

# Impact of Selection on Genetic Variance

## The Bulmer Effect

Jack Dekkers

Truncation selection  $\rightarrow \sigma_g^2$  among selected group  $< \sigma_g^2$  of 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:

$$\sigma_y^{*2} = (1 - k) \sigma_y^2 \quad k = i(i-t)$$

$i$  = sel.intensity

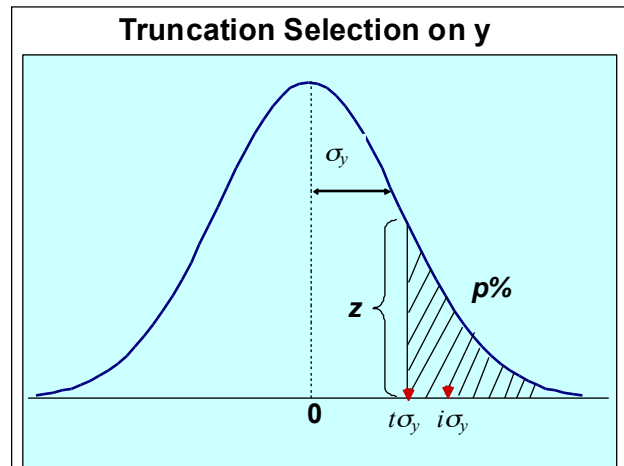
$t$  = trunc.point

- 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:

$$\sigma_g^{*2} = (1 - k) \sigma_g^2$$

- Genetic variance selected individuals:

$$\sigma_g^{*2} = (1 - k r_{gg}^2) \sigma_g^2 \quad r_{gg} = \text{accuracy}$$

- BV of progeny:  $g_o = 1/2 g_s + 1/2 g_d + g_m$

o  $g_m$  = Mendelian sampling

- Genetic variance of progeny

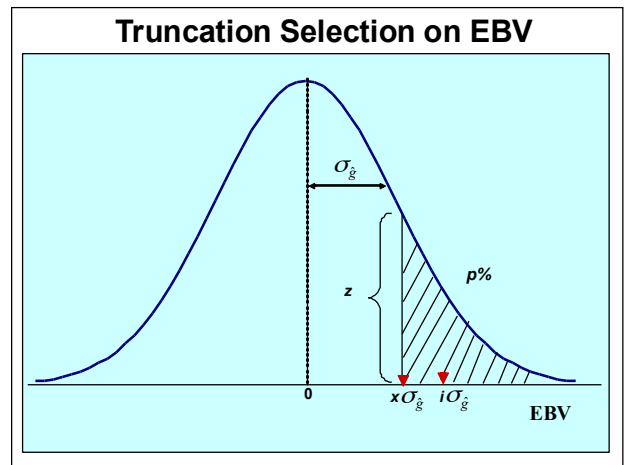
Without selection of parents:  $\sigma_{g_o}^2 = 1/4 \sigma_g^2 + 1/4 \sigma_g^2 + 1/2 \sigma_g^2$

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

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

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

Mend. sampling variance unaffected



Recursive prediction of genetic variance:

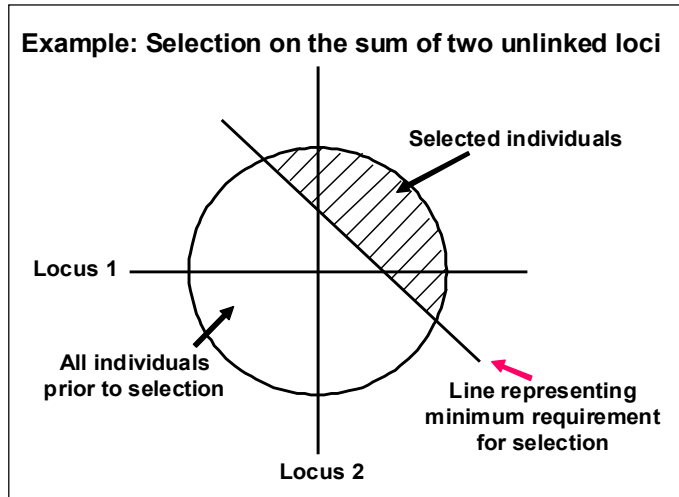
$$\sigma_{g(t+1)}^2 = 1/4 \sigma_{g_s(t)}^{*2} + 1/4 \sigma_{g_d(t)}^{*2} + \sigma_{g_m}^2$$

$$\sigma_{g(t+1)}^2 = 1/4 (1 - k_s r_s^2) \sigma_{g(t)}^2 + 1/4 (1 - k_d r_d^2) \sigma_{g(t)}^2 + 1/2 \sigma_{g(o)}^2$$

