

## Modeling the Effects of Selection on Genetic Variance

**Changes in genetic variance  
affect the amount of change  
that can be made in future generations**

### Objectives:

- to model the effect of selection on genetic variance
- to incorporate its effects in derivation of selection indexes
- to incorporate its effects in response to selection

basis of the models

### infinitesimal genetic model

the trait is assumed to be affected by a large number of unlinked loci with small effect

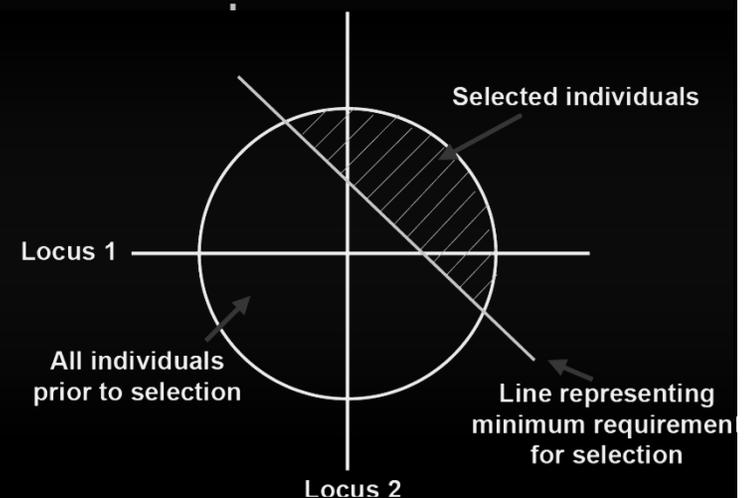
## Gametic phase disequilibrium

Bulmer (1971, 1976, 1981):

Effect of **selection** on **genetic variance**  
referred to as the "**Bulmer Effect**"

A more appropriate term is Falconer's "**gametic phase disequilibrium**"

## Selection on the sum of two unlinked loci



The genetic variance in the trait is equal to the variance in the sum of the gene effects at the two loci:

$$\sigma_g^2 = \sigma_{g_1}^2 + \sigma_{g_2}^2 + 2\sigma_{g_1g_2}$$

Prior to selection  $\sigma_{g_1g_2} = 0$

After selection  $\sigma_{g_1g_2} < 0$

**Reduce genetic variance in the group of selected individuals**

### Selection on genetic variance in Mass Selection

Distribution of phenotypes prior to selection

will have a standard deviation, *but*, the standard deviation will be considerably less than among the proportion, *p*, of animals selected for breeding

### Mass Selection

With truncation selection on *y*:

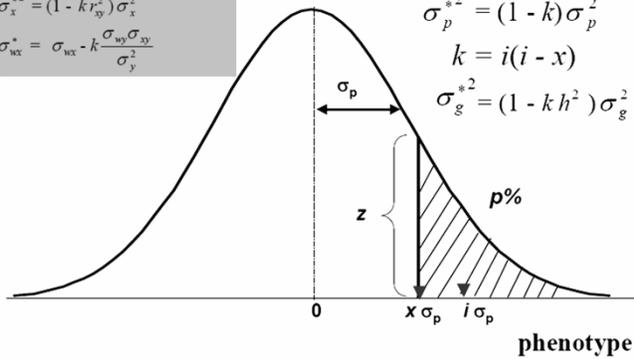
$$\sigma_x^{*2} = (1 - k r_{xy}^2) \sigma_x^2$$

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

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

$$k = i(i - x)$$

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



### EBV Selection

Without selection  $\sigma_g^2 = \frac{1}{4} \sigma_{g_s}^2 + \frac{1}{4} \sigma_{g_d}^2 + \sigma_{g_m}^2$

