Selection Theory – Change of variance

Selection intensity

Superiority of selected group (in SD units)

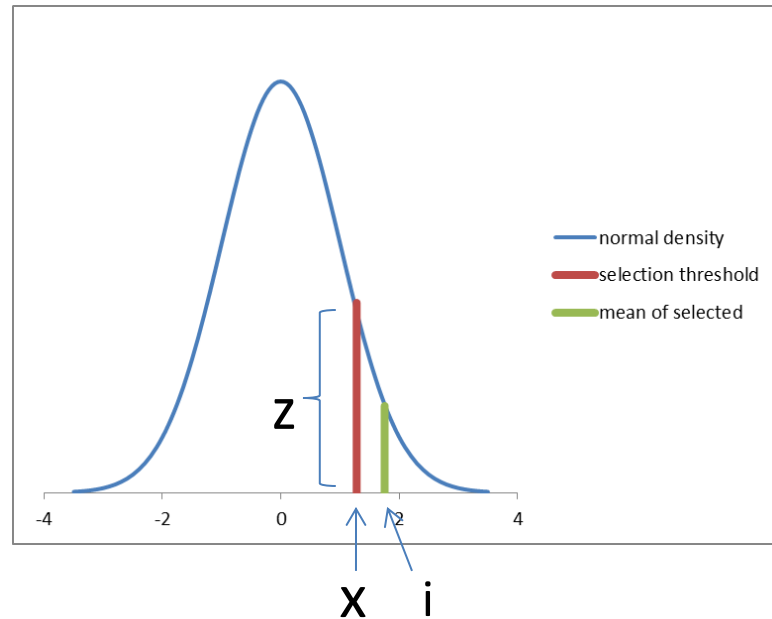|		
proportion selected	p	10.00%
Selection threshold	x	1.282
Height at threshold	z	0.1755
Selection intensity	i	1.755

X: cumulative density function(x > ∞) = p

x= -NORMSINV(p) in excel

$$z = e^{-0.5x^2}/\sqrt{2\pi}$$

i = z/p

Loss of variance due to selection
"Bulmer Effect"

Variance among selected individuals is reduced

Selected parents have a reduced variance

$\qquad$ select of phenotype: $V_{Ps} = (1-k)V_P$ $\qquad$ $k = i\,(i-x)$

Both Environmental en Genetic variance are reduced

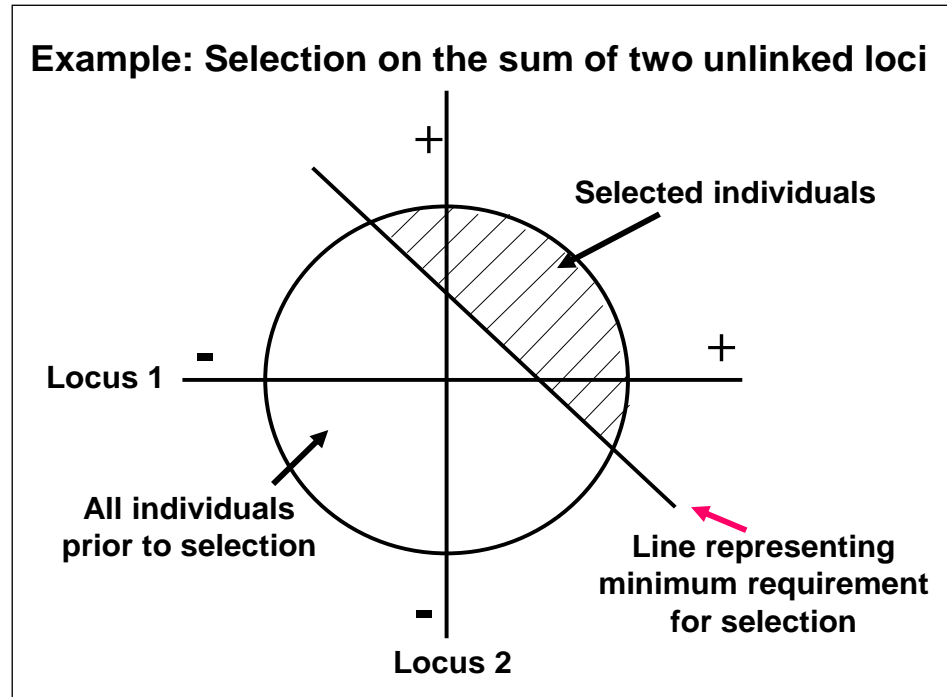Genetic Variance in selected group is reduced to proportion $(1-r^2k)$

$\qquad$ where r is the correlation(selection criterion, breeding value)

$\qquad$ i.e. r = selection accuracy

$\qquad$ select of phenotype: $V_{As} = (1-h^2k)V_A$

Why is genetic variance reduced?