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

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

Select on  $g = g_1 + g_2$   
 Genetic var. =  $\sigma_g^2 = \sigma_{g_1}^2 + \sigma_{g_2}^2 + 2\sigma_{g_1g_2}$   
 Prior to selection  $\sigma_{g_1g_2} = 0$  (LE)  
 After selection  $\sigma_{g_1g_2} < 0$  (LD)  
 $\rightarrow \sigma_g^{*2} < \sigma_g^2$



LD created among the selected parents is eroded by recombination during meiosis to produce the progeny – by 1/2 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:  $\bar{g}_{(t+1)} = \bar{g}_{(t)} + ih_{(t)}\sigma_{g(t)}$

**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  $\mathbf{P}$  and  $\mathbf{G}$

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

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

$$\mathbf{P}_{(t)} = \begin{bmatrix} \sigma_{x_1}^2 & \sigma_{x_1x_2} \\ \sigma_{x_1x_2} & \sigma_{x_2}^2 \end{bmatrix} \quad \mathbf{G}_{(t)} = \begin{bmatrix} \sigma_{x_1g} \\ \sigma_{x_2g} \end{bmatrix}$$

$$\begin{aligned} \sigma_{x_1}^2 &= 1/4\sigma_{g_s(t-1)}^{*2} + 1/4\sigma_{g_d(t-1)}^{*2} + \sigma_{g_m}^2 + \sigma_e^2 \\ \sigma_{x_2}^2 &= 1/4\sigma_{g_s(t-1)}^{*2} + 1/4\sigma_{g_d(t-1)}^{*2} + (\sigma_{g_m}^2 + \sigma_e^2)/m \\ \sigma_{x_1x_2} &= 1/4\sigma_{g_s(t-1)}^{*2} + 1/4\sigma_{g_d(t-1)}^{*2} \\ \sigma_{x_1g} &= 1/4\sigma_{g_s(t-1)}^{*2} + 1/4\sigma_{g_d(t-1)}^{*2} + \sigma_{g_m}^2 \\ \sigma_{x_2g} &= 1/4\sigma_{g_s(t-1)}^{*2} + 1/4\sigma_{g_d(t-1)}^{*2} \end{aligned}$$

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

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

$$r_{(0)} = \sqrt{\frac{\mathbf{b}_{(0)}' \mathbf{G}_{(0)}}{\sigma_{g(0)}^2}} = 0.77$$

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

$$\begin{aligned} \sigma_{g_s(1)}^{*2} &= \sigma_{g_d(1)}^{*2} = (1 - k r_{(0)}^2) \sigma_{g(0)}^2 = (1 - 0.863 \times 0.77^2) 25 = 12.21 \\ \sigma_{g(1)}^2 &= 1/4 \sigma_{g_s(t-1)}^{*2} + 1/4 \sigma_{g_d(t-1)}^{*2} + \sigma_{g_m}^2 = 18.61 \end{aligned}$$

$$\mathbf{P}_{(1)} = \begin{bmatrix} 43.61 & 6.11 \\ 6.11 & 13.61 \end{bmatrix} \quad \mathbf{G}_{(1)} = \begin{bmatrix} 18.61 \\ 6.11 \end{bmatrix} \quad \mathbf{b}_{(1)} = \mathbf{P}_{(1)}^{-1} \mathbf{G}_{(1)} = \begin{bmatrix} .3883 \\ .2746 \end{bmatrix}$$

$$r_{(1)} = \sqrt{\frac{\mathbf{b}_{(1)}' \mathbf{G}_{(1)}}{\sigma_{g(1)}^2}} = 0.69$$

