Impact of Selection on Genetic Variance
The Bulmer Effect

Jack Dekkers

Truncation selection ➔ σ_g^2 among selected group $< \sigma_g^2$ all selection candidates.

This reduction in genetic variance can be predicted using Normal distribution theory:

With truncation **selection on *y***
(* indicates value after selection)

- Variance selected variable:

$$\sigma_y^{*2} = (1 - k)\,\sigma_y^2 \quad k = i(i-t)$$
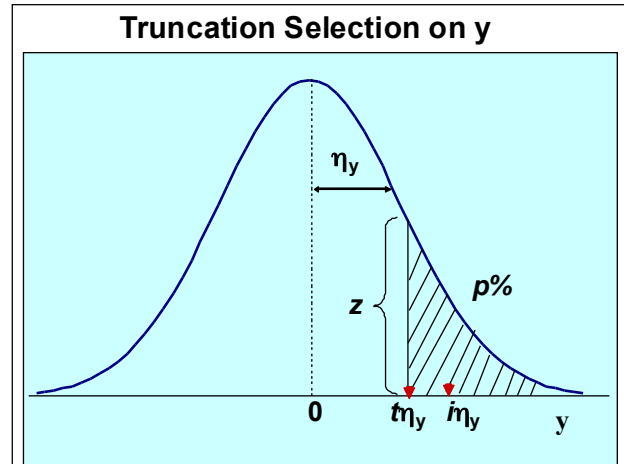
$$i = \text{sel.intensity}$$
$$t = \text{trunc.point}$$

- Variance of correlated variable:

$$\sigma_x^{*2} = (1 - k\,r_{xy}^2)\,\sigma_x^2$$

- Covariance betw. two correlated variables

$$\sigma_{wx}^* = \sigma_{wx} - k\frac{\sigma_{wy}\sigma_{xy}}{\sigma_y^2}$$

Selection on EBV:

- EBV variance selected individuals:

$$\sigma_{\hat{g}}^{*2} = (1 - k)\,\sigma_{\hat{g}}^2$$

- Genetic variance selected individuals:

$$\sigma_g^{*2} = (1 - k\,r_{\hat{g}g}^2)\,\sigma_g^2 \qquad r_{\hat{g}g} = \text{accuracy}$$

- BV of progeny: $g_o = \tfrac{1}{2}g_s + \tfrac{1}{2}g_d + g_m$

- Genetic variance of progeny

Without selection of parents: $\sigma_{go}^2 = \tfrac{1}{4}\sigma_g^2 + \tfrac{1}{4}\sigma_g^2 + \tfrac{1}{2}\sigma_g^2$

With selection of parents: $\sigma_{go}^2 = \tfrac{1}{4}\sigma_{g_s}^{*2} + \tfrac{1}{4}\sigma_{g_d}^{*2} + \tfrac{1}{2}\sigma_g^2$

$$\sigma_{g_s}^{*2} = (1 - k_s\,r_s^2)\,\sigma_g^2$$

$$\sigma_{g_d}^{*2} = (1 - k_d\,r_d^2)\,\sigma_g^2$$

Mend. sampling variance unaffected
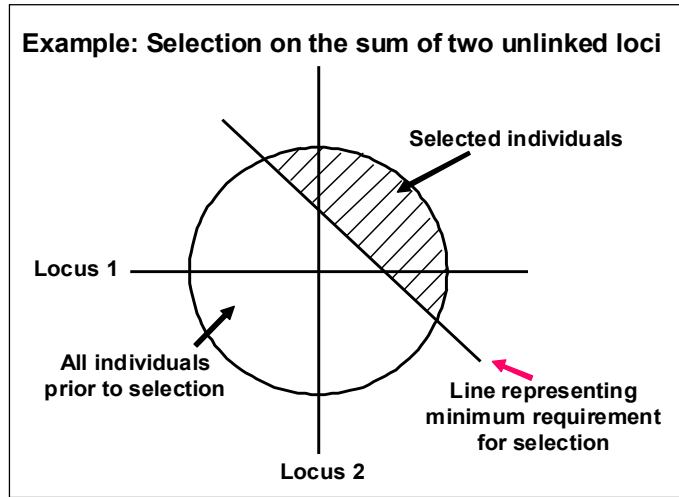
Recursive prediction of genetic variance:

$$\sigma_{g(t+1)}^2 = \tfrac{1}{4}\,\sigma_{g_s(t)}^{*2} + \tfrac{1}{4}\,\sigma_{g_d(t)}^{*2} + \sigma_{g_m}^2$$

$$\sigma_{g(t+1)}^2 = \tfrac{1}{4}(1 - k_s\,r_{s(t)}^2)\,\sigma_{g(t)}^2 + \tfrac{1}{4}(1 - k_d\,r_{d(t)}^2)\,\sigma_{g(t)}^2 + \tfrac{1}{2}\sigma_{g(o)}^2$$

Note: both genetic variance and accuracy are affected by selection.

