Lecture 4
Short-Term Selection Response: Breeder's Equation

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Introduction to Quantitative Genetics
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First PAUSE at Slide 15

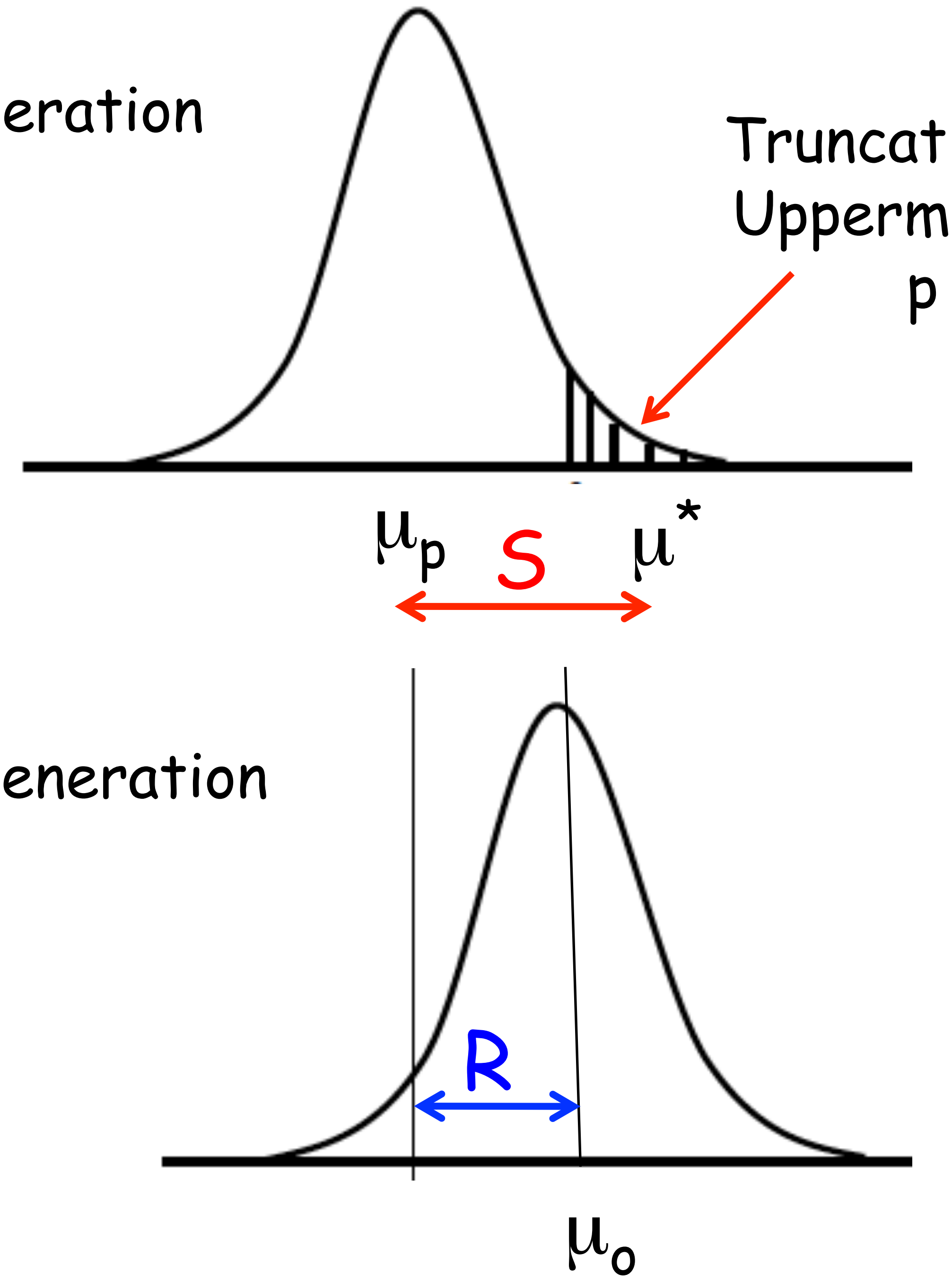
Response to Selection

- Selection can change the distribution of phenotypes, and we typically measure this by changes in mean
  - This is a within-generation change
- Selection can also change the distribution of breeding values
  - This is the response to selection, the change in the trait in the next generation (the between-generation change)

The Selection Differential and the Response to Selection

- The selection differential S measures the within-generation change in the mean
  - $S = \mu^* - \mu$
- The response R is the between-generation change in the mean
  - $R(t) = \mu(t+1) - \mu(t)$

Parental Generation



Truncation selection
Uppermost fraction
p saved

Offspring Generation

The Breeders' Equation: Translating S into R

Recall the regression of offspring value on midparent value

$$y_O = \mu_P + h^2 \left(\frac{P_f + P_m}{2} - \mu_P \right)$$

Averaging over the selected midparents,

$E[\ (P_f + P_m)/2\ ] = \mu^*,$

Likewise, averaging over the regression gives

$$E[\ y_o - \mu\ ] = h^2 (\ \mu^* - \mu\ ) = h^2\ S$$

Since $E[\ y_o - \mu\ ]$ is the change in the offspring mean, it represents the response to selection, giving:

$\boxed{R = h^2\ S}$ The Breeders' Equation (Jay Lush)

- Note that no matter how strong S, if h^2 is small, the response is small
- S is a measure of selection, R the actual response. One can get lots of selection but no response
- If offspring are asexual clones of their parents, the breeders' equation becomes
  - $R = H^2 S$
- If males and females subjected to differing amounts of selection,
  - $S = (S_f + S_m)/2$
  - Example: Selection on seed number in plants -- pollination (males) is random, so that $S = S_f/2$

Pollen control

- Recall that $S = (S_f + S_m)/2$
- An issue that arises in plant breeding is pollen control --- is the pollen from plants that have also been selected?
- Not the case for traits (i.e., yield) scored after pollination. In this case, $S_m = 0$, so response only half that with pollen control
- Tradeoff: with an additional generation, a number of schemes can give pollen control, and hence twice the response
  - However, takes twice as many generations, so response per generation the same