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

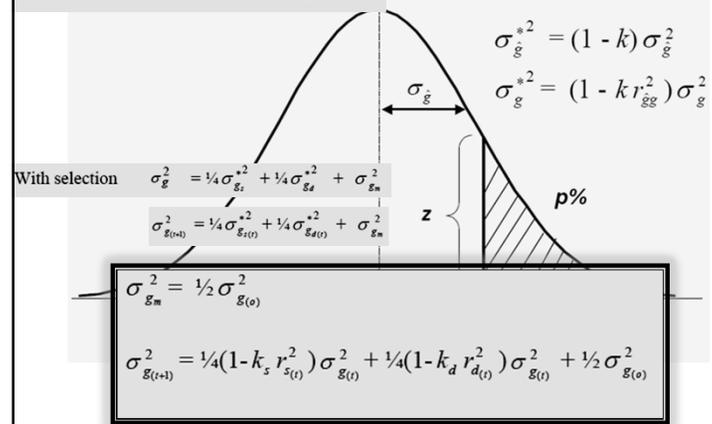
$$\sigma_{g_d}^{*2} = (1 - k r_{gg}^2) \sigma_{g_d}^2$$

With selection  $\sigma_g^2 = \frac{1}{4} \sigma_{g_s}^{*2} + \frac{1}{4} \sigma_{g_d}^{*2} + \sigma_{g_m}^2$

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

$$\sigma_{g_m}^2 = \frac{1}{2} \sigma_{g(t)}^2$$

$$\sigma_{g(t+1)}^2 = \frac{1}{4} (1 - k_s r_{s(t)}^2) \sigma_{g_s(t)}^2 + \frac{1}{4} (1 - k_d r_{d(t)}^2) \sigma_{g_d(t)}^2 + \frac{1}{2} \sigma_{g(t)}^2$$



## Prediction of Genetic Variance and Response for Mass Selection

Response to selection from one generation to the next can be predicted as

$$\bar{g}_{(t+1)} = \bar{g}_{(t)} + ih_{(t)}\sigma_{g(t)}$$

but with the parameters that apply to the parental generation

Effect of truncation selection ( $p=5\%$  in both sexes,  $i=2.063$ ,  $x=1.645$ ), 5 generations ( $t=0$  to 4) on **additive variance** and **average genetic merit** of individuals. Heritability in generation 0 was  $1/2$  (no inbreeding)

$t$	$\sigma_{g(t)}^2$	$h_{(t)}^2$	$\bar{g}_{(t)}$	$\bar{g}_{(t)} - \bar{g}_{(t-1)}$
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

**Genetic variance** reaches an **equilibrium** after 3 gen. selection

**Genetic variance**= 74, doesn't decrease further

(**asymptotic genetic variance**)

Then, gametic phase disequilibrium by selection = *gametic phase dis.* which is broken down during meiosis (Mendelian sampling)

When selection is stopped, no new *gametic phase dis.* is created in parents => variance reduction is halved each generation as a result of Mendelian sampling

## Asymptotic Genetic Variance and Response to Selection

Enable recursive prediction of changes in var. and R

Both reach steady state or asymptotic values after a number of generations

In case of mass selection (and BLUP selection), these steady state parameters can be derived directly

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

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

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

For mass selection:  $r_{s(t)} = r_{d(t)} = h(t)$

With equal selection in both sexes  $k_s = k_d = k$

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

$$\sigma_{g(L)}^2 = \frac{1}{2}(1 - k h_{(L)}^2) \sigma_{g(L)}^2 + \frac{1}{2} \sigma_{g(o)}^2$$