Truncation Selection on y

Truncation Selection on EBV

Reduction of genetic variance is caused by selection-induced gametic phase disequilibrium (LD) between QTL.

Select on $\quad g = g_1 + g_2$

Genetic var. = $\sigma_g^2 = \sigma_{g_1}^2 + \sigma_{g_2}^2 + 2\sigma_{g_1 g_2}$

Prior to selection $\quad \sigma_{g_1 g_2} = 0 \quad$ (LE)

After selection $\quad \sigma_{g_1 g_2} < 0 \quad$ (LD)

$\quad \rightarrow \sigma_g^{*2} < \sigma_g^2$

Example: Selection on the sum of two unlinked loci

Selected individuals

Locus 1

All individuals prior to selection

Line representing minimum requirement for selection

Locus 2

LD created among the selected parents is eroded by recombination during meiosis to produce the progeny – by ½ if loci are unlinked.

This is reflected by the variance of Mendelian sampling terms = $\frac{1}{2}\sigma_{g_{(o)}}^2$

Prediction of Genetic Variance and Response for Selection on Own phenotype

Response: $\quad\quad\quad \bar{g}_{(t+1)} = \bar{g}_{(t)} + i h_{(t)} \sigma_{g_{(t)}}$

Table 1. Effect of truncation selection with $p=5\%$ in both males and females ($i=2.063$, $t=1.645$) during five generations on the additive genetic variance $\sigma_{g_{(t)}}^2$ and the average additive genetic merit of individuals ($\bar{g}_{(t)}$).

Gener.	$\sigma_{g_{(t)}}^2$	$h_{(t)}^2$	$\bar{g}_{(t)}$	$\bar{g}_{(t)} - \bar{g}_{(t-1)}$
0	100	0.50	50.0	0
1	78	0.43	64.6	14.6
2	74	0.43	76.7	12.1
3	74	0.42	88.3	11.6
4	73	0.42	99.8	11.5
5	73	0.42	111.3	11.5
Selection stopped (random selection from here on)				
6	87	0.47	111.3	0
7	93	0.48	111.3	0
8	97	0.49	111.3	0
9	98	0.49	111.3	0
10	99	0.49	111.3	0

Incorporating the Bulmer in Selection Index Calculations

Bulmer effect affects elements of **P** and **G**

Example: x_1 = individual's performance
x_2 = mean performance of that individual's m full sibs

$$\hat{g}_{(t)} = b_{1_{(t)}} x_1 + b_{2_{(t)}} x_2$$

$$\mathbf{P}_{(t)} = \begin{bmatrix} \sigma_{x_1}^2 & \sigma_{x_1 x_2} \\ \sigma_{x_1 x_2} & \sigma_{x_2}^2 \end{bmatrix} \qquad\qquad \mathbf{G}_{(t)} = \begin{bmatrix} \sigma_{x_1 g} \\ \sigma_{x_2 g} \end{bmatrix}$$

$$\sigma_{x_1}^2 = \tfrac{1}{4}\sigma_{g_{s(t-1)}}^{*2} + \tfrac{1}{4}\sigma_{g_{d(t-1)}}^{*2} + \sigma_{g_m}^2 + \sigma_e^2$$

$$\sigma_{x_2}^2 = \tfrac{1}{4}\sigma_{g_{s(t-1)}}^{*2} + \tfrac{1}{4}\sigma_{g_{d(t-1)}}^{*2} + (\sigma_{g_m}^2 + \sigma_e^2)/m$$

$$\sigma_{x_1 x_2} = \tfrac{1}{4}\sigma_{g_{s(t-1)}}^{*2} + \tfrac{1}{4}\sigma_{g_{d(t-1)}}^{*2}$$

$$\sigma_{x_1,g} = \tfrac{1}{4}\sigma_{g_{s(t-1)}}^{*2} + \tfrac{1}{4}\sigma_{g_{d(t-1)}}^{*2} + \sigma_{g_m}^2$$

$$\sigma_{x_2,g} = \tfrac{1}{4}\sigma_{g_{s(t-1)}}^{*2} + \tfrac{1}{4}\sigma_{g_{d(t-1)}}^{*2}$$