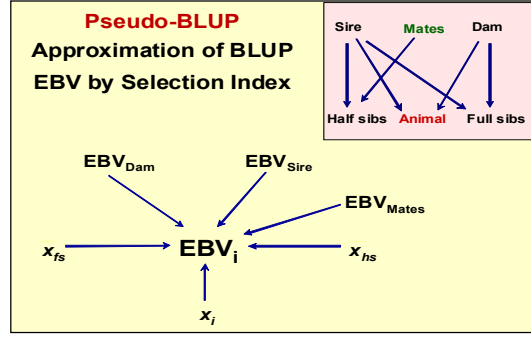
**→ → SELECTION**

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



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

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

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

With 
$$x_{hs} = \left( \sum_{k=1}^{m-1} \sum_{l=1}^n \frac{x_{kl}}{n} \right) / (m-1)$$

Where 
$$x_{kl} = 1/2 g_s + 1/2 g_{d_k} + g_{ms_{kl}} + c_{kl} + e_{kl}$$

Thus 
$$x_{hs} = 1/2 g_s + 1/2 \frac{\sum_{k=1}^{m-1} (g_{d_k} + c_k)}{m-1} + \frac{\sum_{k=1}^{m-1} \sum_{l=1}^n (g_{ms_{kl}} + e_{kl})}{n(m-1)}$$

And 
$$\sigma_{x_{hs}}^2 = 1/4 \sigma_{g_s(t)}^{*2} + \frac{1/4 \sigma_{g_{d(t)}}^{*2} + c^2}{m-1} + \frac{1/2 \sigma_{g^{(0)}}^2 + \sigma_e^2}{n(m-1)}$$

Also, 
$$\sigma_{\hat{g}^{(t)}}^2 = r_{g, \hat{g}^{(t)}}^2 \sigma_{g^{(t)}}^2$$

And 
$$\sigma_{x_i \hat{g}_s} = \sigma_{(1/2 g_s + 1/2 g_d + g_{m_i} + e_i, \hat{g}_s)} = \sigma_{(1/2 g_s, \hat{g}_s)} = 1/2 \sigma_{g_s, \hat{g}_s} = 1/2 r_{s(t)}^2 \sigma_{g^{(t)}}^2$$

$$\mathbf{b} = \mathbf{P}^{-1}\mathbf{G}$$

$$r_{g,\hat{g}(t)} = \sqrt{\mathbf{b}'\mathbf{P}\mathbf{b}/\sigma_{g(t)}^2}$$

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:

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

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

$$\sigma_{\varepsilon(0)}^2 = (1-r_{(0)}^2)\sigma_{g(0)}^2 \quad \text{but also as} \quad \sigma_{\varepsilon(t)}^2 = (1-r_{(t)}^2)\sigma_{g(t)}^2$$

$$\text{PEV unaffected by selection} \rightarrow \sigma_{\varepsilon(0)}^2 = \sigma_{\varepsilon(t)}^2$$

$$(1-r_{(0)}^2)\sigma_{g(0)}^2 = (1-r_{(t)}^2)\sigma_{g(t)}^2$$

$$\text{Thus: accuracy can be derived as} \quad r_{(t)}^2 = 1 - (1-r_{(0)}^2)\sigma_{g(0)}^2 / \sigma_{g(t)}^2$$

$$\text{As before:} \quad \sigma_{g(t+1)}^2 = 1/4(1-k_s r_{s(t)}^2)\sigma_{g(t)}^2 + 1/4(1-k_d r_{d(t)}^2)\sigma_{g(t)}^2 + 1/2\sigma_{g(0)}^2$$

→ 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 $t-1$        |           | $\sqrt{\frac{(1-(1-r_{(0)}^2)\sigma_{g(0)}^2)}{\sigma_{g(0)}^2}}$ | $\bar{g}_{(0)} +$<br>$1/2(i_s+i_d)r_{(0)}\sigma_{g(0)}$ | $\bar{g}_{(t+1)} - \bar{g}_{(t)}$ | $(1-r_{(t)}^2k_s)\sigma_{g(t)}^2$ | $(1-r_{(t)}^2k_d)\sigma_{g(t)}^2$ | $1/2\sigma_{gs(t)}^2 + 1/2\sigma_{gd(t)}^2 + 1/2\sigma_{g(0)}^2$ |
| 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:  $\sigma_{g(t+1)}^2 = 1/4(1-k_s r_{s(t)}^2) \sigma_{g(t)}^2 + 1/4(1-k_d r_{d(t)}^2) \sigma_{g(t)}^2 + 1/2 \sigma_{g(o)}^2$

At steady state (L):  $\sigma_{g(t+1)}^2 = \sigma_{g(t)}^2 = \sigma_{g(L)}^2$      $r_{s(t+1)} = r_{s(t)} = r_{s(L)}$     and  $r_{d(t+1)} = r_{d(t)} = r_{d(L)}$

