

Lecture 3: Univariate and Multivariate Selection

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Response to Selection

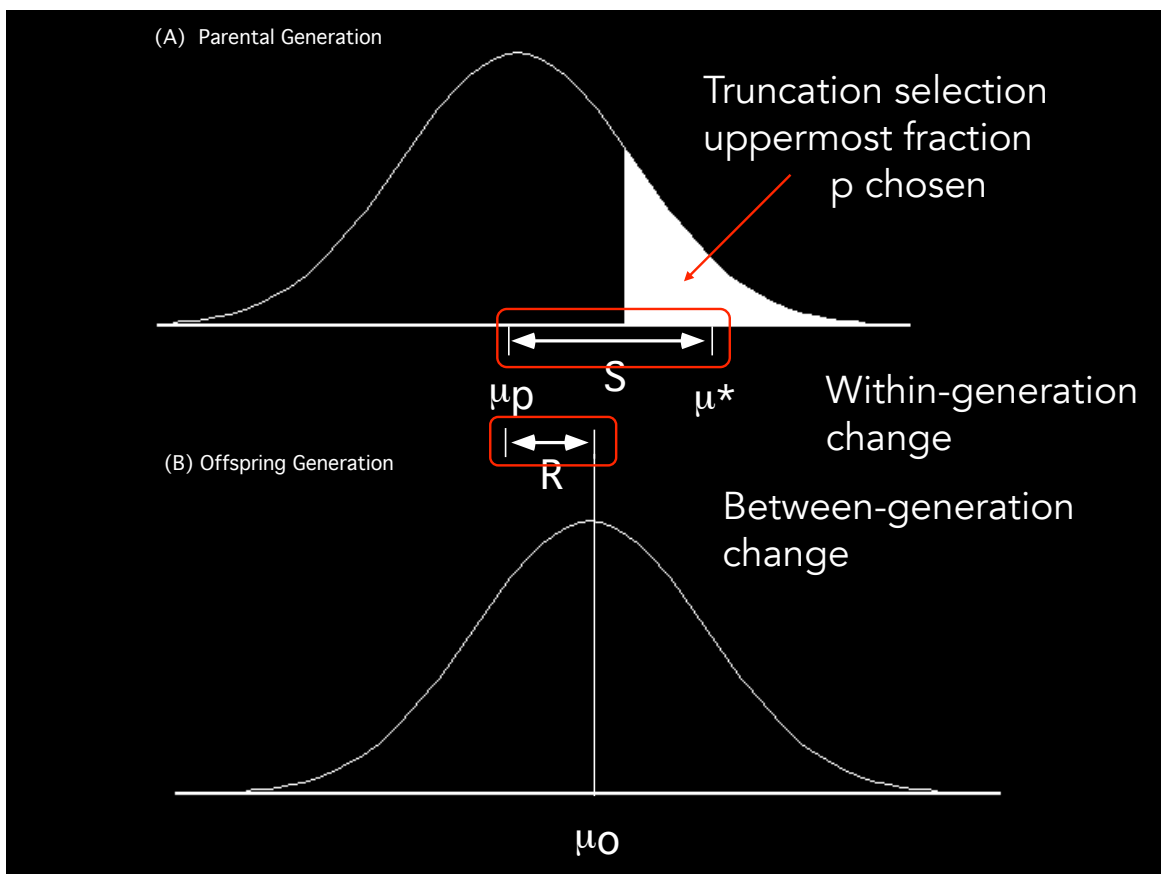
- Selection can change the distribution of phenotypes, and we typically measure this by changes in mean
 - This is a **within-generation change**
- Selection can also change the **distribution of breeding values**
 - This is the **response to selection**, the change in the trait in the next generation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

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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
 - $R(t) = \mu(t+1) - \mu(t)$

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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:

$$R = h^2 S$$

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,
 - $S = (S_f + S_m)/2$

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

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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 broad 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.

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Price-Robertson identity

- $S = \text{cov}(w, z)$
- The covariance between trait value z and relative fitness ($w = W/\bar{W}$, scaled to have mean fitness = 1)
- VERY! Useful result
- $R = \text{cov}(w, A_z)$, as response = within generation change in BV
 - This is called [Robertson's secondary theorem of natural selection](#)