E.g. $h^2 = 0.5,\ \sigma_{g_{(0)}}^2 = 25,\ \sigma_{P_{(0)}}^2 = 50,\ m=5$

$$\mathbf{P}_{(0)} = \begin{bmatrix} 50 & 12.5 \\ 12.5 & 20 \end{bmatrix} \qquad \mathbf{G}_{(0)} = \begin{bmatrix} 25 \\ 12.5 \end{bmatrix} \quad\text{and}\quad \boxed{\mathbf{b}_{(0)} = \mathbf{P}_{(0)}^{-1}\mathbf{G}_{(0)} = \begin{bmatrix} .4074 \\ .3704 \end{bmatrix}}$$

$$\boxed{r_{(0)} = \sqrt{\dfrac{\mathbf{b}_{(0)}'\mathbf{G}_{(0)}}{\sigma_{g_{(0)}}^2}} = 0.77}$$

$p_s = p_d = 5\% \rightarrow k = 0.863$

$$\sigma_{g_{s(1)}}^{*2} = \sigma_{g_{d(1)}}^{*2} = (1 - k\,r_{(0)}^2)\sigma_{g_{(0)}}^2 = (1 - 0.863 \times 0.77^2)25 = 12.21$$

$$\sigma_{g_{(t)}}^2 = \tfrac{1}{4}\sigma_{g_{s(t-1)}}^{*2} + \tfrac{1}{4}\sigma_{g_{d(t-1)}}^{*2} + \sigma_{g_m}^2 = 18.61$$

$$\mathbf{P}_{(1)} = \begin{bmatrix} 43.61 & 6.11 \\ 6.11 & 13.61 \end{bmatrix} \qquad \mathbf{G}_{(1)} = \begin{bmatrix} 18.61 \\ 6.11 \end{bmatrix} \qquad \boxed{\mathbf{b}_{(1)} = \mathbf{P}_{(1)}^{-1}\mathbf{G}_{(1)} = \begin{bmatrix} .3883 \\ .2746 \end{bmatrix}}$$
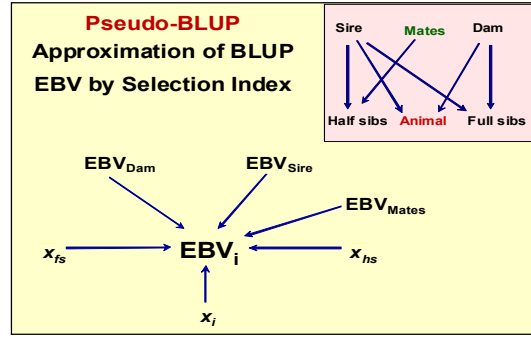
$$\boxed{r_{(1)} = \sqrt{\dfrac{\mathbf{b}_{(1)}'\mathbf{G}_{(1)}}{\sigma_{g_{(1)}}^2}} = 0.69} \qquad \rightarrow\rightarrow \text{SELACTION}$$

Incorporating the Bulmer Effect in BLUP EBV

Information sources:

x_i = animal's own record,

x_{fs} = average of n-1 full sibs

x_{hs} = average of $(m-1)n$ half sibs

$\hat{g}_s$ = EBV of the sire

$\hat{g}_d$ = EBV of the dam

$\overline{\hat{g}}_m$ = average EBV of $(m-1)$ mates of the sire that produced the half sibs

Pseudo-BLUP Approximation of BLUP EBV by Selection Index

Pseudo BLUP EBV $= I_i = \hat{g}_i = b_1 x_i + b_2 x_{fs} + b_3 x_{hs} + b_4 \hat{g}_s + b_5 \hat{g}_d + b_6 \overline{\hat{g}}_m$

$$\mathbf{P} = \begin{bmatrix} \sigma^2_{x_i} & \sigma_{x_i x_{fs}} & \sigma_{x_i x_{hs}} & \sigma_{x_i \hat{g}_s} & \sigma_{x_i \hat{g}_d} & \sigma_{x_i \overline{\hat{g}}_m} \\ & \sigma^2_{x_{fs}} & \sigma_{x_{fs} x_{hs}} & \sigma_{x_{fs} \hat{g}_s} & \sigma_{x_{fs} \hat{g}_d} & \sigma_{x_{js} \overline{\hat{g}}_m} \\ & & \sigma^2_{x_{hs}} & \sigma_{x_{hs} \hat{g}_s} & \sigma_{x_{hs} \hat{g}_d} & \sigma_{x_{hs} \overline{\hat{g}}_m} \\ & & & \sigma^2_{\hat{g}_s} & \sigma_{\hat{g}_s \hat{g}_d} & \sigma_{\hat{g}_s \overline{\hat{g}}_m} \\ & & & & \sigma^2_{\hat{g}_d} & \sigma_{\hat{g}_d \overline{\hat{g}}_m} \\ & & & & & \sigma^2_{\overline{\hat{g}}_m} \end{bmatrix}$$

$$\mathbf{G} = \begin{bmatrix} \sigma_{g_i x_i} & \sigma_{g_i x_{fs}} & \sigma_{g_i x_{hs}} & \sigma_{g_i \hat{g}_s} & \sigma_{g_i \hat{g}_d} & \sigma_{g_i \overline{\hat{g}}_m} \end{bmatrix}$$

