Short-term changes
In the additive variance

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Uppsala EQG 2012 course
version 5 Feb 2012

Detailed reading: WL Chapter 13,
Online Chapter 22
Short-term changes in variance

- The genetic variance can change for two (genetic) reasons
  - Allele frequency change
  - Selection-induced LD
  - Short-term changes are due to LD, not allele frequencies
  - Nice feature: can easily predict short-term response, but NOT long-term response
Changes in the Variance under Selection

The infinitesimal model --- each locus has a very small effect on the trait.

Under the infinitesimal, require many generations for significant change in allele frequencies.

However, can have significant change in genetic variances due to selection creating linkage disequilibrium.

With positive linkage disequilibrium, \( f(AB) > f(A)f(B) \), so that \( AB \) gametes are more frequent.

With negative linkage disequilibrium, \( f(AB) < f(A)f(B) \), so that \( AB \) gametes are less frequent.
Additive variance with LD:

Additive variance is the variance of the sum of allelic effects,

\[
\sigma^2 \left( \sum_{k=1}^{n} \left( a_1^{(k)} + a_2^{(k)} \right) \right) = 2 \sum_{k=1}^{n} \sigma^2 \left( a^{(k)} \right) + 4 \sum_{k<j}^{n} \sigma \left( a^{(j)}, a^{(k)} \right) \\
= 2 \sum_{k=1}^{n} C_{kk} + 4 \sum_{k<j}^{n} C_{jk}
\]

\[
\sigma_A^2 = \sigma_a^2 + d
\]

Additive variance

Has two parts: one from the current allele Frequencies, the other part (d) from LD
Additive variance with LD:

Additive variance is the variance of the sum of allelic effects,

\[ \sigma^2 \left( \sum_{k=1}^{n} (a_1^{(k)} + a_2^{(k)}) \right) = 2 \sum_{k=1}^{n} \sigma^2 (a^{(k)}) + 4 \sum_{k<j}^{n} \sigma (a^{(j)}, a^{(k)}) \]

\[ = 2 \sum_{k=1}^{n} C_{kk} + 4 \sum_{k<j}^{n} C_{jk} \]

\[ \sigma_A^2 = \sigma_a^2 + d \]

**Genic variance:** value of \( \text{Var}(A) \) in the absence of disequilibrium function of allele frequencies

**Disequilibrium contribution** (d). Requires covariances between allelic effects at different loci = LD
Key: Under the infinitesimal model, no (selection-induced) changes in genic variance $\sigma^2_a$

Selection-induced changes in $d$ change $\sigma^2_A, \sigma^2_z, h^2$

\[
\sigma_z^2(t) = \sigma_E^2 + \sigma_D^2 + \sigma_A^2(t) = \sigma_z^2 + d(t)
\]

\[
h^2(t) = \frac{\sigma_A^2(t)}{\sigma_z^2(t)} = \frac{\sigma_a^2 + d(t)}{\sigma_z^2 + d(t)}
\]

Dynamics of $d$: With unlinked loci, $d$ loses half its value each generation (i.e., $d$ in offspring is $1/2$ of their parents,

\[
d(t + 1) = \frac{d(t)}{2}
\]
Dynamics of \( d \): Computing the effect of selection in generating \( d \)

Consider the parent-offspring regression

\[
    z_o = \mu + \frac{h^2}{2}(z_m - \mu) + \frac{h^2}{2}(z_f - \mu) + e
\]

\[
    \sigma_e^2 = \left(1 - \frac{h^4}{2}\right) \sigma_z^2
\]

Taking the variance of the offspring given the selected parents gives

\[
    \sigma^2(z_o) = \frac{h^4}{4} \left[ \sigma^2(z_m^*) + \sigma^2(z_f^*) \right] + \sigma_e^2
\]

\[
    = \frac{h^4}{2} \left[ \sigma_z^2 + \delta(\sigma_z^2) \right] + \left(1 - \frac{h^4}{2}\right) \sigma_z^2
\]

\[
    = \sigma_z^2 + \frac{h^4}{2} \delta(\sigma_z^2)
\]