$$h_{(L)}^2 = \sigma_{g(L)}^2 / (\sigma_{g(L)}^2 + \sigma_e^2)$$

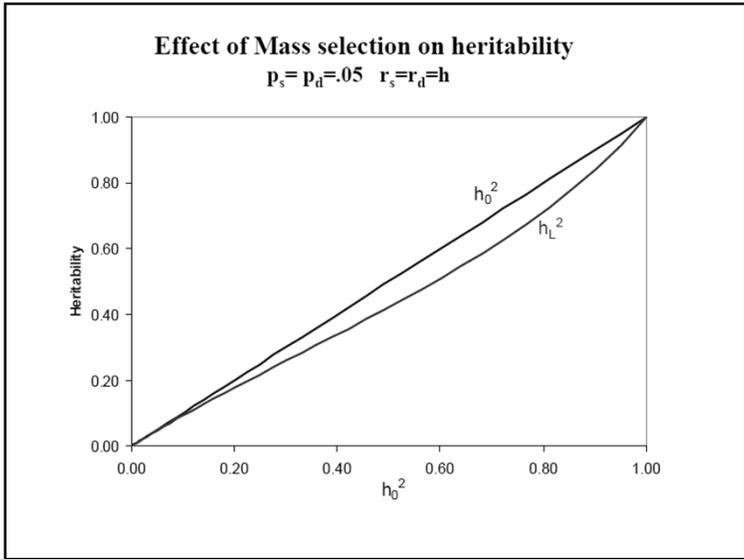
$$\sigma_e^2 = \frac{1 - h_{(0)}^2}{h_0^2} \sigma_{g(o)}^2$$

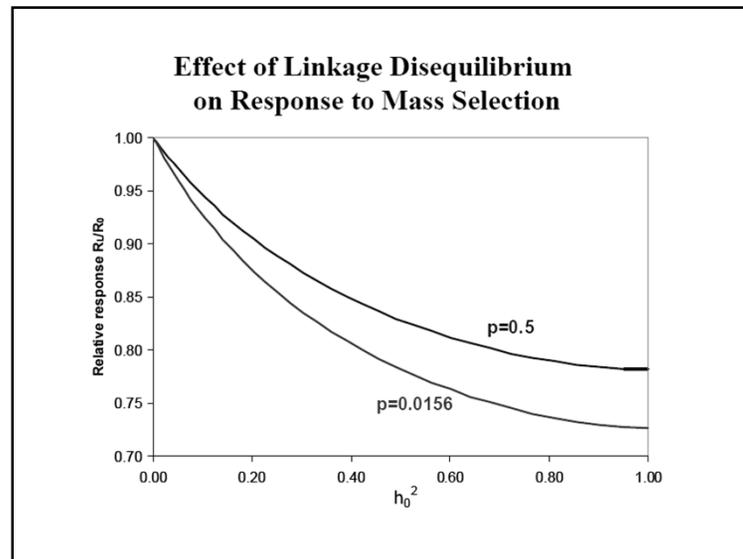
$$h_{(L)}^2 = \frac{h_{(0)}^2}{1 + (1 - h_{(0)}^2) k h_{(L)}^2} = \frac{-1 + \sqrt{1 + 4 h_{(0)}^2 k (1 - h_{(0)}^2)}}{2 k (1 - h_{(0)}^2)}$$

**Steady state genetic variance**  
in terms of base population parameters:

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

**Relative Response to mass selection**  
in the limit to the initial generation:

$$R_{(L)}/R_{(1)} = \frac{i h_{(L)} \sigma_{g(L)}}{i h_{(0)} \sigma_{g(0)}} = \sqrt{\frac{h_{(L)}^2}{h_{(0)}^2 (1 + k h_{(L)}^2)}}$$




### Incorporating Gametic Phase Dis. in Selection Index

Selection affects genetic (co)variances =>  
affects elements of the **P** and **G** matrices  
(needed to derive the optimal weights for SI)

This section:

- How changes in genetic parameters incorporate in SI
- The impact on accuracy of the index

Selection affects between and within-family  
variances differentially

Elements of the **P** and **G** must be based on the  
partition of the genetic value of individuals  
into their **parental** and **Mendelian sampling**  
**components**