With	$x_{hs} = \left(\sum\limits_{k=1}^{m-1} \sum\limits_{l=1}^{n} \dfrac{x_{kl}}{n} \right) /(m\text{-}1)$
Where	$x_{kl} = {}^1/_2\, g_s + {}^1/_2\, g_{d_k} + g_{ms_{kl}} + c_{kl} + e_{kl}$
Thus	$x_{hs} = {}^1/_2\, g_s + {}^1/_2\, \dfrac{\sum\limits_{k=1}^{m-1}\left(g_{d_k} + c_k\right)}{m\text{-}1} + \dfrac{\sum\limits_{k=1}^{m-1}\sum\limits_{l=1}^{n}\left(g_{ms_{kl}} + e_{kl}\right)}{n(m\text{-}1)}$
And	$\sigma^2_{x_{hs}} = {}^1/_4\, \sigma^{*2}_{g_{s(t)}} + \dfrac{{}^1/_4\, \sigma^{*2}_{g_{d(t)}} + c^2}{m\text{-}1} + \dfrac{{}^1/_2\, \sigma^2_{g(0)} + \sigma^2_e}{n(m\text{-}1)}$
Also,	$\sigma^2_{\hat{g}(t)} = r^2_{g,\hat{g}(t)}\, \sigma^2_{g(t)}$
And	$\sigma_{x_i \hat{g}_s} = \sigma_{({}^1/_2\, g_s + {}^1/_2\, g_d + g_{m_i} + e_i,\, \hat{g}_s)} = \sigma_{({}^1/_2 g_s,\, \hat{g}_s)} = {}^1/_2\, \sigma_{g_s,\, \hat{g}_s} = {}^1/_2\, r^2_{s(t)} \sigma^2_{g(t)}$

$$\mathbf{b} = \mathbf{P^{-1}G} \qquad\qquad r_{g,\hat{g}(t)} = \sqrt{\mathbf{b'Pb}/\sigma^2_{g(t)}} \qquad\qquad \textbf{\textcolor{blue}{See BLUP\_EBV.xls}}$$

NOTE: Incorporating Bulmer effect into pseudo-BLUP index does NOT affect index weights.
→ BLUP EBV can be derived without considering the Bulmer effect.

However, the accuracy of BLUP EBV is affected by the Bulmer effect and needs to be derived.

Important Henderson (1975) result: Prediction error variance (PEV) of BLUP EBV does not depend on selection, but only on the amount of effective information used:

$$\text{Prediction error Var-Cov matrix} = \sigma^2_\varepsilon = \text{Var}(\hat{g} - g) = C_{22} \quad \text{from MME}$$

Thus the PEV of a BLUP-EBV based on a given set of information sources can be derived as:

$$\sigma^2_{\varepsilon_{(0)}} = (1 - r^2_{(0)})\sigma^2_{g_{(o)}} \qquad\qquad \text{but also as} \qquad\qquad \sigma^2_{\varepsilon_{(t)}} = (1 - r^2_{(t)})\sigma^2_{g_{(t)}}$$

PEV unaffected by selection → $\qquad\qquad \sigma^2_{\varepsilon_{(0)}} \quad = \quad \sigma^2_{\varepsilon_{(t)}}$

$$(1 - r^2_{(0)})\sigma^2_{g_{(o)}} = (1 - r^2_{(t)})\sigma^2_{g_{(t)}}$$

Thus: accuracy can be derived as $\qquad r^2_{(t)} = 1 - (1 - r^2_{(0)})\sigma^2_{g_{(o)}}/\sigma^2_{g_{(t)}}$

As before: $\qquad\qquad \sigma^2_{g_{(t+1)}} = \tfrac{1}{4}(1 - k_s r^2_{s_{(t)}})\sigma^2_{g_{(t)}} + \tfrac{1}{4}(1 - k_d r^2_{d_{(t)}})\sigma^2_{g_{(t)}} + \tfrac{1}{2}\sigma^2_{g_{(o)}}$