Change in variance from selection
Change in $d =$ change from recombination plus change from selection

$$d(t + 1) = \frac{d(t)}{2} + \frac{h^4}{2} \delta(\sigma_z^2) = d(t + 1) = \frac{d(t)}{2} + \frac{h^4(t)}{2} \delta(\sigma_z^2(t))$$

Recombination Selection

In terms of change in $d$,

$$\Delta d(t) = \Delta \sigma_z^2(t) = \Delta \sigma_A^2(t)$$

$$= - \frac{d(t)}{2} + \frac{h^4(t)}{2} \delta(\sigma_z^2(t))$$

This is the Bulmer Equation (Michael Bulmer), and it is akin to a breeder’s equation for the change in variance

At the selection-recombination equilibrium,

$$\bar{d} = \bar{h}^4 \delta(\sigma_z^2)$$
Application: Egg Weight in Ducks

Rendel (1943) observed that while the change in mean weight weight (in all vs. hatched) was negligible, but there was a significance decrease in the variance, suggesting stabilizing selection.

Before selection, variance = 52.7, reducing to 43.9 after selection. Heritability was $h^2 = 0.6$

$$\tilde{d} = \tilde{h}^4 \delta (\sigma_z^2) = 0.6^2 (43.9 - 52.7) = -3.2$$

Var(A) = 0.6*52.7 = 31.6. If selection stops, Var(A) is expected to increase to 31.6+3.2 = 34.8

Var(z) should increase to 55.9, giving $h^2 = 0.62$
Contribution of within- vs. between-family effects to $\text{Var}(A)$

The total additive variance arises from two sources: differences between the mean BVs of families and variation of BVs within families.

When no LD is present, both these sources contribute equally, $\frac{\text{Var}(A)}{2}$.

When LD is present, the within-family variance is still $\frac{\text{Var}(A)}{2}$, as it is due to segregation of alleles in heterozygous parents. If parents are inbred, then $\frac{\text{Var}(A)(1-f)}{2}$ is the segreg. variance.
Consider parent-offspring regression in BV

\[ A_o = \frac{1}{2} A_m + \frac{1}{2} A_f + e \]

\[
\sigma^2_A(t + 1) = \sigma^2_{A_o}(t + 1) = \sigma^2 \left( \frac{A_m(t)}{2} + \frac{A_f(t)}{2} \right) + \sigma^2_e
\]

\[
= \frac{1}{4} \left[ \sigma^2_{A_m}(t) + \sigma^2_{A_f}(t) \right] + \frac{1}{2} \sigma^2_A(0)
\]

\[
= \frac{1}{2} \sigma^2_{A^*}(t) + \frac{1}{2} \sigma^2_a
\]

The within-family (or mendelian segregation variance) is simply the genic variance and is a constant (if allele frequencies not changing).

LD is a function the between-family variance in BV

When LD < 0, families are more similar than expected,
When LD > 0, families are more dissimilar
Changes in phenotypic variance generate $d$

- If the population variance is reduced after selection (the variance of the trait among the selected parents),
  - Negative $d$ generated
  - Occurs with directional and stabilizing selection

- If the trait variance of the selected parents is larger than the original population variance
  - Positive $d$ generated
  - Occurs with disruptive selection or positive assortative mating
Specific models of selection-induced changes in variances

Proportional reduction model:
constant fraction $k$ of variance removed

Bulmer equation simplifies to

$$d(t + 1) = \frac{d(t)}{2} - \frac{k}{2} h^2(t) \sigma_A^2(t)$$

$$= \frac{d(t)}{2} - \frac{k}{2} \left[ \frac{\sigma_A^2 + d(t)}{\sigma_z^2 + d(t)} \right]^2$$