Bulmer 1971: Due to LD between loci (even if unlinked)

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

In the selected group, there will be a negative covariance between loci

$$\text{var}(x_1+x_2) = \text{car}(x_1) + \text{var}(x_2) + 2\text{cov}(x_1,x_2) = \text{reduced}$$

This reduction will disappear if you stop selecting, i.e. no loss due to allele fixation

Reduction in genetic variance after selection

Variance among parents is reduced
    What of this reduction do we find back in progeny?

we find again full residual variance
    ....but genetic variance is still reduced

Only the part coming from the parents is reduced

$$\sigma^2_{As\_t} = (1 - r_2 k_s)\sigma^2_{At}$$

$$\sigma^2_{Ad\_t} = (1 - r_2 k_d)\sigma^2_{At}$$

New variance is generated due to Mendelian Sampling
This is NOT affected by selection

$$\sigma^2_{At+1} = \tfrac{1}{4}\sigma^2_{As_t} + \tfrac{1}{4}\sigma^2_{Ad_t} + \tfrac{1}{2}\sigma^2_{A0}$$

Genetic variance stabilizes after a few generations

Change of variance over time

(P-males=10%, P-females = 50%, $h^2 = 0.5$)

Generation	Phenotypic Variance	Genetic Variance	Mendelian Sampling Variance	Variance among selected sires (% of unselected)	Variance among selected dams (% of unselected)	Heritability	Genetic mean	Response to selection
0	200.0	100.0	50.0	58.5	68.2	0.500	0.0	9.03
1	181.7	81.7	50.0	51.2	58.3	0.450	9.0	7.73
2	177.4	77.4	50.0	49.3	55.9	0.436	16.8	7.41
3	176.3	76.3	50.0	48.9	55.3	0.433	24.2	7.34
4	176.0	76.0	50.0	48.7	55.1	0.432	31.5	7.32
5	176.0	76.0	50.0	48.7	55.1	0.432	38.8	7.31
6	176.0	76.0	50.0	48.7	55.1	0.432	46.1	7.31
7	175.9	75.9	50.0	48.7	55.1	0.432	53.4	7.31
8	175.9	75.9	50.0	48.7	55.1	0.432	60.8	7.31
9	175.9	75.9	50.0	48.7	55.1	0.432	68.1	7.31
10	175.9	75.9	50.0	48.7	55.1	0.432	75.4	7.31

- Variance, heritability, and response decline rapidly (about 15-25%)

- Stabilize after few generations   = asymptotic response

Less response over time due to Bulmer effect (here 16%)

(P-males=10%, P-females = 50%, $h^2 = 0.5$)
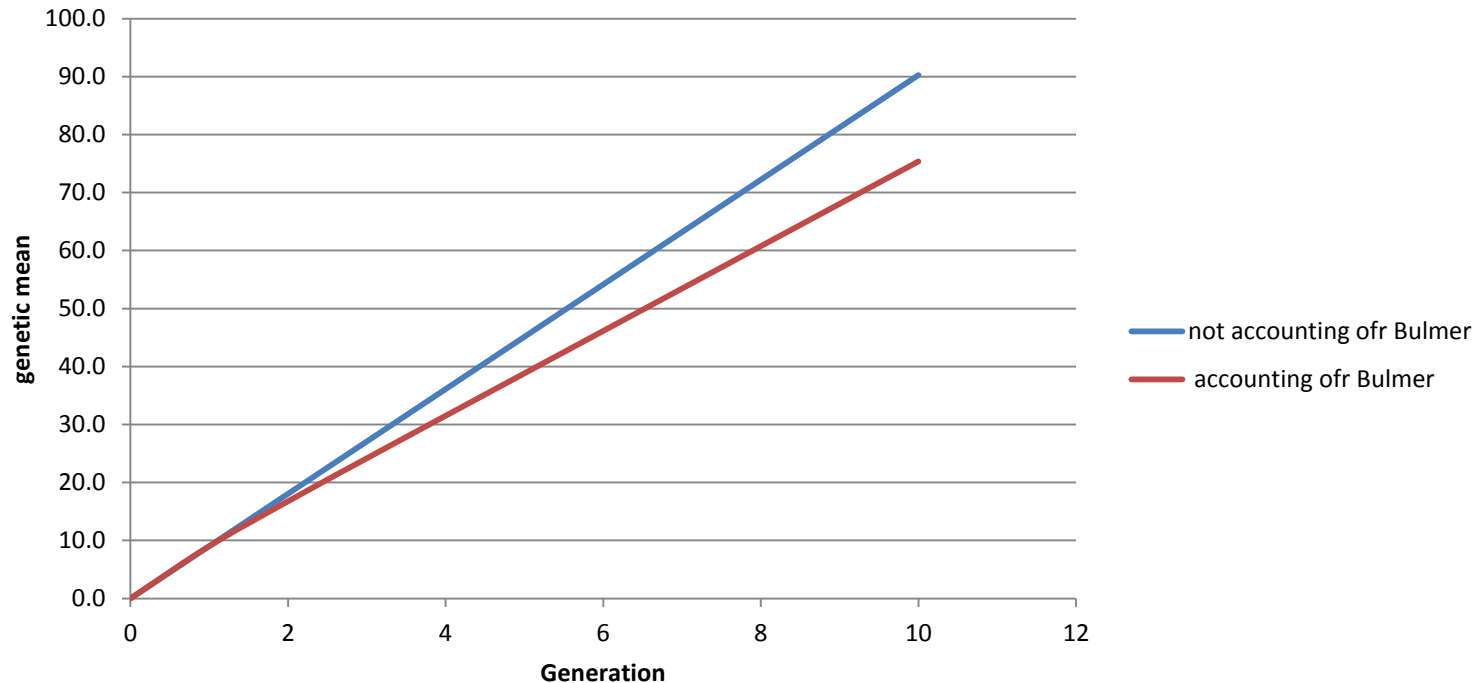
Conclusion:
The Bulmer effect accounts for a reduction in genetic variance, heritability, selection response in populations under selection