Selection on clones

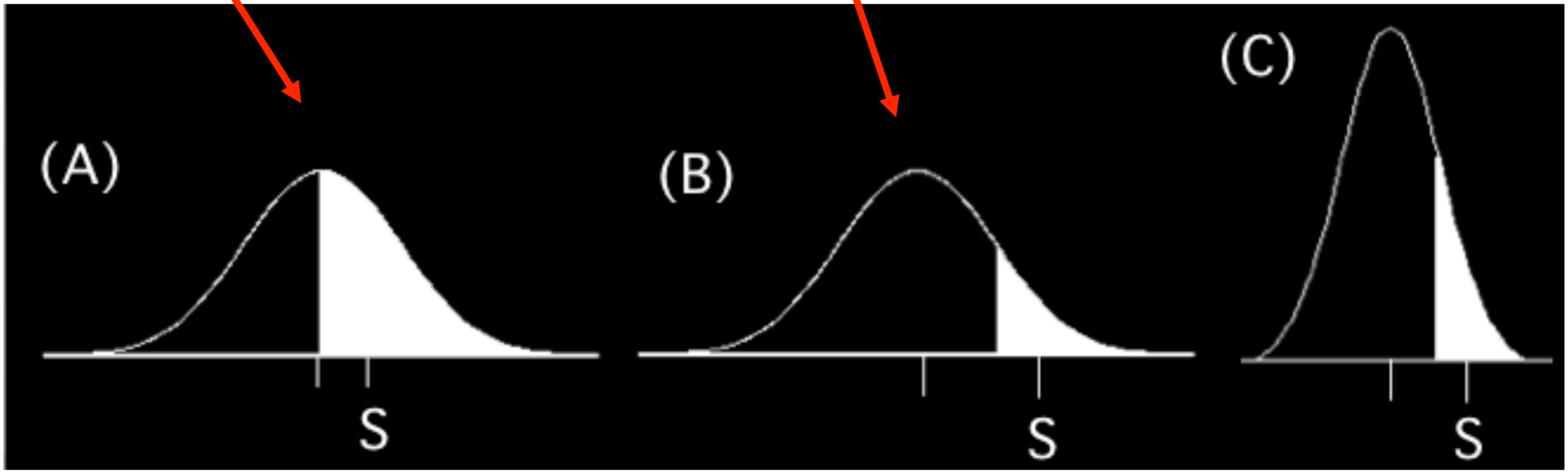
- Although we have framed response in an outcrossed population, we can also consider selecting the best individual clones from a large population of different clones (e.g., inbred lines)
- $R = H^2S$, now a function of the board sense heritability. Since $H^2 \geq h^2$, the single-generation response using clones exceeds that using outcrossed individuals
- However, the genetic variation in the next generation is significantly reduced, reducing response in subsequent generations
  - In contrast, expect an almost continual response for several generations in an outcrossed population.

The selection differential is a function of both the phenotypic variance and the fraction selected

50% selected
$V_p = 4$, $S = 1.6$

20% selected
$V_p = 4$, $S = 2.8$

20% selected
$V_p = 1$, $S = 1.4$



The Selection Intensity, i

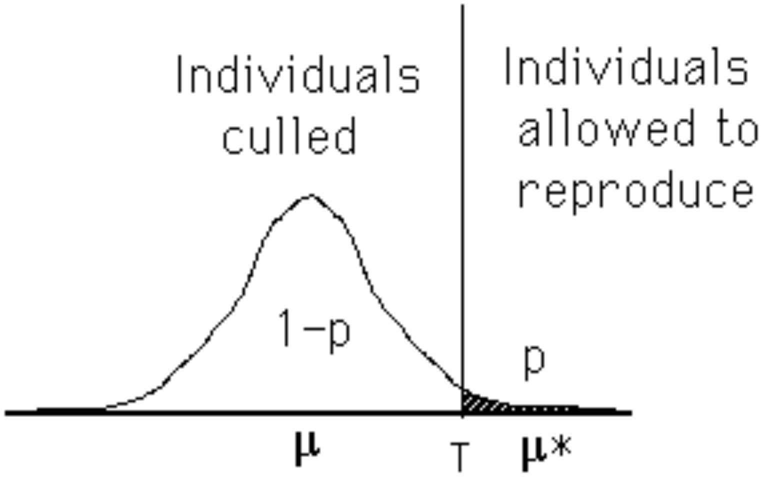
As the previous example shows, populations with the same selection differential (S) may experience very different amounts of selection

The selection intensity i provides a suitable measure for comparisons between populations,

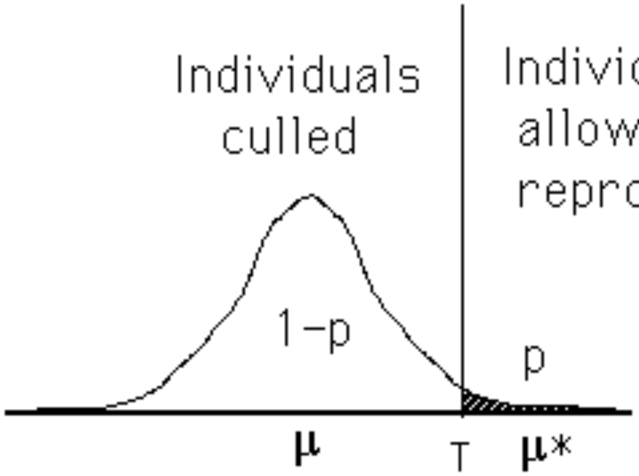
$$i = \frac{S}{\sqrt{V_P}} = \frac{S}{\sigma_p}$$

Truncation selection

- A common method of artificial selection is truncation selection --- all individuals whose trait value is above some threshold (T) are chosen.
- Equivalent to only choosing the uppermost fraction p of the population



Selection Differential Under Truncation Selection



S =μ*- μ

$$S = \varphi\left(\frac{T-\mu}{\sigma}\right)\,\frac{\sigma}{p}$$

Likewise,

$$\bar{\imath} = \frac{S}{\sigma} = \frac{\varphi(z_{[1-p]})}{p}$$

R code for i: `dnorm(qnorm(1-p))/p`

Truncation selection

- The fraction p saved can be translated into an expected selection intensity (assuming the trait is normally distributed),
  - allows a breeder (by setting p in advance) to chose an expected value of i before selection, and hence set the expected response

$$\bar{\imath} = \frac{S}{\sigma} = \frac{\varphi(z_{[1-p]})}{p}$$

Height of a unit normal at the threshold value corresponding to p

p	0.5	0.2	0.1	0.05	0.01	0.005
i	0.798	1.400	1.755	2.063	2.665	2.892

R code for i: `dnorm(qnorm(1-p))/p`

Selection Intensity Version of the Breeders' Equation

$$R = h^2 S = h^2 \frac{S}{\sigma_p} \sigma_p = i\, h^2 \sigma_p$$

Since $h^2\sigma_P = (\sigma^2_A/\sigma^2_P)\,\sigma_P = \sigma_A(\sigma_A/\sigma_P) = h\,\sigma_A$

$$R = i\, h\, \sigma_A$$

Since h = correlation between phenotypic and breeding values, $h = r_{PA}$

$$\boxed{R = i\, r_{PA} \sigma_A}$$

Response = Intensity * Accuracy * spread in Va

When we select an individual solely on their phenotype, the accuracy (correlation) between BV and phenotype is h

PAUSE

- Suppose that you save the upper 5% of a population each generation.
  - What is the selection intensity?
  - If $h^2 = 0.25$, how many generations of selection would be required to shift the trait mean by 5 phenotypic standard deviations?
  - Hint: recall that

$$R = i\, h^2\, \sigma_p$$

- Next pause at slide 25

- From table on slide 13, the selection intensity for 5% is i ~ 2
- $R/\sigma_P = i\ h^2$. Hence, with $h^2 = 0.25$, and i = 2, a single generation of selection gives $R/\sigma_P = 0.25*2 = ½$. Hence, 10 generations of selection gives a total response of 5 standard deviations.