→ recursive system for prediction of accuracy and genetic variance

Table 2. Recursive prediction of genetic variance, accuracy and response with selection on BLUP EBV. Selected fractions are 0.2 and 0.5 for males and females, respectively, for a trait with heritability 0.25 and phenotypic variance 100. Selection is on BLUP EBV from an hierarchical mating structure with 20 mates per sire and 10 offspring per dam. Accuracy in generation zero is derived in section 4.5

t	$\frac{(i_s + i_d)}{2}$	k_s	k_d	$\sigma_{g(0)}^2$	$\sigma_{g(t)}^2$	$r_{(0)}$	$r_{(t)}=$	$\bar{g}_{(t+1)}=$	$R_{(t)}=$	$\sigma_{gs(t)}^2=$	$\sigma_{gd(t)}^2=$	$\sigma_{g(t+1)}^2=$
					from t-1		$\sqrt{\frac{(1-(1-r_{(0)}^2)\sigma_{g(0)}^2}{\sigma_{g(t)}^2}}$	$\bar{g}_{(t)} + \frac{1}{2}(i_s+i_d)r_{(t)}\sigma_{g(t)}$	$\bar{g}_{(t+1)} - \bar{g}_{(t)}$	$(1-r_{(t)}^2 k_s)\sigma_{g(t)}^2$	$(1-r_{(t)}^2 k_d)\sigma_{g(t)}^2$	$\frac{1}{2}\sigma_{gs(t)}^2 + \frac{1}{2}\sigma^*_{gd(t)}^2 + \frac{1}{2}\sigma_{g(0)}^2$
0	1.1	0.78	0.64	25	25.00	0.704	0.704	3.871	3.871	15.326	17.074	20.600
1	1.1	0.78	0.64	25	20.60	0.704	0.623	6.979	3.108	14.363	15.490	19.963
2	1.1	0.78	0.64	25	19.96	0.704	0.607	9.961	2.982	14.224	15.261	19.871
3	1.1	0.78	0.64	25	19.87	0.704	0.604	12.924	2.963	14.204	15.228	19.858
4	1.1	0.78	0.64	25	19.86	0.704	0.604	15.884	2.960	14.201	15.223	19.856
5	1.1	0.78	0.64	25	19.86	0.704	0.604	18.843	2.960	14.200	15.223	19.856

Direct Derivation of Asymptotic
or Steady State Genetic Variance and Response

Recursive equation: $\sigma^2_{g_{(t+1)}} = \frac{1}{4}(1 - k_s\, r^2_{s_{(t)}})\sigma^2_{g_{(t)}} + \frac{1}{4}(1 - k_d\, r^2_{d_{(t)}})\sigma^2_{g_{(t)}} + \frac{1}{2}\sigma^2_{g_{(o)}}$

At steady state (L): $\sigma^2_{g_{(t+1)}} = \sigma^2_{g_{(t)}} = \sigma^2_{g_{(L)}}$ $\qquad r_{s_{(t+1)}} = r_{s_{(t)}} = r_{s_{(L)}}$ $\qquad$ and $r_{d_{(t+1)}} = r_{d_{(t)}} = r_{d_{(L)}}$

➔ $\quad \sigma^2_{g_{(L)}} = \frac{1}{4}(1 - k_s\, r^2_{s_{(L)}})\sigma^2_{g_{(L)}} + \frac{1}{4}(1 - k_d\, r^2_{d_{(L)}})\sigma^2_{g_{(L)}} + \frac{1}{2}\sigma^2_{g_{(o)}}$

Mass selection: $\quad r_{s_{(t)}} = r_{d_{(t)}} = h_{(t)}$ $\qquad$ Assume equal selection in both sexes ➔ $k_s = k_d = k$

➔ $\quad \sigma^2_{g_{(t+1)}} = \frac{1}{2}(1 - k\, h^2_{(t)})\sigma^2_{g_{(t)}} + \frac{1}{2}\sigma^2_{g_{(o)}}$

At the limit $\quad \sigma^2_{g_{(L)}} = \frac{1}{2}(1 - k\, h^2_{(L)})\sigma^2_{g_{(L)}} + \frac{1}{2}\sigma^2_{g_{(o)}}$ $\qquad$ with $h^2_{(L)} = \sigma^2_{g_{(L)}} / (\sigma^2_{g_{(L)}} + \sigma^2_e)$

Using $\quad \sigma^2_e = \dfrac{1 - h^2_{(0)}}{h^2_0}\sigma^2_{g_{(o)}}$

$$h^2_{(L)} = \frac{h^2_{(0)}}{1 + (1 - h^2_{(0)})k h^2_{(L)}} = \frac{-1 + \sqrt{1 + 4h^2_{(0)}k(1 - h^2_{(0)})}}{2k(1 - h^2_{(0)})} \quad \text{and} \quad \sigma^2_{g_{(L)}} = \frac{2\sigma^2_{g_{(0)}}(1 - h^2_{(0)})}{1 - 2h^2_{(0)} + \sqrt{1 + 4h^2_{(0)}k(1 - h^2_{(0)})}}$$