$$g_{\text{offspring}} = \frac{1}{2} g_s + \frac{1}{2} g_d + g_m$$

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

$$\sigma_{g_s(t-1)}^{*2} = (1 - k_s r_{s(t-1)}^2) \sigma_{g(t-1)}^2$$

$$\sigma_{g_d(t-1)}^{*2} = (1 - k_d r_{d(t-1)}^2) \sigma_{g(t-1)}^2$$

$$\sigma_{g_m}^2 = \frac{1}{2} \sigma_{g(o)}^2$$

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

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

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

$$\mathbf{G}_{(t)} = \begin{bmatrix} \sigma_{x_1g} \\ \sigma_{x_2g} \end{bmatrix} \quad \begin{aligned} \sigma_{x_1g} &= 1/4\sigma_{g_s(t-1)}^{*2} + 1/4\sigma_{g_d(t-1)}^{*2} + \sigma_{g_m}^2 \\ \sigma_{x_2g} &= 1/4\sigma_{g_s(t-1)}^{*2} + 1/4\sigma_{g_d(t-1)}^{*2} \end{aligned}$$

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

$$\mathbf{P}_{(0)} = \begin{bmatrix} 50 & 12.5 \\ 12.5 & 20 \end{bmatrix}$$

$$\mathbf{G}_{(0)} = \begin{bmatrix} 25 \\ 12.5 \end{bmatrix}$$

$$\mathbf{b}_{(0)} = \mathbf{P}_{(0)}^{-1} \mathbf{G}_{(0)} = \begin{bmatrix} .4074 \\ .3704 \end{bmatrix}$$

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

$$p_s = p_d = 5\%$$

$$k = 0.863$$

$$\sigma_{g_s(1)}^{*2} = \sigma_{g_d(1)}^{*2} = (1 - k r_{(0)}^2) \sigma_{g(0)}^2 = (1 - 0.863 \times 0.77^2) 25 = 12.21$$

$$\sigma_{g(t)}^2 = 1/4 \sigma_{g_s(t-1)}^{*2} + 1/4 \sigma_{g_d(t-1)}^{*2} + \sigma_{g_m}^2 = 18.61$$

$$\mathbf{P}_{(1)} = \begin{bmatrix} 43.61 & 6.11 \\ 6.11 & 13.61 \end{bmatrix} \quad \mathbf{G}_{(1)} = \begin{bmatrix} 18.61 \\ 6.11 \end{bmatrix}$$

$$\mathbf{b}_{(1)} = \mathbf{P}_{(1)}^{-1} \mathbf{G}_{(1)} = \begin{bmatrix} .3883 \\ .2746 \end{bmatrix}$$

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

### Incorporating Gametic Phase Dis. in BLUP EBV

Bulmer effect in BLUP EBV, which facilitates direct derivation of steady state parameters

The method utilizes their prediction error variance (PEV)

- important property of BLUP EBV
- does not depend on selection, but only on the amount of effective information

First by Henderson (1975), using the argument that PEV's, which depends on the design matrices, the matrix of additive genetic relationships, and genetic parameters in the base population

$$\sigma_e^2 = \text{Var}(\hat{g} - g) = C_{22}$$

$$\sigma_{\hat{g}_{(0)}}^2 = (1 - r_{(0)}^2) \sigma_{g_{(0)}}^2$$

$$\sigma_{\hat{g}_{(t)}}^2 = (1 - r_{(t)}^2) \sigma_{g_{(t)}}^2$$

PEV unaffected by selection

$$\sigma_{\hat{g}_{(t)}}^2 = \sigma_{\hat{g}_{(0)}}^2$$

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

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

$$\sigma_{g_{(t+1)}}^2 = 1/4(1 - k_s r_{s(t)}^2) \sigma_{g_{(t)}}^2 + 1/4(1 - k_d r_{d(t)}^2) \sigma_{g_{(t)}}^2 + 1/2 \sigma_e^2$$

This is a recursive system to derive:

- genetic variance
- accuracy of selection
- response to selection

Note: It is assumed that full pedigree information is available in  $g_{(0)}$

### Example:

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, for a trait with heritability 0.25 and phenotypic variance 100

Selection on BLUP EBV from an hierarchical mating structure with 20 mates per sire and 10 offspring per dam