→  $\sigma_{g(L)}^2 = 1/4(1-k_s r_{s(L)}^2) \sigma_{g(L)}^2 + 1/4(1-k_d r_{d(L)}^2) \sigma_{g(L)}^2 + 1/2 \sigma_{g(o)}^2$

**Mass selection:**  $r_{s(t)} = r_{d(t)} = h(t)$     Assume equal selection in both sexes →  $k_s = k_d = k$

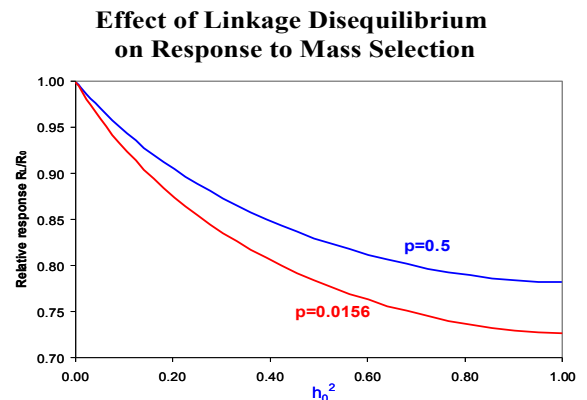
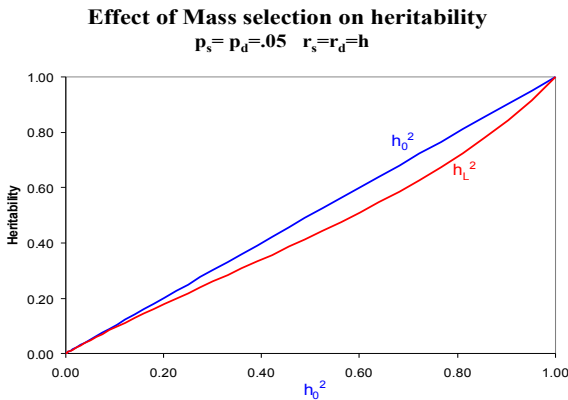
→  $\sigma_{g(t+1)}^2 = 1/2(1-k h_{(t)}^2) \sigma_{g(t)}^2 + 1/2 \sigma_{g(o)}^2$

At the limit  $\sigma_{g(L)}^2 = 1/2(1-k h_{(L)}^2) \sigma_{g(L)}^2 + 1/2 \sigma_{g(o)}^2$     with  $h_{(L)}^2 = \sigma_{g(L)}^2 / (\sigma_{g(L)}^2 + \sigma_e^2)$

Using  $\sigma_e^2 = \frac{1-h_{(0)}^2}{h_0^2} \sigma_{g(o)}^2$

$$h_{(L)}^2 = \frac{h_{(0)}^2}{1 + (1-h_{(0)}^2)kh_{(L)}^2} = \frac{-1 + \sqrt{1 + 4h_{(0)}^2 k(1-h_{(0)}^2)}}{2k(1-h_{(0)}^2)} \quad \text{and} \quad \sigma_{g(L)}^2 = \frac{2\sigma_{g(o)}^2(1-h_{(0)}^2)}{1 - 2h_{(0)}^2 + \sqrt{1 + 4h_{(0)}^2 k(1-h_{(0)}^2)}}$$

Relative reduction in response:  $R_{(L)}/R_{(1)} = \frac{ih_{(L)}\sigma_{g(L)}}{ih_{(0)}\sigma_{g(o)}} = \sqrt{\frac{h_{(L)}^2}{h_{(0)}^2(1+kh_{(L)}^2)}}$



### Select on BLUP EBV

Accuracy at the limit:

Equal selection in males and females:

$$r_{(L)}^2 = 1 - (1-r_{(0)}^2) \sigma_{g(o)}^2 / \sigma_{g(L)}^2$$

Genetic var. at limit:

$$\sigma_{g(L)}^2 = 1/2(1-k r_{(L)}^2) \sigma_{g(L)}^2 + 1/2 \sigma_{g(o)}^2 \quad \rightarrow \quad \sigma_{g(L)}^2 = \sigma_{g(o)}^2 / (1-k r_{(L)}^2)$$