Relative reduction in response: $\qquad R_{(L)}/R_{(1)} = \dfrac{i h_{(L)}\sigma_{g_{(L)}}}{i h_{(0)}\sigma_{g_{(0)}}} = \sqrt{\dfrac{h^2_{(L)}}{h^2_{(0)}(1 + k\, h^2_{(L)})}}$
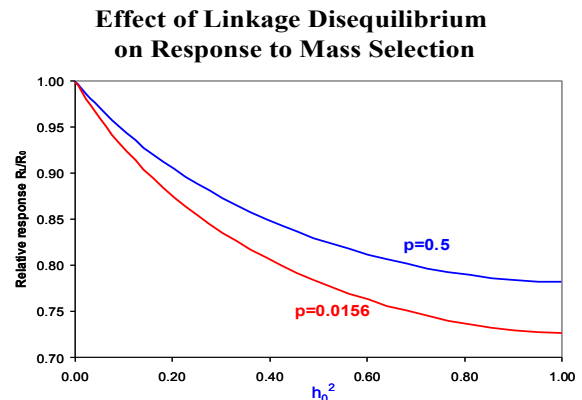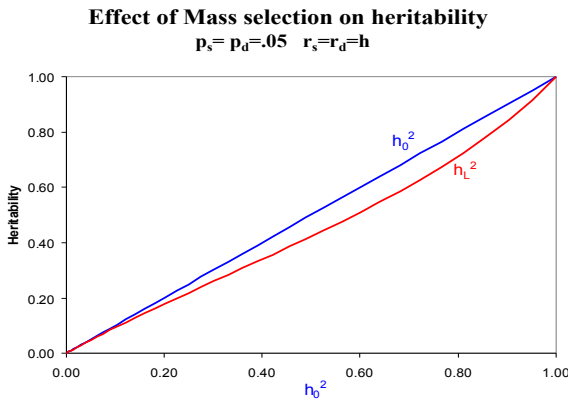
Effect of Mass selection on heritability
$p_s = p_d = .05 \quad r_s = r_d = h$

**Effect of Linkage Disequilibrium
on Response to Mass Selection**

Select on BLUP EBV $\qquad$ *Equal selection in males and females:*

Accuracy at the limit: $\qquad r^2_{(L)} = 1 - (1 - r^2_{(0)})\,\sigma^2_{g_{(o)}}/\sigma^2_{g_{(L)}}$

Genetic var. at limit: $\qquad \sigma^2_{g_{(L)}} = \frac{1}{2}(1 - k\, r^2_{(L)})\sigma^2_{g_{(L)}} + \frac{1}{2}\sigma^2_{g_{(o)}}$ $\qquad$ ➔ $\qquad \sigma^2_{g_{(L)}} = \sigma^2_{g_{(o)}}/(1 - k\, r^2_{(L)})$

➔ $\qquad \sigma^2_{g_{(L)}} = [1 + k(1 - r^2_{(0)})]\sigma^2_{g_{(o)}}/(1 + k)$

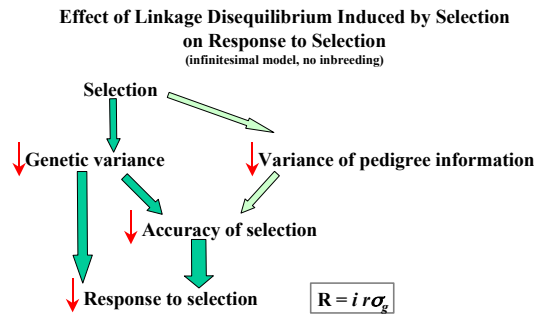Response at the limit: $\qquad R_{(L)}/R_{(0)} = r_{(L)}\,\sigma_{g_{(L)}}/r_{(0)}\,\sigma_{g_{(o)}} = \dfrac{1}{\sqrt{1+k}}$

Unequal selection in males and females:

$$R_{(L)}/R_{(0)} = \frac{i_s\sqrt{2\dfrac{r^2_{s_{(0)}}}{r^2_{d_{(0)}}} - k_d\left(\dfrac{r^2_{s_{(0)}}}{r^2_{d_{(0)}}} - 1\right)} + i_d\sqrt{2 + k_s\left(1 - \dfrac{r^2_{s_{(0)}}}{r^2_{d_{(0)}}}\right)}}{\left(i_s\dfrac{r_{s_{(0)}}}{r_{d_{(0)}}} + i_d\right)\sqrt{2 + k_s + k_d}} \qquad \text{IF } r_s = r_d \blacktriangleright R_{(L)}/R_{(0)} = \sqrt{\dfrac{2}{2 + k_s + k_d}}$$