$t$	$\frac{(i_s + i_d)}{2}$	$k_s$	$k_d$	$\sigma_{g(0)}^2$	$\sigma_{g(t)}^2$	$r_{(0)}$	$r_{(t)}$	$\bar{g}_{(t+1)}$	$R_{(t)}$	$\sigma_{g(t)}^2 = \sigma_{g(t)}^2$	$\sigma_{g(t)}^2 = \sigma_{g(t)}^2$	$\sigma_{g(t+1)}^2 = \sigma_{g(t+1)}^2$
					from t-1		$\sqrt{\frac{(1 - r_{(0)}^2) \sigma_{g(0)}^2}{\sigma_{g(t)}^2}}$	$\bar{g}_{(t)} + \frac{1}{2} \frac{(i_s + i_d) r_{(t)} \sigma_{g(t)}}{\sigma_{g(t)}}$	$\bar{g}_{(t-1)} \bar{g}_{(t)}$	$(1 - r_{(0)}^2 k_s) \sigma_{g(t)}^2$	$(1 - r_{(0)}^2 k_d) \sigma_{g(t)}^2$	$\frac{1}{2} \sigma_e^2 + \frac{1}{2} \sigma_{g(t)}^2$
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

### Asymptotic Genetic Variance and Response to Selection

Assuming for simplicity equal selection in males and females

Accuracy at the limit:  $r_{(L)}^2 = 1 - (1 - r_{(0)}^2) \sigma_{g(0)}^2 / \sigma_{g(L)}^2$

$$\sigma_{g(L)}^2 = \frac{1}{2}(1 - k r_{(L)}^2) \sigma_{g(L)}^2 + \frac{1}{2} \sigma_{g(0)}^2$$



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

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

Response at the limit:  $R_{(L)} = i r_{(L)} \sigma_{g(L)}$

Response at  $t=0$ :  $R_{(0)} = i r_{(0)} \sigma_{g(0)}$

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

Therefore reduction in response:

- under **BLUP selection** depends only on selection intensity
- under **mass selection** depends on selection intensity initial, accuracy and heritability

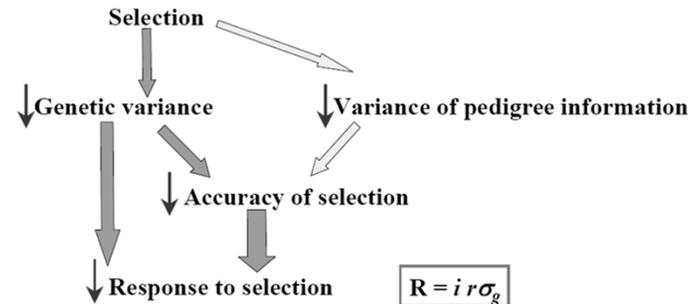
*Unequal selection in males and females:*