Accuracy of selection

More generally, we can express the breeders equation as

$$\boxed{R = i\, r_{uA}\, \sigma_A}$$

Where we select individuals based on the index u (for example, the mean of n of their sibs).

r_{uA} = the accuracy of using the measure u to predict an individual's breeding value = correlation between u and an individual's BV, A

Example 10.4. **Progeny testing**, using the mean of a parent's offspring to predict the parent's breeding value, is an alternative predictor of an individual's breeding value. In this case, the correlation between the mean x of n offspring and the breeding value A of the parent is

$$\rho(x, A) = \sqrt{\frac{n}{n+a}}, \quad \text{where} \quad a = \frac{4-h^2}{h^2}$$

From Equation 10.11, the response to selection under progeny testing is

$$R = i\sigma_A \sqrt{\frac{n}{n+a}} = i\sigma_A \sqrt{\frac{h^2 n}{4 + h^2(n-1)}}$$

Note that for very large n that the accuracy approaches one. Progeny testing gives a larger response than simple selection on the phenotypes of the parents (**mass selection**) when

$$\sqrt{\frac{n}{4 + h^2(n-1)}} > 1, \quad \text{or} \quad n > \frac{4-h^2}{1-h^2}$$

In particular, $n > 4$, 5, and 7, for $h^2 = 0.1$, 0.25, and 0.5. Also note that the ratio of response for progeny testing (R_{pt}) to mass selection (R_{ms}) is just

$$\frac{R_{pt}}{R_{ms}} = \frac{1}{h}\sqrt{\frac{h^2 n}{4 + h^2(n-1)}} = \sqrt{\frac{n}{4 + h^2(n-1)}}$$

which approaches $1/h$ for large n.

Improving accuracy

- Predicting either the breeding or genotypic value from a single individual often has low accuracy --- h^2 and/or H^2 (based on a single individuals) is small
  - Especially true for many plant traits with high G x E
  - Need to replicate either clones or relatives (such as sibs) over regions and years to reduce the impact of G x E
  - Likewise, information from a set of relatives can give much higher accuracy than the measurement of a single individual

Stratified mass selection

- In order to accommodate the high environmental variance with individual plant values, Gardner (1961) proposed the method of stratified mass selection
  - Population stratified into a number of different blocks (i.e., sections within a field)
  - The best fraction p within each block are chosen
  - Idea is that environmental values are more similar among individuals within each block, increasing trait heritability.

Overlapping Generations

L_x = Generation interval for sex x
= Average age of parents when progeny are born

The yearly rate of response is

$$R_y = \frac{i_m + i_f}{L_m + L_f} h^2 \sigma_p$$

Trade-offs: Generation interval vs. selection intensity:
If younger animals are used (decreasing L), i is also lower,
as more of the newborn animals are needed as replacements

Computing generation intervals

OFFSPRING	Year 2	Year 3	Year 4	Year 5	total
Number (sires)	60	30	0	0	90
Number (dams)	400	600	100	40	1140

$$L_s = \frac{2 \cdot 60 + 3 \cdot 30}{60 + 30} = 2.33,$$

$$L_d = \frac{2 \cdot 400 + 3 \cdot 600 + 4 \cdot 100 + 5 \cdot 40}{400 + 600 + 100 + 40} = 2.81$$

Generalized Breeder's Equation

$$R_y = \frac{i_m + i_f}{L_m + L_f} \; r_{uA}\sigma_A$$

Tradeoff between generation length L and accuracy r

The longer we wait to replace an individual, the more accurate the selection (i.e., we have time for progeny testing and using the values of its relatives)

Example 10.8. As an example of the tradeoff between accuracy and generation intervals, consider a trait with $h^2 = 0.25$ and selection only on sires. One scheme is to simply select on the sire's phenotype, which results in a sire generation interval of 1.5 years. Alternatively, one might perform progeny testing to improve the accuracy of the selected sires. This results in an increase of the sire generation interval to (say) 2.5 years. Suppose in both cases, the dam interval is steady at 1.5 years.

Since the intensity of selection and additive genetic variation are the same in both schemes, the ratio of response under mass selection to response under progeny testing is just

$$\frac{R(\text{Sire phenotype})}{R(\text{progeny mean})} = \frac{\rho(A, \text{Sire phenotype})/(L_s + L_d)}{\rho(A, \text{progeny mean})/(L_s + L_d)}$$

Here, $\rho(A, \text{Sire phenotype}) = h = \sqrt{0.25} = 0.5$, with generation intervals $L_s + L_d = 1.5{+}1.5 = 3$. With progeny testing, (Example 10.4)

$$\rho(A, \text{progeny mean}) = \sqrt{\frac{n}{n+a}} = \sqrt{\frac{n}{n+15}}$$

as $a = (4 - h^2)/(h^2) = 15$, with a total generation interal of $L_s + L_d = 2.5{+}1.5 = 4$. Hence,

$$\frac{R(\text{Sire phenotype})}{R(\text{progeny mean})} = \frac{0.5/3.0}{\sqrt{\frac{n}{n+15}}/4} = \frac{2}{3} \cdot \sqrt{\frac{n+15}{n}}$$

If (say) $n = 2$ progeny are tested per sire, this ratio is 1.95, giving a much larger rate of response under sire-only selection. For $n = 12$, the ratio is exactly one, while for a very large number of offspring tested per sire, the ratio approaches 2/3, or a 1.5-fold increase in the rate of response under progeny testing, despite the increase in sire generation interval.