Linkage Disequilibrium under BLUP Selection

Predicting Response to Selection

Effect of Linkage Disequilibrium Induced by Selection on Response to Selection
(infinitesimal model, no inbreeding)

Selection

↓ Genetic variance   ↓ Variance of pedigree information

↓ Accuracy of selection

↓ Response to selection $R = i\, r\, \sigma_g$

BLUP Selection - Example

$p_s = p_d = 0.2$ ➡ $i = 1.4$ $k = 0.79$

$\sigma_{g,0} = 1$

$r_0^2 = 0.15$ ➡ $PEV = (1-.15)*1 = 0.85$ | $r_0^2 = 0.80$ ➡ $PEV = 0.85$

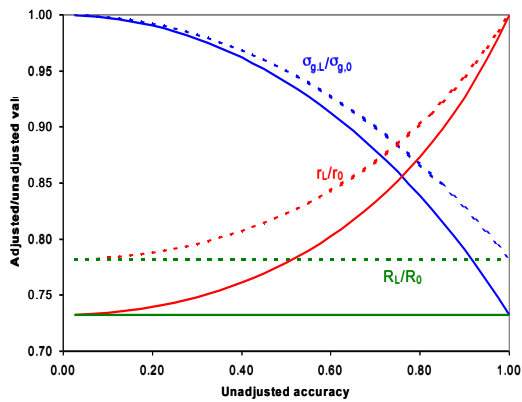$\sigma_{g,L}^2 = \dfrac{1+k(1-r_0^2)}{1+k}\,\sigma_{g,0}^2$ $= 0.93$ | $= 0.65$

$\sigma_{g,L}^2/\sigma_{a,0}^2$ $= 0.93$ | $= 0.65$

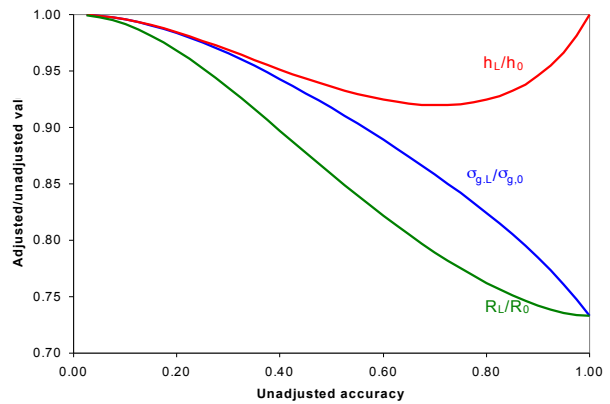$r_L^2 = 1 - (1-r_0^2)\dfrac{\sigma_{g,0}^2}{\sigma_{g,L}^2}$ $= 0.09$ | $= 0.69$

r_L^2/r_0^2 $= 0.60$ | $= 0.86$

$R_L/R_0 = \dfrac{1}{\sqrt{1+k}}$ $= 0.747$ | $= 0.747$

Effect of BLUP Selection on Asymptotic Parameters
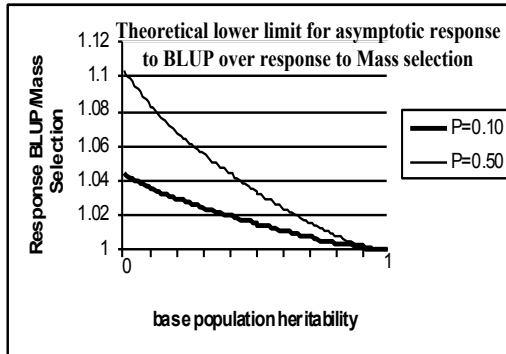$r_s = r_d$ Broken lines: $p_s = p_d = .5$ Solid lines: $p_s = p_d = .05$

Adjusted/unadjusted val (y-axis, 0.70 to 1.00)
Unadjusted accuracy (x-axis, 0.00 to 1.00)

$\sigma_{g,L}/\sigma_{g,0}$
r_L/r_0
R_L/R_0

Effect of Mass Selection on Asymptotic Parameters
$p_s = p_d = .05$ $r_s = r_d = h$

Adjusted/unadjusted val (y-axis, 0.70 to 1.00)
Unadjusted accuracy (x-axis, 0.00 to 1.00)

h_L/h_0
$\sigma_{g,L}/\sigma_{g,0}$
R_L/R_0

Reduction with BLUP selection > Reduction with Mass selection

Is BLUP selection better than Mass selection at the limit?
(Ignore effect of Inbreeding)

Lower limit to BLUP accuracy: 1 progeny per parent

Response BLUP/Mass Selection (y-axis, 1 to 1.12)

Theoretical lower limit for asymptotic response to BLUP over response to Mass selection

