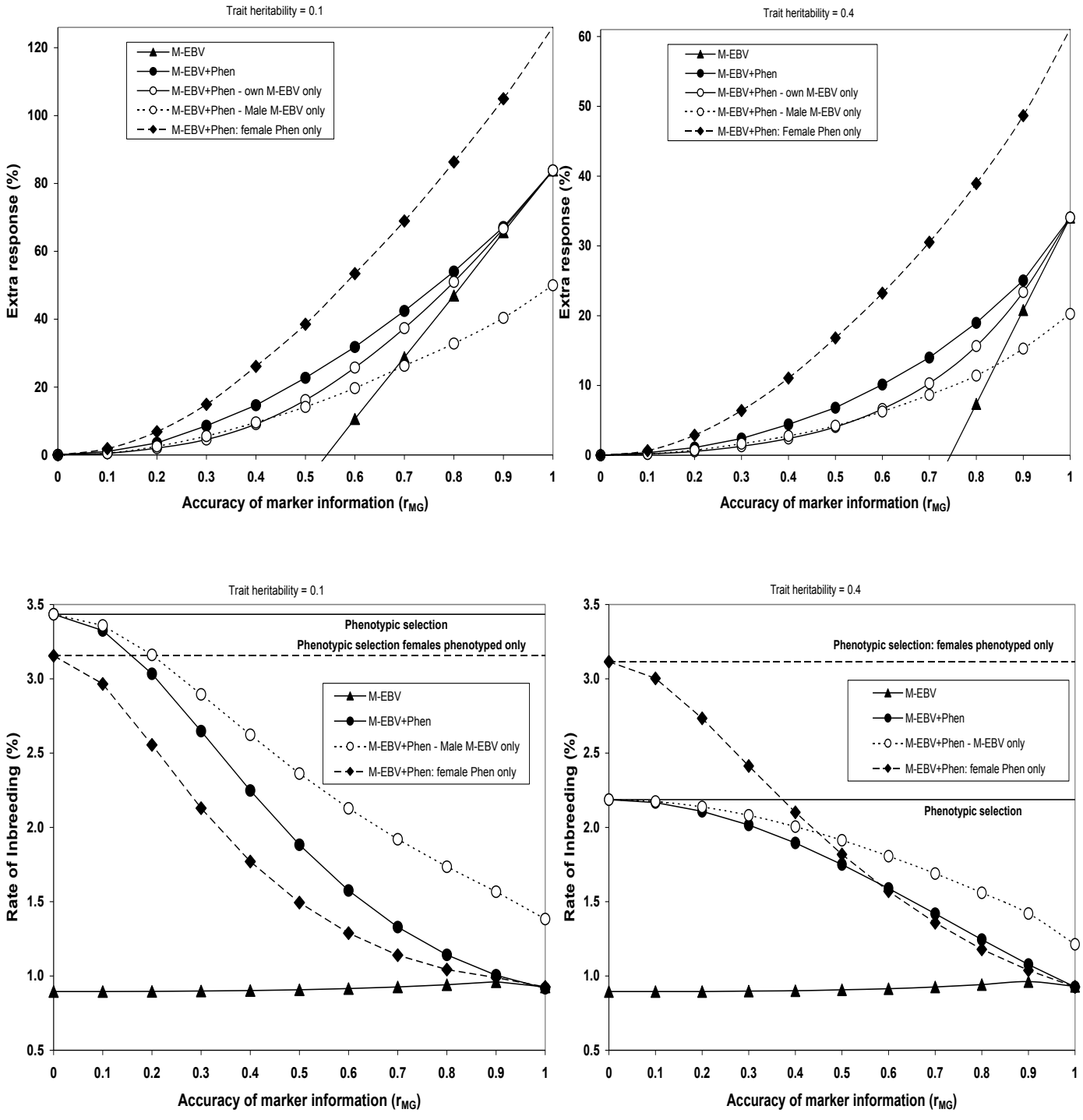


Table 2. Genetic parameters for selection on a breeding goal of two traits (P_1 and P_2) with and without marker information and resulting responses to selection in individual traits and the breeding goal (ΔH) and rates of inbreeding (ΔF). Marker-based EBV ($\hat{Q}_1$ and $\hat{Q}_2$) have accuracies of 0.8, based on markers explaining 62.4% of the genetic variance.