PAUSE

Most of the theory of optimal selection design is based on the generalized breeders equation

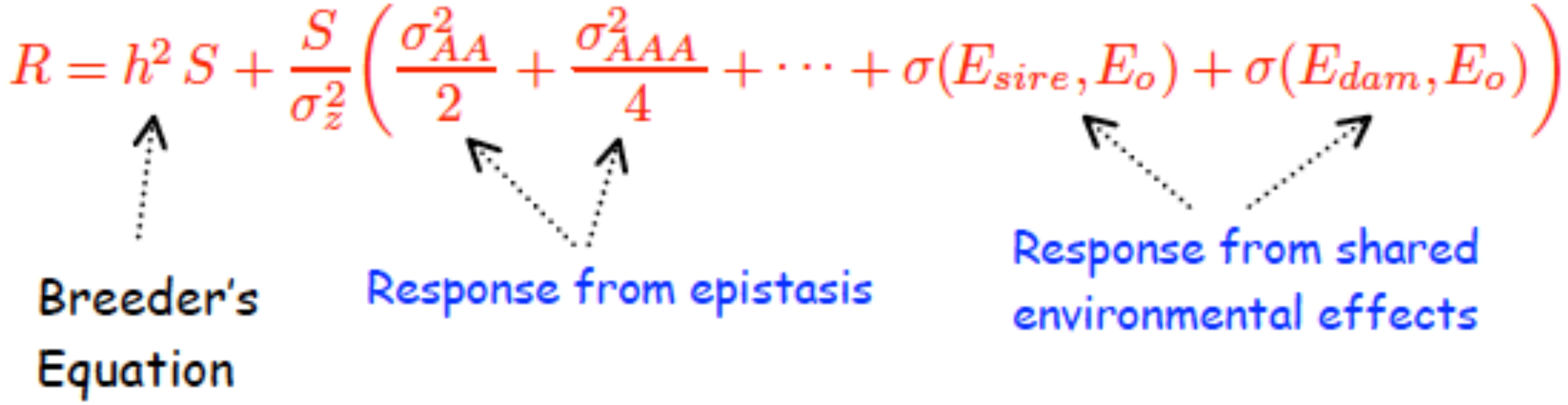
$$R_y = \frac{i_m + i_f}{L_m + L_f} \quad r_{uA} \sigma_A$$

i, L and r are components that a breeder can modify by their breeding design

Next PAUSE, slide 39

Permanent Versus Transient Response

Considering epistasis and shared environmental values, the single-generation response follows from the midparent-offspring regression



$$R = h^2\, S + \frac{S}{\sigma_z^2}\left(\frac{\sigma^2_{AA}}{2} + \frac{\sigma^2_{AAA}}{4} + \cdots + \sigma(E_{sire}, E_o) + \sigma(E_{dam}, E_o)\right)$$

Breeder's Equation

Response from epistasis

Response from shared environmental effects

Permanent component of response

Transient component of response --- contributes to short-term response. Decays away to zero over the long-term

Permanent Versus Transient Response

The reason for the focus on h^2S is that this component is permanent in a random-mating population, while the other components are transient, initially contributing to response, but this contribution decays away under random mating

Why? Under HW, changes in allele frequencies are permanent (don't decay under random-mating), while LD (epistasis) does, and environmental values also become randomized

Response with Epistasis

The response after one generation of selection from an unselected base population with A x A epistasis is

$$R = S\left(h^2 + \frac{\sigma^2_{AA}}{2\,\sigma^2_z}\right)$$

The contribution to response from this single generation after τ generations of no selection is

$$R(1+\tau) = S\left(h^2 + (1-c)^\tau \frac{\sigma^2_{AA}}{2\sigma^2_z}\right)$$

c is the average (pairwise) recombination between loci involved in A x A

Response with Epistasis

$$R(1+\tau) = S\left(h^2 + (1-c)^\tau \frac{\sigma^2_{AA}}{2\sigma^2_z}\right)$$

Response from additive effects (h^2 S) is due to changes in allele frequencies and hence is permanent. Contribution from A x A due to linkage disequilibrium

Contribution to response from epistasis decays to zero as linkage disequilibrium decays to zero

Why breeder's equation assumption of an unselected base population? If history of previous selection, linkage disequilibrium may be present and the mean can change as the disequilibrium decays

For t generation of selection followed by
τ generations of no selection (but recombination)

$$R(t+\tau) = t\,h^2\,S + (1-c)^{\tau}\,R_{AA}(t)$$

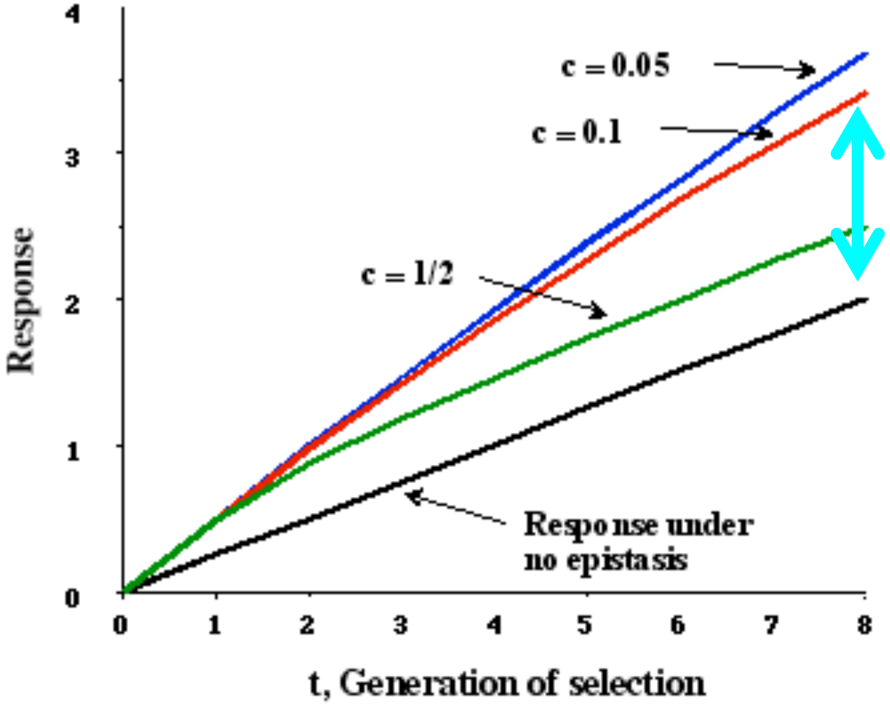
R_{AA} has a limiting value given by

$$\widetilde{R}_{AA} = \lim_{t\to\infty} R_{AA}(t) = \frac{1}{c}\left(S\,\frac{\sigma^2_{AA}}{2\,\sigma^2_z}\right)$$

Time to equilibrium a function of c

$$t_{1/2} = \frac{-\ln(2)}{\ln(1-c)}$$

Decay half-life



$$= \frac{1}{c}\left(S\,\frac{\sigma^2_{AA}}{2\,\sigma^2_z}\right)$$

Fixed incremental difference that decays when selection stops

What about response with higher-order epistasis?