Closed-form solution to equilibrium $h^2$

$$\tilde{h}^2 = \frac{-1 + \sqrt{1 + 4h^2(1 - h^2)\kappa}}{2\kappa (1 - h^2)}$$
Directional Truncation Selection: Uppermost (or lowermost) $p$ saved

$$\kappa = \frac{\varphi \left( z_{[1-p]} \right)}{p} \left( \frac{\varphi \left( z_{[1-p]} \right)}{p} - z_{[1-p]} \right) = \bar{t} \left( \bar{t} - z_{[1-p]} \right)$$

Stabilizing Truncation Selection: Middle fraction $p$ of the distribution saved

$$\kappa = \frac{2 \varphi \left( z_{[1/2+p/2]} \right) \left( z_{[1/2+p/2]} \right)}{p}$$

Disruptive Truncation Selection: Uppermost and lowermost $p/2$ saved

$$\kappa = -\frac{2 \varphi \left( z_{[1-p/2]} \right) \left( z_{[1-p/2]} \right)}{p}$$
Equilibrium $h^2$ under direction truncation selection
Directional truncation selection

\[ \kappa = \bar{t} \left( \bar{t} - z_{[1-p]} \right) \]

**Example 13.2.** Suppose directional truncation selection is performed (equally on both sexes) on a normally distributed character with \( \sigma^2_z = 100, h^2 = 0.5, \) and \( p = 0.20 \) (the upper 20 percent of the population is saved). From normal distribution tables,

\[ \Pr(U \leq 0.84) = 0.8, \quad \text{hence} \quad z_{[0.8]} = 0.84 \]

Likewise, evaluating the unit normal gives \( \varphi(0.84) = 0.2803, \) so that (Equation 10.26a)

\[ \bar{t} = \varphi(0.84)/p = 0.2803/0.20 = 1.402 \]

From Equation 13.15b, the fraction of variance removed by selection is

\[ \kappa = 1.402 (1.402 - 0.84) = 0.787. \]

Hence, Equation 13.12 gives

\[ d(t + 1) = \frac{d(t)}{2} - 0.394 \frac{[50 + d(t)]^2}{100 + d(t)} \]

<table>
<thead>
<tr>
<th>Generation</th>
<th>( d(t) )</th>
<th>( \sigma^2_A(t) )</th>
<th>( h^2(t) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.00</td>
<td>50.00</td>
<td>0.50</td>
</tr>
<tr>
<td>1</td>
<td>-9.84</td>
<td>40.16</td>
<td>0.45</td>
</tr>
<tr>
<td>2</td>
<td>-11.96</td>
<td>38.04</td>
<td>0.43</td>
</tr>
<tr>
<td>3</td>
<td>-12.45</td>
<td>37.55</td>
<td>0.43</td>
</tr>
<tr>
<td>4</td>
<td>-12.56</td>
<td>37.44</td>
<td>0.43</td>
</tr>
<tr>
<td>5</td>
<td>-12.59</td>
<td>37.41</td>
<td>0.43</td>
</tr>
<tr>
<td>( \infty )</td>
<td>-12.59</td>
<td>37.41</td>
<td>0.43</td>
</tr>
</tbody>
</table>
Changes in the variance = changes in $h^2$ and even $S$ (under truncation selection)

$$R(t) = h^2(t) \cdot S(t)$$

How does this reduction in $\sigma_A^2$ influence the per-generation change in mean, $R(t)$? Since the selection $7$ is unchanged (being entirely a function of the fraction $p$ of adults saved), but $h^2$ and $\sigma_z^2$ change over time, Equation 10.6b gives the response as

$$R(t) = h^2(t) \cdot \sigma_z(t) = 1.402 \cdot h^2(t) \cdot \sqrt{\sigma_z^2 + d(t)} = 1.402 \cdot h^2(t) \cdot \sqrt{100 + d(t)}$$