→  $\sigma_{g(L)}^2 = [1+k(1-r_{(0)}^2)] \sigma_{g(o)}^2 / (1+k)$

Response at the limit:

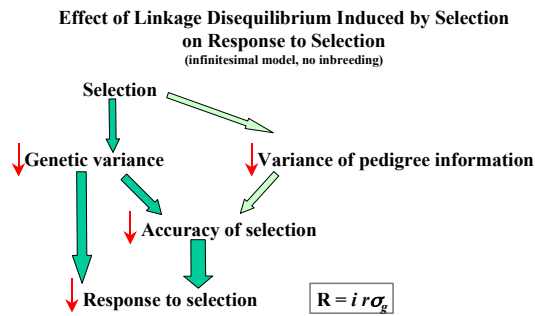
$$R_{(L)}/R_{(0)} = r_{(L)} \sigma_{g(L)} / r_{(0)} \sigma_{g(o)} = \frac{1}{\sqrt{1+k}}$$

Unequal selection in males and females:

$$R_{(L)}/R_{(0)} = \frac{i_s \sqrt{2 \frac{r_{s(0)}^2}{r_{d(0)}^2} - k_d \left( \frac{r_{s(0)}^2}{r_{d(0)}^2} - 1 \right) + i_d \sqrt{2 + k_s \left( 1 - \frac{r_{s(0)}^2}{r_{d(0)}^2} \right)}}{\left( i_s \frac{r_{s(0)}^2}{r_{d(0)}^2} + i_d \right) \sqrt{2 + k_s + k_d}}$$

IF  $r_s = r_d \rightarrow R_{(L)}/R_{(0)} = \sqrt{\frac{2}{2 + k_s + k_d}}$

### Linkage Disequilibrium under BLUP Selection Predicting Response to Selection

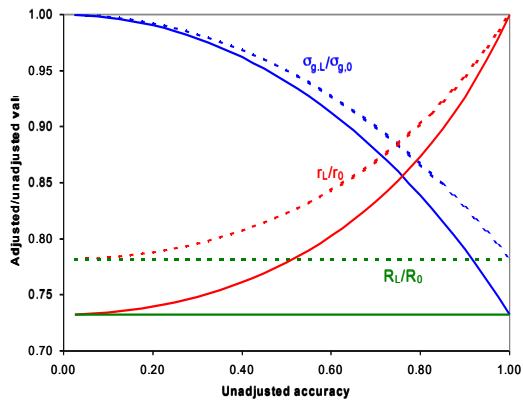


### BLUP Selection - Example

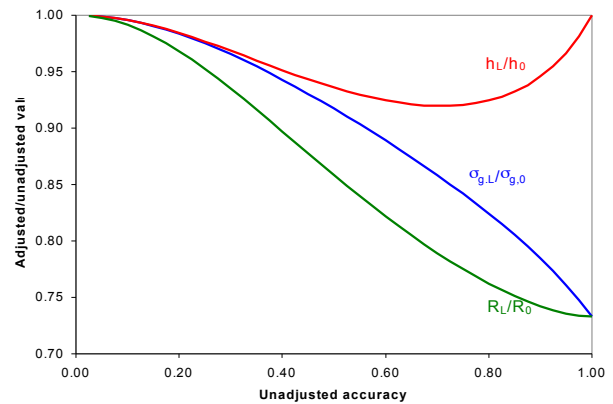
$p_s = p_d = 0.2 \Rightarrow i = 1.4 \quad k = 0.79$   
 $\sigma_{g,0} = 1$

|  |                                       |
|--|---------------------------------------|
| $r_0^2 = 0.15 \Rightarrow PEV = (1 - r_0^2) * 1 = 0.85$              | $r_0^2 = 0.80 \Rightarrow PEV = 0.20$ |
| $\sigma_{g,L}^2 = \frac{1+k(1-r_0^2)}{1+k} \sigma_{g,0}^2 = 0.93$    | $= 0.65$                              |
| $\sigma_{g,L}^2 / \sigma_{a,0}^2 = 0.93$                             | $= 0.65$                              |
| $r_L^2 = 1 - (1-r_0^2) \frac{\sigma_{g,0}^2}{\sigma_{g,L}^2} = 0.09$ | $= 0.69$                              |
| $r_L^2 / r_0^2 = 0.60$   | $= 0.86$                              |
| $R_L / R_0 = \frac{1}{\sqrt{1+k}} = 0.747$                           | $= 0.747$                             |