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

Equal accuracy  $\rightarrow R_{(L)}/R_{(0)} = \sqrt{\frac{2}{2 + k_s + k_d}}$

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

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



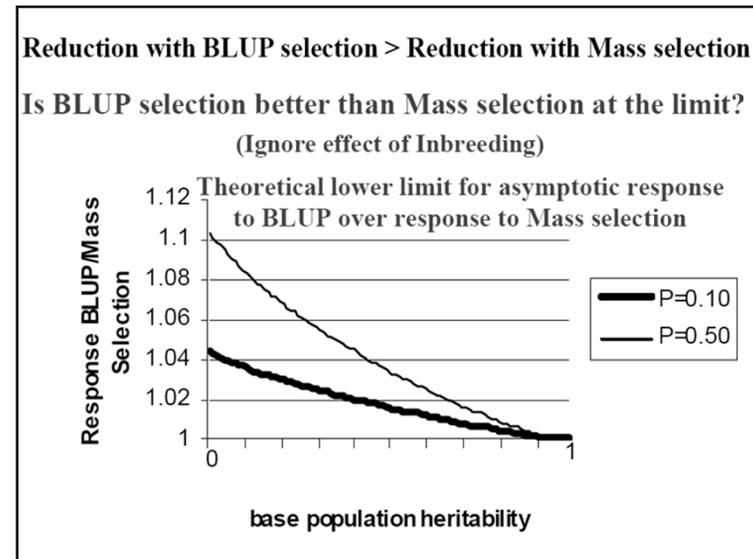
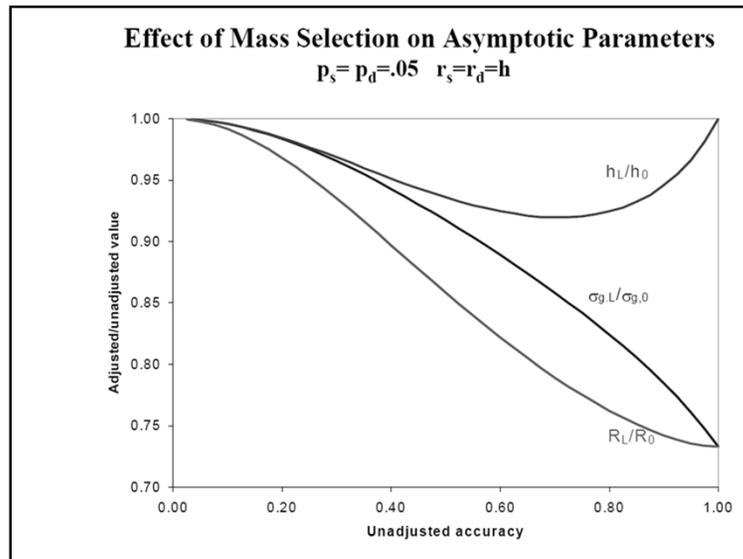
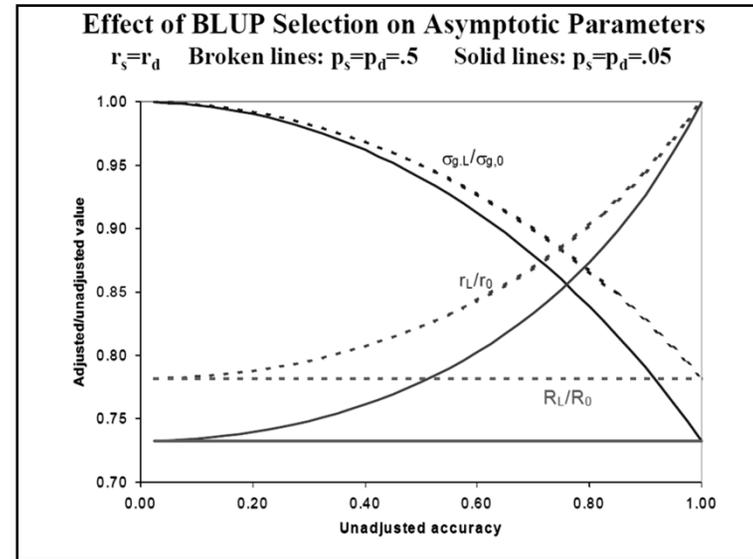
### BLUP Selection - Example