P=0.10
P=0.50

base population heritability (x-axis, 0 to 1)

Example Programs with Four Selection Paths

Breeding plan	I	II	III	IV
Pathway p_{SS}	.05	.03	.03	.03
p_{SD}	.20	.10	.10	.10
p_{DS}	.05	.01	.01	.01
p_{DD}	.90	.80	.80	.80
r_s	.85	.85	.85	.85
r_d	.65	.65	.50	.75
$\sigma_{Sg,L}^2/\sigma_{g,0}^2$	.736	.732	.773	.699
$\sigma_{Dg,L}^2/\sigma_{g,0}^2$	.774	.759	.783	.741
$r_{S,L}/r_{S,0}$	.929	.927	.942	.914
$r_{D,L}/r_{D,0}$	.775	.753	.408	.853
R_L/R_0	.759	.743	.685	.752

Relative reductions in response to BLUP due to LD range from 22 to 32% for most practical programs

Modelling Genetic Variance with Selection across (age) Groups

Age group	Relative # of candidates	Mean within group	Accuracy w/in group	Genetic var. within group	Fraction selected w/in group	Genetic superiority w/in group	Mean selected individuals	Genetic var. within the selected group
1	w_1	$\bar{g}_1$	r_1	σ^2_{g1}	p_1	$S_1 = i_1 r_1 \sigma_{g1}$	$\bar{g}^*_1 = \bar{g}_1 + S_1$	$\sigma^{*2}_{g1} = (1 - k_1 r_1^2)\sigma^2_{g1}$
2	w_2	$\bar{g}_2$	r_2	σ^2_{g2}	p_2	$S_2 = i_2 r_2 \sigma_{g2}$	$\bar{g}^*_2 = \bar{g}_2 + S_2$	$\sigma^{*2}_{g2} = (1 - k_2 r_2^2)\sigma^2_{g2}$
3	w_3	$\bar{g}_3$	r_3	σ^2_{g3}	p_3	$S_3 = i_3 r_3 \sigma_{g3}$	$\bar{g}^*_3 = \bar{g}_3 + S_3$	$\sigma^{*2}_{g3} = (1 - k_3 r_3^2)\sigma^2_{g3}$

$\Sigma w_i = 1$

Genetic mean of all selected individuals $= \bar{g}^* = \dfrac{1}{P}\Sigma p_i\, w_i\, \bar{g}^*_i$

Genetic variance

among all selected individuals = pooled within/group variance + between group variance

$$\sigma^{*2}_g = \frac{1}{P}\Sigma p_i\, w_i\, \sigma^{*2}_{g_i} \quad + \quad \frac{1}{P}\Sigma p_i\, w_i\, (\bar{g}^*_i - \bar{g}^*)^2$$

Recursive equations:

Pooled sire variance:
$$\sigma^{*2}_{g_{s(t)}} = \frac{1}{P_s}\Sigma p_{si}\, w_{si}\, \sigma^{*2}_{g_{si(t)}} + \frac{1}{P_s}\Sigma p_{si}\, w_{si}\, (\bar{g}^*_{si_{(t)}} - \bar{g}^*_{s_{(t)}})^2$$

Pooled dam variance:
$$\sigma^{*2}_{g_{d(t)}} = \frac{1}{P_d}\Sigma p_{di}\, w_{di}\, \sigma^{*2}_{g_{di(t)}} + \frac{1}{P_d}\Sigma p_{di}\, w_{di}\, (\bar{g}^*_{di_{(t)}} - \bar{g}^*_{d_{(t)}})^2$$

Genetic variance at time t+1: $\sigma^2_{g_{(t+1)}} = \tfrac{1}{4}\sigma^{*2}_{g_{s(t)}} + \tfrac{1}{4}\sigma^{*2}_{g_{d(t)}} + \tfrac{1}{2}\sigma^2_{g0}$

Effect of finite population size on genetic variance

$\sigma^{*2}_g = (1 - k\, r^2_{\hat{g}g})\sigma^2_g = $ variance of a population that the selected individuals are sampled from

To convert this to the variance of the sample, use: $\sigma^{*2}_g = \dfrac{n-1}{n}(1 - k\, r^2_{\hat{g}g})\sigma^2_g$

Effect of Inbreeding on Genetic Variance

Inbreeding (F) reduces Mendelian sampling variance from a parent by a factor (1-F)

$\sigma^2_{g_{m(t+1)}} = \left(1 - \tfrac{1}{2}(\bar{F}_{s(t)} + \bar{F}_{d(t)})\right)\tfrac{1}{2}\sigma^2_{g_{(o)}}$ $\bar{F}_{s(t)}$, $\bar{F}_{d(t)} = $ average F of selected sires, dams