Another consequence of the Bulmer effect

Estimation of breeding values is based on information sources that combine

- Information about between family
  - All pedigree and collateral sib information

- Information about Mendelian sampling variation
  - Own performance and progeny information

Under selection, the variation between family is reduced
But the Mendelian sampling variance is not

→ Under selection, the family (pedigree) information becomes less important
→ The information from own performance and progeny becomes more important

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

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

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

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

$p_s = p_d = 5\%$ → $k = 0.863$

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

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

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

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

How accurate is the parent average EBV?

STEBVaccurcay.xls

	selected proportion males	5%	Index weight			
	selected proportion females	5%				
Information used		Nr.Records				
nr of own records		0	-	-	-	
nr. of dams per sire		0	0.500	EBV	dam	
nr of progeny per dam		0	0.500	EBV	sire	
nr. of progeny		0	-	-	-	

No Bulmer Correction

Equilibrium Va	0.500
Equilibrium h2	0.500
SD of EBV	0.383
Accuracy of EBV	**0.5412**

correlation EBV FS	1.000
correlation EBV HS	0.500

With Bulmer Correction

Equilibrium Va	0.364
Equilibrium h2	0.422
SD of EBV	0.104
Accuracy of EBV	**0.1730**

correlation EBV FS	1.000
correlation EBV HS	0.500

Parameters	
Heritability	0.5
Repeatability of subsequent records	0.5
c-squared (among full sibs)	0
selected proportion males	5%
selected proportion females	5%

Information used	Nr.Records
nr of own records	1
nr. of dams per sire	0
nr of progeny per dam	6
nr. of progeny	0
recorded on	both sexes

STEBVaccurcay.xls

Index weight		
0.381	1	own
0.189	EBV	dam
0.189	EBV	sire
0.240	5	FS
-	-	-
-	-	-
-	-	-

Equilibrium Va	0.500
Equilibrium h2	0.500
SD of EBV	0.556
Accuracy of EBV	**0.7865**

correlation EBV FS	0.500
correlation EBV HS	0.296

No Bulmer Correction

Parameters	
Heritability	0.5
Repeatability of subsequent records	0.5
c-squared (among full sibs)	0
selected proportion males	5%
selected proportion females	5%

Information used	Nr.Records
nr of own records	1
nr. of dams per sire	0
nr of progeny per dam	6
nr. of progeny	0
recorded on	both sexes

STEBVaccurcay.xls

Index weight		
0.382	1	own
0.188	EBV	dam
0.188	EBV	sire
0.242	5	FS
-	-	-
-	-	-
-	-	-

Equilibrium Va	0.356
Equilibrium h2	0.416
SD of EBV	0.409
Accuracy of EBV	**0.6851**

correlation EBV FS	0.229
correlation EBV HS	0.106

With Bulmer Correction

Bulmer effect and BLUP selection (Dekkers, 1992)

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:

PEV unaffected by selection ➜

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

As a result, can derive Asymptotic or Steady State Genetic Variance and Response

Select on BLUP EBV

Equal selection in males and females:

Accuracy at the limit:

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

Genetic var. at limit:

$$\sigma^2_{g_{(L)}} = \tfrac{1}{2}(1 - k \, r^2_{(L)}) \sigma^2_{g_{(L)}} + \tfrac{1}{2}\sigma^2_{g_{(o)}} \qquad \Rightarrow \qquad \sigma^2_{g_{(L)}} = \sigma^2_{g_{(o)}} /(1 - k \, r^2_{(L)})$$

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

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:

$$R_{(L)}/R_{(0)} = \frac{i_s \sqrt{2\dfrac{r^2_{s_{(0)}}}{r^2_{d_{(0)}}} - k_d (\dfrac{r^2_{s_{(0)}}}{r^2_{d_{(0)}}} - 1)} + i_d \sqrt{2 + k_s (1 - \dfrac{r^2_{s_{(0)}}}{r^2_{d_{(0)}}})}}{(i_s \dfrac{r_{s_{(0)}}}{r_{d_{(0)}}} + i_d)\sqrt{2 + k_s + k_d}}$$

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

So with BLUP selection, the reduction in response does not depend on the initial selection accuracy

Summary

In populations under selection, the variance decreases rapidly by about 20% due to LD between loci under selection
→ Bulmer effect

Predicted responses will be reduced by a similar amount (compared with assuming no reduced variance

As a result, the value of 'family information' (ancestors and collateral sibs), will be reduced, as the variation between families is reduced
(e.g. parental mean)

→ Effectively less accuracy as predicted by selection index