$S\sigma^2(A^i)/\sigma^2_z$,	AA	AAA	AAAA	AAAAA
$R(1)$	0.500	0.250	0.125	0.063
Limit	1.000	0.333	0.143	0.067
% $R(1)$/limit	50.0	75.0	87.5	93.8

Response in autotetraploids

- Autotetraploids pass along two alleles at each locus to their offspring
- Hence, dominance variance is passed along
- However, as with A x A, this depends upon favorable combinations of alleles, and these are randomized over time by transmission, so D component of response is transient.

Autotetraploids

P-O covariance

$$\sigma(z_p, z_o) = \frac{\sigma_A^2}{2} + \frac{\sigma_D^2}{6},$$

Single-generation response

$$R = S\left(h^2 + \frac{\sigma_D^2}{3\sigma_z^2}\right)$$

Response to t generations of selection with constant selection differential S

$$R(t) = th^2S + R_D(t)$$

$$R_D(t) = S\,\frac{3}{2}\left[1 - \left(\frac{1}{3}\right)^t\right]\frac{\sigma_D^2}{3\sigma_z^2}$$

Response remaining after t generations of selection followed by τ generations of random mating

$$t\,h^2\,S + (1/3)^\tau\,R_D(t)$$

Contribution from dominance quickly decays to zero

Maternal Effects:

Falconer’s dilution model

$$z = G + m\, z_{dam} + e$$

G = Direct genetic effect on character

$G = A + D + I$. $E[A] = (A_{sire} + A_{dam})/2$

maternal effect passed from dam to offspring $m\, z_{dam}$ is just a fraction m of the dam’s phenotypic value

The presence of the maternal effects means that response is not necessarily linear and time lags can occur in response

m can be negative --- results in the potential for a reversed response

Parent-offspring regression under the dilution model

In terms of parental breeding values,

$$E(z_o \mid A_{dam}, A_{sire}, z_{dam}) = \frac{A_{dam}}{2} + \frac{A_{sire}}{2} + m\, z_{dam}$$

Regression of BV on phenotype

$$A = \mu_A + b_{Az}\,(z - \mu_z) + e$$

The resulting slope becomes $b_{Az} = h^2\, 2/(2-m)$

With no maternal effects, $b_{az} = h^2$

Parent-offspring regression under the dilution model

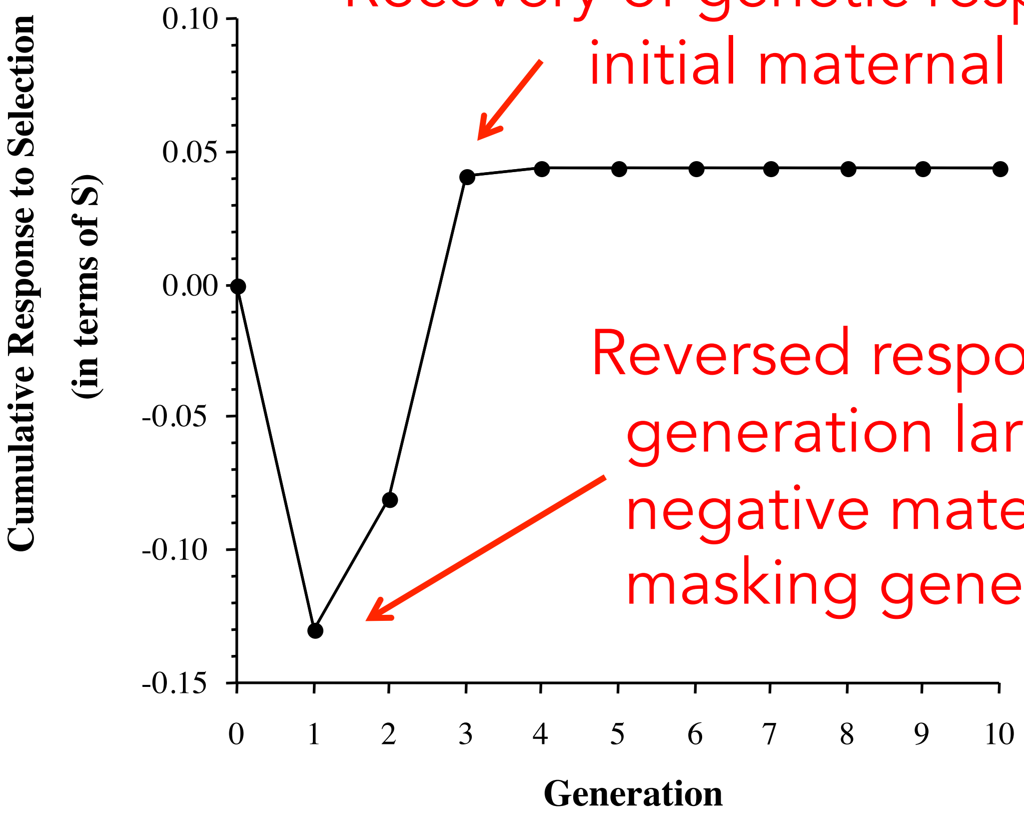
With maternal effects, a covariance between BV and maternal effect arises, with $\sigma_{A,M} = m\,\sigma_A^2 \,/\, (2 - m)$

The response thus becomes

$$\Delta\mu_z = S_{dam}\left(\frac{h^2}{2 \quad m} + m\right) + S_{sire}\,\frac{h^2}{2 - m}$$

Response to a single generation of selection

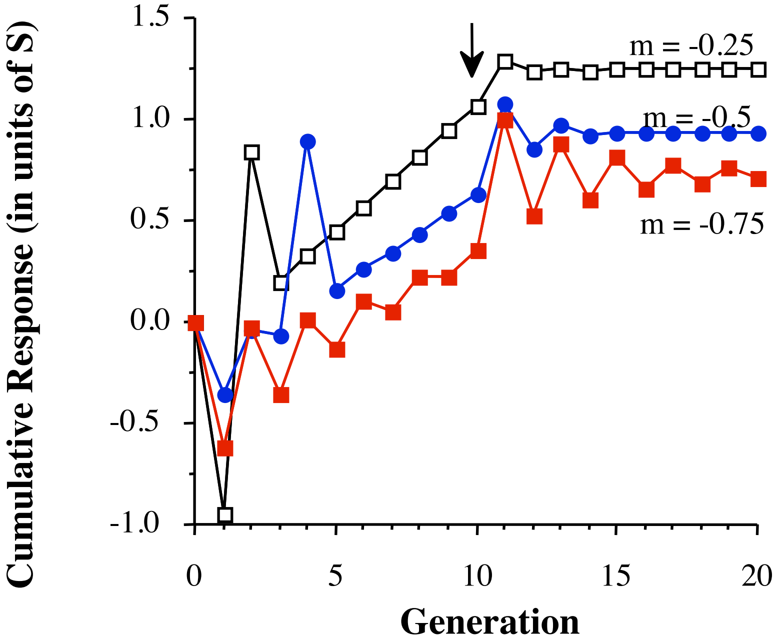
$h^2 = 0.11$, $m = -0.13$ (litter size in mice)



Recovery of genetic response after initial maternal correlation decays

Reversed response in 1st generation largely due to negative maternal correlation masking genetic gain

Selection occurs for 10 generations and then stops



$h^2 = 0.35$

PAUSE

- All of the above focus has been on change in the mean.