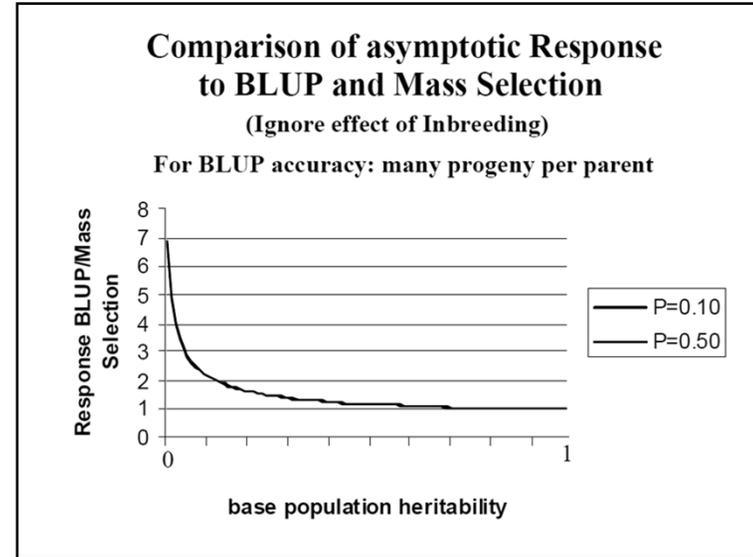
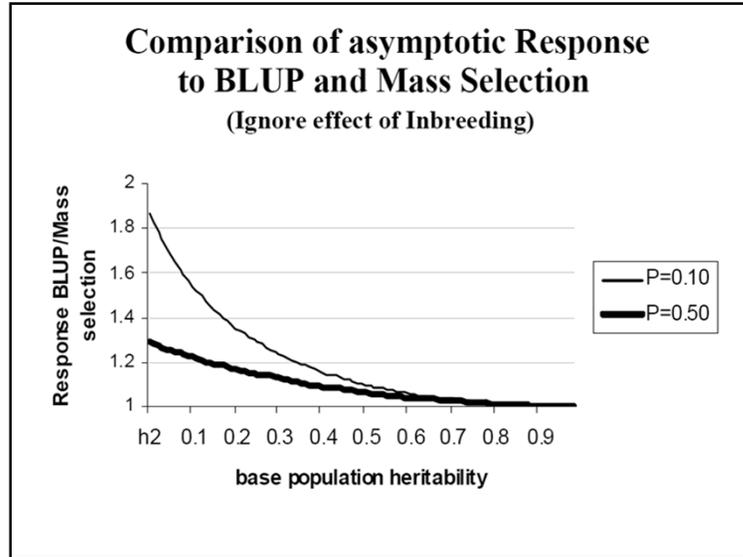
$p_s = p_d = 0.2 \rightarrow i=1.4 \quad k=0.79$

$\sigma_{g,0} = 1$

$r_0^2 = 0.15 \Rightarrow PEV = (1-.15)*1 = 0.85 \quad r_0^2 = 0.80 \Rightarrow PEV = 0.85$

$\sigma_{g,L}^2 = \frac{1+k(1-r_0^2)}{1+k} \sigma_{g,0}^2$	= 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





### 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
$\sigma_{s_g,L}^2/\sigma_{g,0}^2$	.736	.732	.773	.699
$\sigma_{d_g,L}^2/\sigma_{g,0}^2$	.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**

### Selection Across Multiple Age Groups

Means:

$$\bar{g}_{(t+1)} = \frac{1}{2} \bar{g}_{s(t)}^* + \frac{1}{2} \bar{g}_{d(t)}^*$$

For sires:

$$\bar{g}_{s(t)}^* = \frac{1}{P_s} \sum p_{si} w_{si} \bar{g}_{s_i(t)}^*$$

with

$$\bar{g}_{s_i(t)}^* = \bar{g}_{s(t)} + i_{si} r_{s_i(t)} \sigma_{g_i(t)}$$

For dams:

$$\bar{g}_{d(t)}^* = \frac{1}{P_d} \sum p_{di} w_{di} \bar{g}_{d_i(t)}^*$$

with

$$\bar{g}_{d_i(t)}^* = \bar{g}_{d(t)} + i_{di} r_{d_i(t)} \sigma_{g_i(t)}$$

Genetic variance

Among selected sires from age group  $i$  at time  $t$ :

$$\sigma_{g_{si(t)}}^{*2} = (1 - k_{si} r_{si(t)}^2) \sigma_{g_{si(t)}}^2$$

$$k_{si} = i_{si} (i_{si} - x_{si})$$

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  $t+1$ :

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

### Effects of Sample size and Inbreeding

$$\sigma_g^{*2} = \left(1 - \frac{1}{n}\right) (1 - k r_{gg}^2) \sigma_g^2$$

$$\sigma_{g_{m(t+1)}}^2 = \left(1 - \frac{1}{2} (\bar{F}_{s(t)} + \bar{F}_{d(t)})\right) \frac{1}{2} \sigma_{g_0}^2$$