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

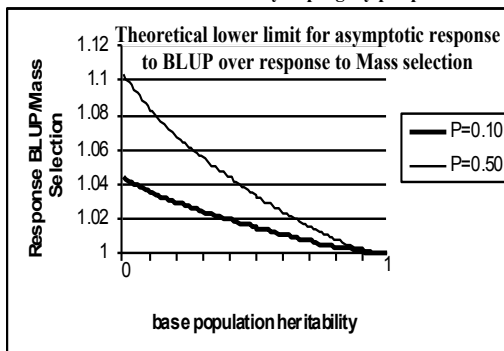


### Effect of Mass Selection on Asymptotic Parameters $p_s = p_d = .05 \quad r_s = r_d = h$



### 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



### 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                | $w_1$                    | $\bar{g}_1$       | $r_1$               | $\sigma_{g1}^2$           | $p_1$                        | $S_1 = i_1 r_1 \sigma_{g1}$    | $\bar{g}_1^* = \bar{g}_1 + S_1$ | $\sigma_{g1}^{*2} = (1 - k_1 r_1^2) \sigma_{g1}^2$ |
| 2                | $w_2$                    | $\bar{g}_2$       | $r_2$               | $\sigma_{g2}^2$           | $p_2$                        | $S_2 = i_2 r_2 \sigma_{g2}$    | $\bar{g}_2^* = \bar{g}_2 + S_2$ | $\sigma_{g2}^{*2} = (1 - k_2 r_2^2) \sigma_{g2}^2$ |
| 3                | $w_3$                    | $\bar{g}_3$       | $r_3$               | $\sigma_{g3}^2$           | $p_3$                        | $S_3 = i_3 r_3 \sigma_{g3}$    | $\bar{g}_3^* = \bar{g}_3 + S_3$ | $\sigma_{g3}^{*2} = (1 - k_3 r_3^2) \sigma_{g3}^2$ |
| $\Sigma w_i = 1$ |                          |                   |                     |                           |                              |                                |                                 |  |

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

Genetic variance selected individuals = pooled within/group variance + between group variance

$$\sigma_g^{*2} = \frac{1}{P} \sum p_i w_i \sigma_{g_i}^{*2} + \frac{1}{P} \sum p_i w_i (\bar{g}_i^* - \bar{g}^*)^2$$

Recursive equations:

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

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

Genetic variance at time  $t+1$ : 
$$\sigma_{g(t+1)}^2 = \frac{1}{4} \sigma_{g_s(t)}^{*2} + \frac{1}{4} \sigma_{g_d(t)}^{*2} + \frac{1}{2} \sigma_{g_0}^2$$

### Effect of finite population size on genetic variance

$\sigma_g^{*2} = (1 - k r_{gg}^2) \sigma_g^2$  = variance of a population that the selected individuals are sampled from

To convert this to the variance of the sample, use: 
$$\sigma_g^{*2} = \frac{n-1}{n} (1 - k r_{gg}^2) \sigma_g^2$$

### Effect of Inbreeding on Genetic Variance

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

$$\sigma_{g_m(t+1)}^2 = (1 - \frac{1}{2}(\bar{F}_{s(t)} + \bar{F}_{d(t)})) \sigma_{g_0}^2 \quad \bar{F}_{s(t)}, \bar{F}_{d(t)} = \text{average F of selected sires, dams}$$

## Summary – Bulmer Effect

- Selection reduces genetic variance, which reduces accuracy and response
- Can be modeled using Normal distribution theory

- Genetic variance selected individuals:  $\sigma_g^{*2} = (1 - k r_{gg}^2) \sigma_g^2$
- Genetic variance of progeny

$$\sigma_{g_0}^2 = \frac{1}{4} \sigma_{g_s}^{*2} + \frac{1}{4} \sigma_{g_d}^{*2} + \frac{1}{2} \sigma_g^2 \quad \sigma_{g_s}^{*2} = (1 - k_s r_s^2) \sigma_g^2 \quad \sigma_{g_d}^{*2} = (1 - k_d r_d^2) \sigma_g^2$$

- Accuracy, variance, and response stabilize to equilibrium (asymptotic) values after a couple of generations → response reduces by 20-30% for most breeding programs
- Important to account for when evaluating response to selection but may not affect ranking of alternative programs