- Predicting change in the variance is more complicated, as allele frequencies can change. The next few slides examine the Bulmer Equation, which predicts the short-term change from linkage disequilbirium (WL Chapter 16). Changes in the variance from allele frequencies are examined in WL Chapters 24-26

Additional material

The Bulmer Equation

(Not covered in class)

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

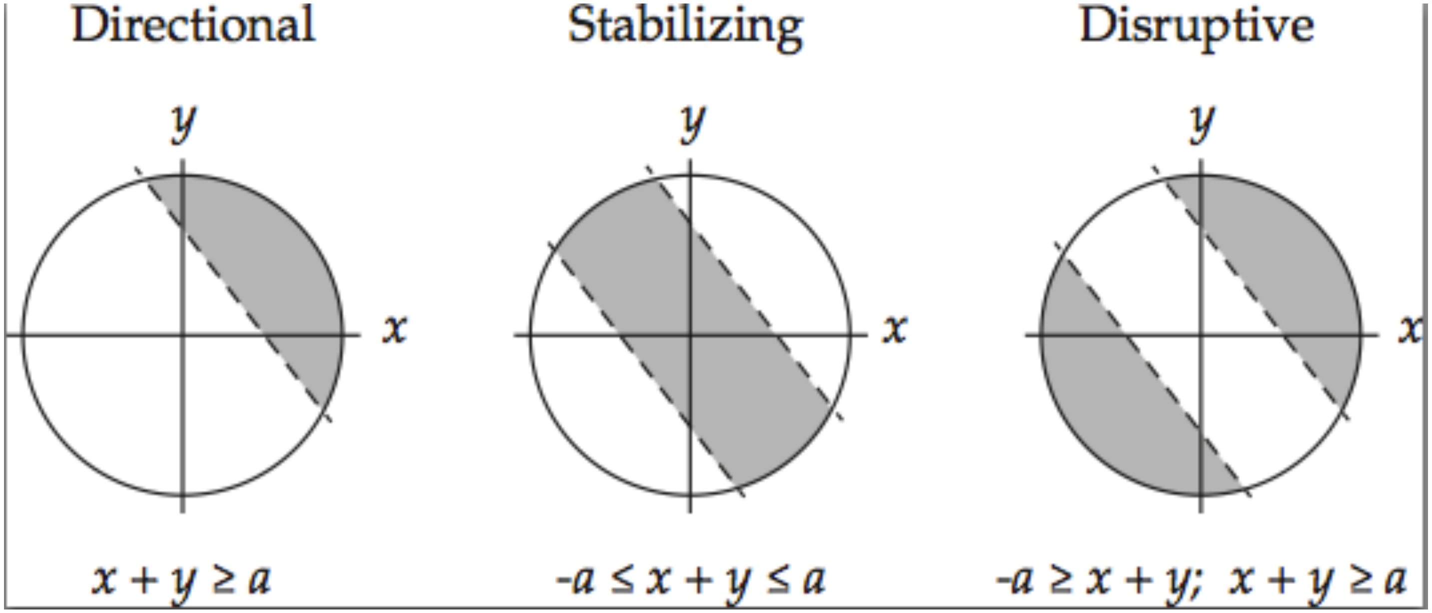
However, can have significant change in genetic variances due to selection creating linkage disequilibrium

Under **linkage equilibrium**, freq(AB gamete) = freq(A)freq(B)

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

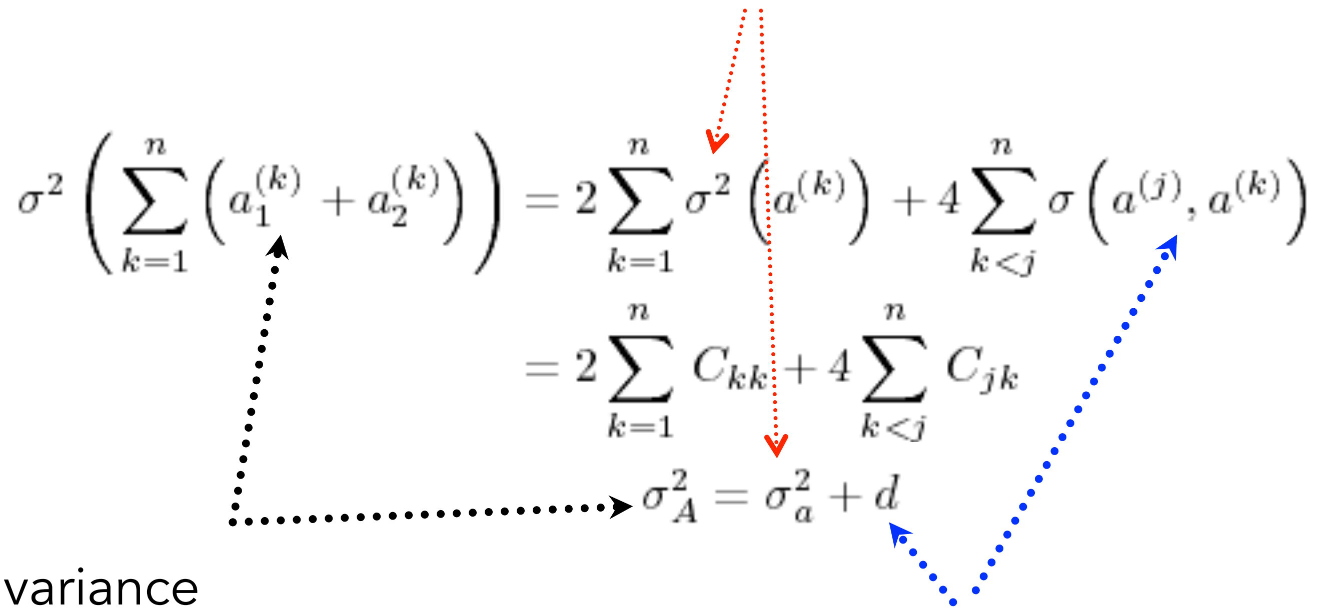
Selection that reduces the variance generates negative d, selection that increases the variance generates positive d