Response declines from an initial value of $R = 1.4 \cdot 0.5 \cdot 10 = 7$ to an asymptotic per-generation value of $\tilde{R} = 1.4 \cdot 0.43 \cdot \sqrt{87.41} = 5.6$. Thus, if we simply used the Breeders’ equation to predict change in mean over several generations without accounting for the Bulmer effect, we would have overestimated the expected response by 25 percent.
In Class Problem 1

You are selecting the upper 5% of a trait with $h^2 = 0.75$ and $\sigma^2_z = 100$ initially in linkage equilibrium

- Compute the response over 3 generations. Also compute $d(t)$, $h^2(t)$, $\sigma^2_z(t)$, and $S(t)$. Compare the total 3 generations of response with the result from the standard breeder’s equation

\[
\kappa = \bar{t} \left( \bar{t} - z_{[1-p]} \right)
\]

\[
z_{[1-p]} = qnorm(1-p), \quad i = \frac{dnorm(z_{[1-p]})}{p}
\]

\[
d(t + 1) = \frac{d(t)}{2} - \frac{\kappa}{2} h^2(t) \sigma^2_A(t)
\]

\[
= \frac{d(t)}{2} - \frac{\kappa}{2} \left[ \frac{\sigma^2_a + d(t)}{\sigma^2_z + d(t)} \right]^2
\]

\[
R(t) = h^2(t) \bar{t} \sigma_z(t)
\]

\[
z_{[1-p]} = qnorm(1-0.05) = 1.645
\]

\[
i = \frac{dnorm(1.645)}{0.05} = 2.062
\]

\[
K = 2.062 \times (2.062 - 1.645) = 0.860
\]
Selection can also focus entirely on the variance (stabilizing & disruptive selection)
Selection can also focus entirely on the variance (stabilizing & disruptive selection)

**Example 13.3.** Consider a normally distributed character with $\sigma_z^2 = 100$ and $h^2 = 0.5$ in a random mating population. To compare the effects of stabilizing and disruptive selection, suppose in one replicate disruptive selection is practiced via double truncation with $p = 0.5$ (the upper and lower 25 percent of the population are culled), while stabilizing selection with $p = 0.5$ (the upper and lower 25 percent are saved) is practiced in the other. To obtain $\kappa$ from Table 13.1, first note that for stabilizing selection, $z_{[1/2+p/2]} = z_{[0.75]}$, while for disruptive selection $z_{[1-p/2]} = z_{[0.75]}$. From normal tables, $\Pr(U \leq 0.675) = 0.75$, giving $z_{[0.75]} = 0.675$. Likewise, $\varphi(0.675) = 0.318$. Hence

$$\kappa = \pm (2 \cdot 0.318 \cdot 0.675)/0.5 = \pm 0.858$$

where the plus is used for stabilizing selection, the minus for disruptive selection. Equation 13.2 becomes

$$d(t + 1) = \frac{d(t)}{2} + 0.429 \frac{[50 + d(t)]^2}{100 + d(t)}$$

where (since the equation is in terms of $-\kappa$) the minus corresponds to stabilizing selection, the plus for disruptive selection. Starting selection on a base population with $d = 0$, iteration yields
### Disruptive selection

<table>
<thead>
<tr>
<th>Generation</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>20</th>
<th>∞</th>
</tr>
</thead>
<tbody>
<tr>
<td>$d(t)$</td>
<td>0.00</td>
<td>10.73</td>
<td>19.65</td>
<td>27.22</td>
<td>33.72</td>
<td>39.34</td>
<td>74.83</td>
<td>82.69</td>
</tr>
<tr>
<td>$\sigma_A^2(t)$</td>
<td>50.00</td>
<td>60.37</td>
<td>69.65</td>
<td>77.22</td>
<td>83.72</td>
<td>89.34</td>
<td>124.83</td>
<td>132.69</td>
</tr>
<tr>
<td>$h^2(t)$</td>
<td>0.50</td>
<td>0.55</td>
<td>0.58</td>
<td>0.61</td>
<td>0.63</td>
<td>0.64</td>
<td>0.71</td>
<td>0.73</td>
</tr>
</tbody>
</table>