Correlations[1]	P_1	P_2	$\hat{Q}_1$	$\hat{Q}_2$		
P_1	--	-0.5	0.438	-0.131		
P_2	-0.3	--	-0.076	0.253		
$\hat{Q}_1$	0.8	-0.24	--	-0.243		
$\hat{Q}_2$	-0.24	0.8	-0.243	--		
Heritability	0.3	0.1	1	1		
Phenotypic SD	1	1	0.8	0.8		
Economic value	1	1	0	0		
Response to selection					ΔH	ΔF(%)
Phenotype only	0.408	0.041	0.394	0.052	0.448	2.36
Markers only	0.418	0.068	0.655	0.167	0.486	0.94
Combined	0.469	0.074	0.582	0.148	0.543	1.29

[1] Phenotypic correlations above the diagonal; genetic correlations below the diagonal

Impact of the Bulmer effect with Genomic Selection

(after Grevenhof, Bijma, van Arendonk GSE 2012, 44:26)

General equation for impact of selection on variable *w* on:

- covariance between variables *x* and *y*: $\sigma^*_{xy} = \sigma_{xy} - k\sigma^*_{xy}\frac{\sigma_{wx}\sigma_{wy}}{\sigma^2_w}$

- variance of variable *w*: $\sigma^{*2}_w = (1-k)\sigma^2_w$

- variance of correlated variable *x*: $\sigma^{*2}_x = (1-kr^2_{wx})\sigma^2_x$

Genomic Selection = select on *w* = MBV = trait with $h^2 = 1$ (equal male/female selection)

Variance MBV candidates generation t = $\sigma^2_{\mathrm{MBV,t}} = r^2_{\mathrm{MBV,t}}\sigma^2_{\mathrm{G,t}}$

Variance MBV selected parents gener t = $\sigma^{*2}_{\mathrm{MBV,t}} = (1-k)\sigma^2_{\mathrm{MBV,t}}$

Variance MBV next generation t+1 = $\sigma^2_{\mathrm{MBV,t+1}} = .5(1-k)\sigma^2_{\mathrm{MBV,t}} + .5\sigma^2_{\mathrm{MBV,0}}$

Genetic variance selected parents gener t = $\sigma^{*2}_{g,\mathrm{t}} = (1-r^2_{\mathrm{MBV,t}}k)\sigma^2_{g,\mathrm{t}}$

Genetic variance next generation t+1 = $\sigma^2_{g,\mathrm{t+1}} = 0.5(1-r^2_{\mathrm{MBV,t}}k)\sigma^2_{g,\mathrm{t}} + .5\sigma^2_{g,0}$

At equilibrium/Limit: $\sigma^2_{\mathrm{MBV,L}} = \sigma^2_{\mathrm{MBV,0}}/(1+k)$ from $\sigma^2_{\mathrm{MBV,t+1}} = \sigma^2_{\mathrm{MBV,t}}$

Response to GS = $i\sigma_{\mathrm{MBV}}$: $R_{(L)}/R_{(0)} = \sigma_{\mathrm{MBV,L}}/\sigma_{\mathrm{MBV,0}} = \frac{1}{\sqrt{1+k}}$

Note: same as BLUP selection

Genetic variance $\sigma^2_{g,L} = \sigma^2_{MBV,L} + \mathrm{PEV}$

$= [r^2_{MBV,0}\sigma^2_{MBV,0}/(1+k)] + (1-r^2_{MBV,0})\sigma^2_{g,0}$

$= \sigma^2_{MBV,0}(1-k\,r^2_{MBV,0})/(1+k)$

$\mathrm{PEV_L} = \mathrm{PEV_0}$ $(1-r^2_{MBV,L})\sigma^2_{g,L} = (1-r^2_{MBV,0})\sigma^2_{g,0}$

Accuracy-squared $r^2_{MBV,L} = 1-[(1-r^2_{MBV,0})\sigma^2_{g,0}/\sigma^2_{g,L}]$

Table 1 Comparison of the Bulmer-effect for mass selection and genomic selection

Selection methoda	h^2	$r_{g\hat{g}_0}$	Equilibrium genetic variance	Equilibrium accuracy	Δ% b
Mass selection	0.25	0.5	0.21	0.47	−14%
Genomic selection	0.25	0.5	0.22	0.39	−27%
Mass selection	0.10	0.32	0.093	0.306	−7%
Mass selection	0.50	0.71	0.367	0.651	−21%
Mass selection	-	any value	-	-	−27%

[a]Comparison of the Bulmer-effect for mass selection and genomic selection with different heritabilities (h^2) and accuracies of EBV ($r_{g\hat{g}_0}$); phenotypic variance equals 1; selected proportion equals 5%; [b]Δ% is the relative difference between the initial response and the Bulmer-equilibrium response.

Note:

GS → greater Bulmer reduction in response than mass selection

GS targets a proportion of the genetic variation with full accuracy

Mass selection targets the full genetic variation with limited accuracy

GS → Bulmer reduction in response unaffected by accuracy

- same as BLUP selection ➔ no need to account for Bulmer effect when comparing GS to BLUP selection with equal intensity