Additive variance with LD:

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

Genic variance: value of Var(A)
in the absence of disequilibrium
function of allele frequencies



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

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

$$\sigma_A^2=\sigma_a^2+d$$

Additive variance

Disequilibrium contribution. Requires covariances
between allelic effects at different loci

Key: Under the infinitesimal model, no (selection-induced) changes in genic variance σ^2_a

Selection-induced changes in d change σ^2_A, σ^2_z , h^2

$$\sigma^2_z(t) = \sigma^2_E + \sigma^2_D + \sigma^2_A(t) = \sigma^2_z + d(t)$$

$$h^2(t) = \frac{\sigma^2_A(t)}{\sigma^2_z(t)} = \frac{\sigma^2_a + d(t)}{\sigma^2_z + d(t)}$$

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

$$\begin{aligned}\sigma^2(z_o) &= \frac{h^4}{4}\left[\,\sigma^2(z_m^*) + \sigma^2(z_f^*)\right] + \sigma_e^2\\ &= \frac{h^4}{2}\left[\,\sigma_z^2 + \delta(\sigma_z^2)\right] + \left(1 - \frac{h^4}{2}\right)\sigma_z^2\\ &= \sigma_z^2 + \frac{h^4}{2}\,\delta(\sigma_z^2)\end{aligned}$$

Change in variance from selection

Change in d = change from recombination plus change from selection

$d(t+1) = \frac{d(t)}{2}$ + $\frac{h^4}{2}\delta(\sigma_z^2)$ = $d(t+1) = \frac{d(t)}{2} + \frac{h^4(t)}{2}\,\delta\left(\sigma^2_{z(t)}\right)$

Recombination Selection

In terms of change in d,

$$\begin{aligned}\Delta d(t) = \Delta\sigma^2_{z(t)} &= \Delta\sigma^2_A(t)\\ &= -\frac{d(t)}{2} + \frac{h^4(t)}{2}\,\delta\left(\sigma^2_{z(t)}\right)\end{aligned}$$

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,

$$\widetilde{d} = \widetilde{h}^4\,\widetilde{\delta}(\sigma_z^2)$$

Application: Egg Weight in Ducks

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

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

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

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 $h^2 = 0.62$

Specific models of selection-induced changes in variances

Proportional reduction model: constant fraction k of variance removed

$$\sigma^2_{z*} = (1-\kappa)\,\sigma^2_z$$

$$\delta\left(\sigma^2_z\right) = \sigma^2_{z*} - \sigma^2_z = -\kappa\,\sigma^2_z$$

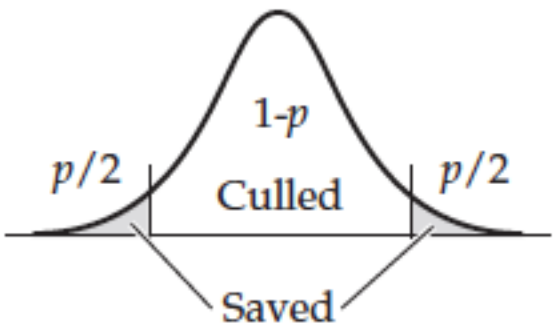
Bulmer equation simplifies to

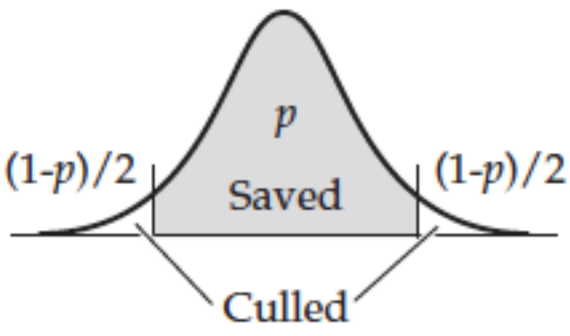
$$d(t+1) = \frac{d(t)}{2} - \frac{\kappa}{2}\,h^2(t)\,\sigma^2_A(t)$$

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

Closed-form solution to equilibrium h^2

$$\widetilde{h}^2 = \frac{-1+\sqrt{1+4h^2(1-h^2)\kappa}}{2\,\kappa\,(1-h^2\,)}$$


Disruptive selection


Stabilizing selection

Directional Truncation Selection: Uppermost (or lowermost) p saved

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

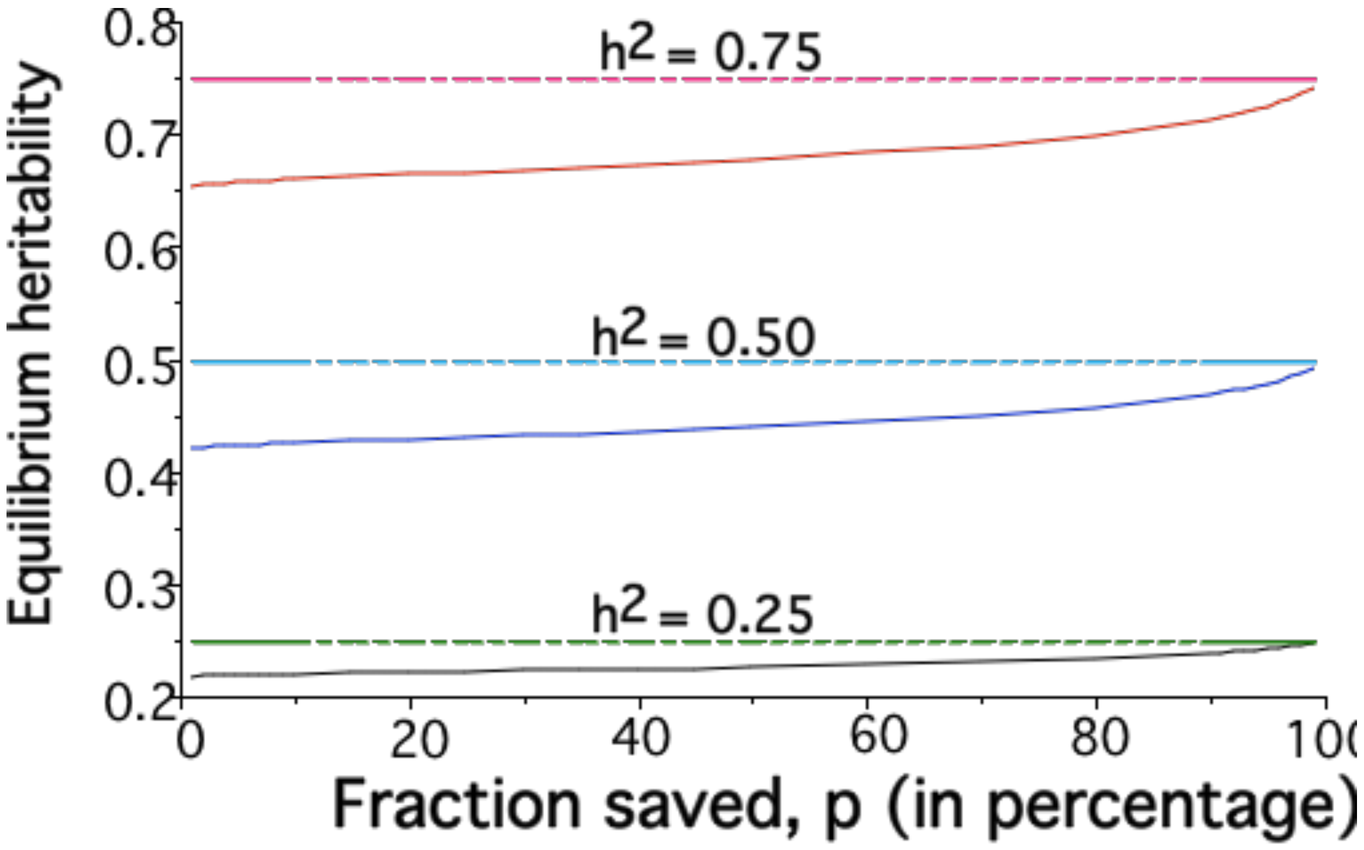
Stabilizing Truncation Selection: Middle fraction p of the distribution saved