Disruptive selection inflates the variance after selection, generating positive $d$

### Stabilizing selection

<table>
<thead>
<tr>
<th>Generation</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>∞</th>
</tr>
</thead>
<tbody>
<tr>
<td>$d(t)$</td>
<td>0.00</td>
<td>-10.73</td>
<td>-12.77</td>
<td>-13.20</td>
<td>-13.29</td>
<td>-13.31</td>
<td>-13.32</td>
</tr>
<tr>
<td>$\sigma_A^2(t)$</td>
<td>50.00</td>
<td>39.27</td>
<td>37.23</td>
<td>36.80</td>
<td>36.71</td>
<td>36.69</td>
<td>36.68</td>
</tr>
<tr>
<td>$h^2(t)$</td>
<td>0.50</td>
<td>0.44</td>
<td>0.43</td>
<td>0.42</td>
<td>0.42</td>
<td>0.42</td>
<td>0.42</td>
</tr>
</tbody>
</table>

Stabilizing selection deflates the variance after selection, generating negative $d$
Suppose that after the equilibrium value of $d$ has been reached, both of the two above populations are then subjected to directional selection. In particular, assume directional truncation selection with the upper 20 percent of the population being saved. The recursion equation for the disequilibrium contribution is given in Example 13.2, but now the initial disequilibrium values are $d_0 = -13.32$ for the population with a previous history of stabilizing selection and $d_0 = 82.69$ for the population with a previous history of disruptive selection.
Selection on the environmental variance

• **Genotypes can differ in their environmental variances**
  - Example: Different inbred lines show different variances
  - Different QTL genotypes can show different trait variances

• **Can get response to selection on the environmental variance**
  - Response for increased cannalization (greater left-right symmetry in traits like bristle number in flies)

• **Hence, selection on a trait can also potentially change its environmental variance**
Models of heritable environmental variation

• Base model is $P = G + E$, where $E$ now varies over genotype and hence we can speak of a breeding value for $E$

• Gavrilets-Hastings multiplicative model
  - $E = \gamma_i * e$, where $e \sim (0, \sigma_e^2)$
  - A genotype-specific effect $\gamma +$ noise ($e$)
  - Hence, $\text{Var}(E \mid G, g) = \gamma^2 * \sigma_e^2$
  - Simplest approach $\gamma = A_v$, the BV for variance
    • Hence, $\text{Var}(E \mid G, A_v) = A_v^2 * \sigma_e^2$
Multiplicative Model (cont)

- Total environmental variance (for population)
  \[ \sigma_E^2 = (\mu_\gamma^2 + \sigma_\gamma^2) \cdot \sigma_e^2 \]

- Selecting \( \mu_\gamma \) to zero minimized population environmental variance

- When \( \gamma = A_v + D_v \), (dominance in environmental sensitivity), then
  \[ \sigma_E^2 = (\mu_{A_v}^2 + \sigma_{A_v}^2) \cdot \sigma_e^2 + \sigma_{D_v}^2 \cdot \sigma_e^2 \]
  - selection can decrease mean of \( A_v \) and also its variance (by generating negative LD), but can’t impact the dominance term
The exponential model

- $E = \exp(A_v/2) \cdot e$
  - Where $e \sim N(0, \sigma_e^2)$, $A_v \sim N(\mu_{A_v}, \sigma_{A_v}^2)$,
- Also called the log-additive model, as
  - $\ln(\sigma^2(E | A_v)) = \ln(\sigma_e^2) + A_v$
- Environmental variation for the population
  - $\sigma_E^2 = \sigma_e^2 \exp(\mu_{A_v} + \sigma_{2A_v}/2)$
  - Under this model, decreasing the mean (to negative values) continues to decrease the variance
The additive model

- While the multiplicative and exponential models ensure a non-zero variance, they can be hard to work with.

- The additive model is easier to use but does not ensure a positive environmental variance.
  
  - Here, \( \sigma_E^2 = \sigma_e^2 + \mu_{Av} \)

\[
E = U \cdot \sqrt{\sigma_e^2 + A_v}, \quad \text{where} \quad U \sim N(0, 1) \quad \text{and} \quad A_v \sim N(\mu_{A_v}, \sigma_{A_v}^2)
\]
Table 13.3. Models for heritable variation in the environmental value $E$. The basic model is $z = \mu + A_m + E$, where $z$ is the trait value and $A_m \sim N(\mu_{A_m}, \sigma_{A_m}^2)$ the breeding value for trait value. The table gives the assumed form of $E$ for different models as a function of the breeding value in variance $A_v \sim N(\mu_{A_v}, \sigma_{A_v}^2)$, some intrinsic environmental value $e \sim N(0, \sigma_e^2)$, and the unit normal $U \sim N(0, 1)$.

<table>
<thead>
<tr>
<th>Model</th>
<th>$E$</th>
<th>$\sigma^2(E \mid A_v)$</th>
<th>$\sigma^2(E)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Multiplicative</td>
<td>$A_v e$</td>
<td>$A_v^2 \sigma_e^2$</td>
<td>$(\mu_{A_v}^2 + \sigma_{A_v}^2) \sigma_e^2$</td>
</tr>
<tr>
<td>Exponential</td>
<td>$\exp (A_v/2) e$</td>
<td>$\sigma_e^2 \exp (A_v)$</td>
<td>$\sigma_e^2 \exp [\mu_{A_v} + \sigma_{A_v}^2/2]$</td>
</tr>
<tr>
<td>(or log-additive)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Additive</td>
<td>$\sqrt{A_v + \sigma_e^2} \cdot U$</td>
<td>$A_v + \sigma_e^2$</td>
<td>$\mu_{A_v} + \sigma_e^2$</td>
</tr>
</tbody>
</table>
Under the additive model, we can define a Heritability as

\[ h_v^2 = \frac{\sigma(A_v, z^2)}{\sigma^2(z^2)} \]

Under normality Assumptions,

\[ h_v^2 = \frac{\sigma^2(A_v)}{2\sigma_z^4 + 3\sigma_{A_v}^2} \]

**Table 13.4.** Literature estimates of the heritability \( h_v^2 \) and evolvability \( \sigma_{A_v}/\sigma_{E}^2 \) of the environmental variance (after Mulder et al. 2007).

<table>
<thead>
<tr>
<th>Species</th>
<th>Trait</th>
<th>( h_v^2 )</th>
<th>( \sigma_{A_v}/\sigma_{E}^2 )</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pig ((Sus))</td>
<td>Meat pH</td>
<td>0.039</td>
<td>0.402</td>
<td>SanCristobal-Gaudy et al. (1998)</td>
</tr>
<tr>
<td></td>
<td>Litter size</td>
<td>0.026</td>
<td>0.307</td>
<td>Sorensen &amp; Waagepetersen (2003)</td>
</tr>
<tr>
<td>Sheep ((Ovis))</td>
<td>Litter size</td>
<td>0.048</td>
<td>0.509</td>
<td>SanCristobal-Gaudy et al. (2001)</td>
</tr>
<tr>
<td>Snail ((Helix))</td>
<td>Body weight</td>
<td>0.017</td>
<td>0.580</td>
<td>Ros et al. (2004)</td>
</tr>
<tr>
<td>Chicken ((Gallus))</td>
<td>Body weight (male)</td>
<td>0.029</td>
<td>0.399</td>
<td>Rowe et al. (2006)</td>
</tr>
<tr>
<td></td>
<td>Body weight (female)</td>
<td>0.031</td>
<td>0.318</td>
<td>Rowe et al. (2006)</td>
</tr>
</tbody>
</table>
Selection response (additive model)