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

DisruptiveTruncation Selection: Uppermost and lowermost $p/2$ saved

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

Equilibrium h^2 under direction truncation selection



Directional truncation selection

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

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

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

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

$$\bar{\imath} = \varphi(0.84)/p = 0.2803/0.20 = 1.402$$

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

$$\kappa = 1.402\,(1.402 - 0.84) = 0.787.$$

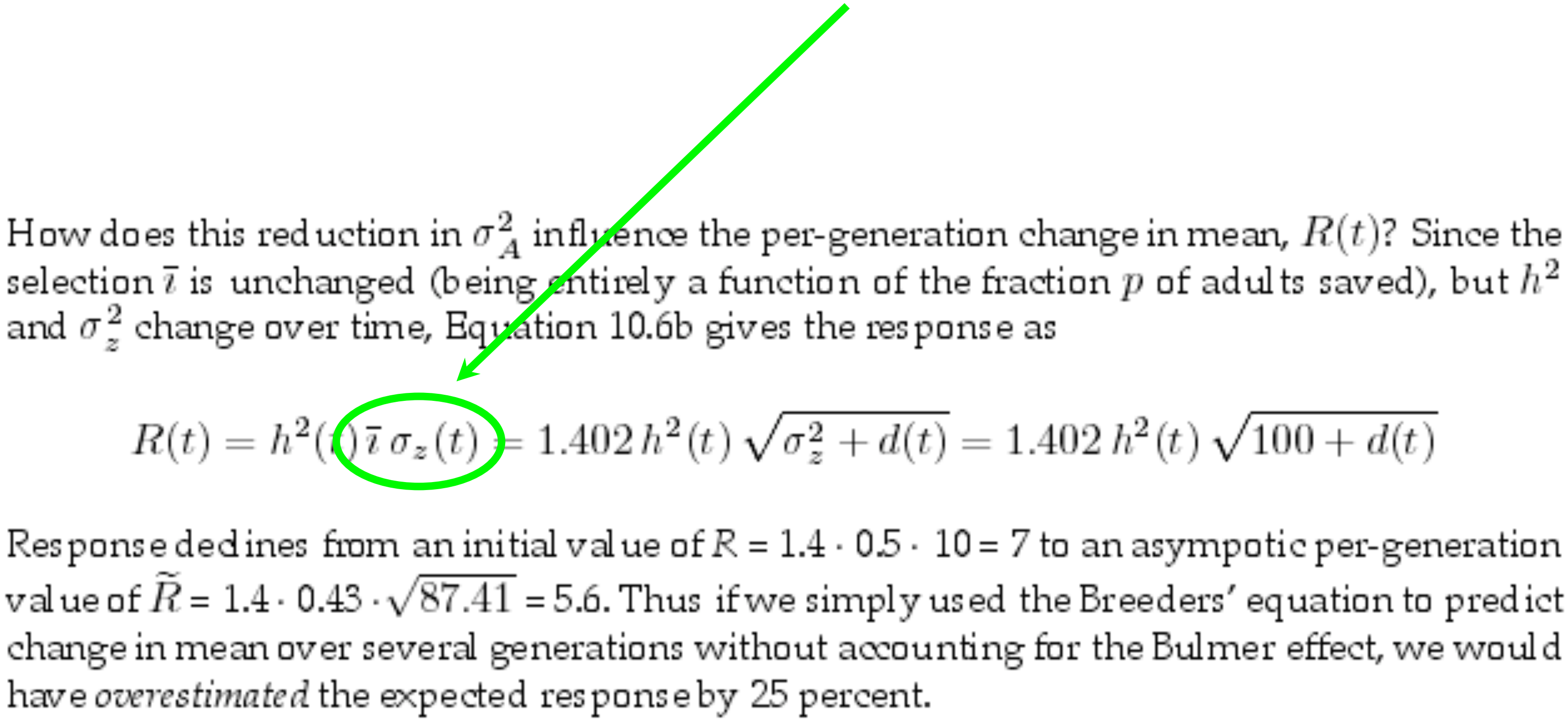
Hence, Equation 13.12 gives

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

Generation	0	1	2	3	4	5	∞
$d(t)$	0.00	–9.84	–11.96	–12.45	–12.56	–12.59	–12.59
$\sigma_A^2(t)$	50.00	40.16	38.04	37.55	37.44	37.41	37.41
$h^2(t)$	0.50	0.45	0.43	0.43	0.43	0.43	0.43

Changes in the variance = changes in h^2 and even S (under truncation selection)

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



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

$$R(t) = h^2(t)\, \bar{\imath}\, \sigma_z(t) = 1.402\, h^2(t)\, \sqrt{\sigma^2_z + d(t)} = 1.402\, h^2(t)\, \sqrt{100 + d(t)}$$

Response declines from an initial value of $R = 1.4 \cdot 0.5 \cdot 10 = 7$ to an asympotic per-generation value of $\widetilde{R} = 1.4 \cdot 0.43 \cdot \sqrt{87.41} = 5.6$. 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.