Assume the additive model for $\sigma^2_E$ (Equation 13.26b) and truncation selection on a normally-distributed trait. Recall (Equation 10.26) that for a given fraction $p$ saved under truncation selection on a normally-distributed trait, the selection intensity is $\bar{t} = \varphi(x_{[1-p]})/p$, where $\varphi(x)$ is the unit normal distribution function evaluated at $x$, while for a unit normal $U$, $x_{[1-p]}$ satisfies $\Pr(U \geq x_{[1-p]}) = p$. For the special case where $A_m$ and $A_v$ are uncorrelated, the expected responses become simply

$$R_{A_m} = h^2_m \bar{t} \sigma_z$$
$$R_{A_v} = h^2_v \bar{t} x_{[1-p]} \sigma_z^2$$

where $h^2_m$ is the heritability for trait mean and $h^2_v$ is the heritability for the additive component of trait variance (Equation 13.27b). Equation 13.31a is simply our standard result for the change in mean under truncation selection, while 13.31b is the analog for the change in the breeding value of the variance (under the additive model).

Hence strong directional selection (by selecting outliers) can result in a significant increase in $\text{Var}(E)$, reducing $h^2$. 
Truncation selection

Selection on variance

Selection on mean

\[ R_{A_m} = h_m^2 \bar{x} \sigma_z \]

\[ R_{A_v} = h_v^2 \bar{x} [1 - p] \sigma_z^2 \]
Example 13.8. Consider a trait with $h_m^2 = 0.3$ and $h_v^2 = 0.03$ (which is a typical value of the known estimates, see Table 13.4). Suppose $\sigma_z^2 = 100$. What is the expected response in the mean and $\sigma_E^2$ following a single generation of truncation selection with $p = 0.1$? Noting that $\Pr(U > 1.282) = 0.1$, we have $x_{[1-p]} = 1.282$ and $\bar{t} = \phi(1.282)/0.1 = 1.755$, giving

$$R_{Am} = 0.3 \cdot 1.755 \cdot 10 = 5.265, \quad \text{and} \quad R_{Av} = 0.03 \cdot 1.755 \cdot 1.282 \cdot 100 = 6.750$$

Here selection increased the mean by 5.3 and the environmental variance by 6.75. Now consider stronger selection, $p = 0.01$. Here $x_{[1-p]} = 2.326$ and $\bar{t} = 2.666$, giving

$$R_{Am} = 0.3 \cdot 2.666 \cdot 10 = 7.998, \quad \text{and} \quad R_{Av} = 0.03 \cdot 2.666 \cdot 2.326 \cdot 100 = 18.603$$

This is roughly a 50% increase in the mean, but a 275% increase in the variance.
Stabilizing selection

• Selection to minimize deviations from some optimal value can occur through three pathways
  - To the mean to the optimal value
  - Reduce the additive genetic variation (generation of negative LD)
  - Reduce the environmental variance
Stabilizing selection (cont)

Assume \[ W(z) = 1 - s(z - \theta)^2. \] Multiplicative model

\[
W(A_m, A_v) = 1 - s \mathbb{E} \left[ (A_m + A_v e - \theta)^2 \right] \\
= 1 - s \left[ (A_m - \theta)^2 + 2(A_m - \theta)A_v \mathbb{E} [e] + A_v^2 \mathbb{E} (e^2) \right] \\
= 1 - s \left[ (A_m - \theta)^2 + A_v^2 \sigma_e^2 \right]
\] (13.29b)

Thus, under phenotypic stabilizing selection, there is selective pressure to shift the breeding value of the trait towards \( \theta \) and to decrease \( A_v \) towards zero (and hence direct selection to decrease \( \sigma_E^2 \)). There are two important consequences of this. First, the reduction in phenotypic variance can be much greater than predicted from the simple reduction in the additive variance from the Bulmer effect. Second, there can be cases where the heritability will increase under stabilizing selection. Since both additive and environmental variances are decreased, if the decrease in environmental variance is sufficiently larger, \( h^2 \) can actually increase.