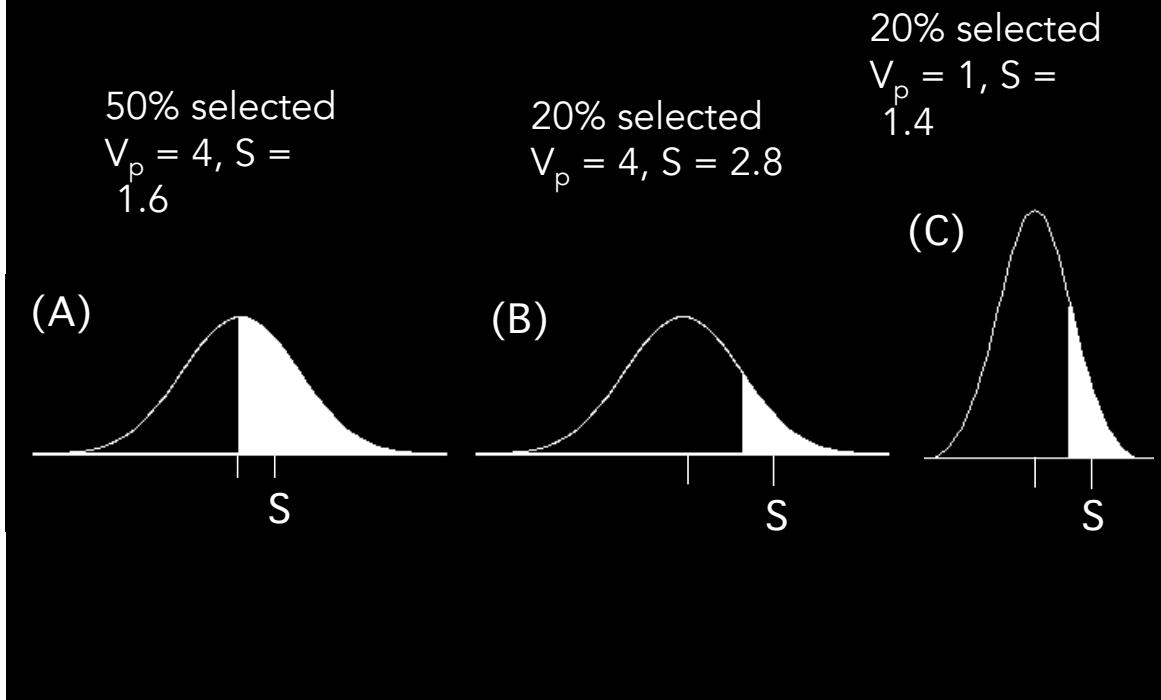
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Response over multiple generations

- Strictly speaking, the breeders' equation only holds for predicting a **single generation** of response from an **unselected base population**
- Practically speaking, the breeders' equation is usually pretty good for 5-10 generations
- The validity for an initial h^2 predicting response over several generations depends on:
 - The reliability of the initial h^2 estimate
 - Absence of environmental change between generations
 - The absence of genetic change between the generation in which h^2 was estimated and the generation in which selection is applied

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



The Selection Intensity, i

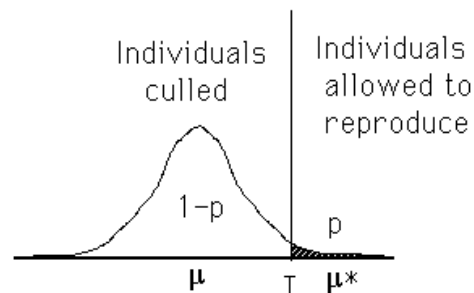
As the previous example shows, populations with the same selection differential (S) may experience very different amounts of selection

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

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

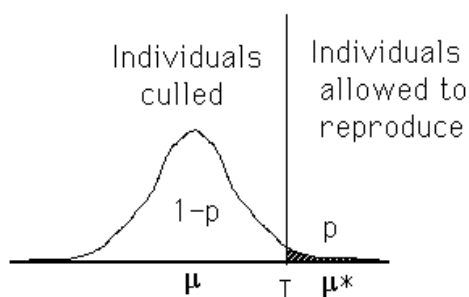
Truncation selection

- 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



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Selection Differential Under Truncation Selection



$$S = \mu^* - \mu$$

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

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

R code for \bar{i} : `dnorm(qnorm(1-p)) / p`

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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

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

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`

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Selection Intensity Version of the Breeders' Equation

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

$$\text{Since } h^2 \sigma_p = (\sigma_A^2 / \sigma_p^2) \sigma_p = \sigma_A (\sigma_A / \sigma_p) = h \sigma_A$$

$$R = i h \sigma_A$$

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

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

$$\text{Response} = \text{Intensity} * \text{Accuracy} * \text{spread in } V_a$$

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

Accuracy of selection

More generally, we can express the breeders equation as

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

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

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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

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

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

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

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 $n.$

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

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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

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

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

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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)

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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 interval 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.

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**, $\text{freq}(AB \text{ gamete}) = \text{freq}(A)\text{freq}(B)$

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

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Additive variance with LD:

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

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

$$\begin{aligned} \sigma^2 \left(\sum_{k=1}^n (a_1^{(k)} + a_2^{(k)}) \right) &= 2 \sum_{k=1}^n \sigma^2 (a^{(k)}) + 4 \sum_{k < j}^n \sigma (a^{(j)}, a^{(k)}) \\ &= 2 \sum_{k=1}^n C_{kk} + 4 \sum_{k < j}^n C_{jk} \\ &\rightarrow \sigma_A^2 = \sigma_a^2 + d \end{aligned}$$

Additive variance

Disequilibrium contribution. Requires covariances between allelic effects at different loci

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

Selection-induced changes in d change $\sigma_A^2, \sigma_z^2, h^2$

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

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

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

$$d(t+1) = \frac{d(t)}{2}$$

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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

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

Change in variance from selection

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Change in d = change from recombination plus change from selection

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

Recombination Selection

In terms of change in d ,

$$\Delta d(t) = \Delta \sigma_{z(t)}^2 = \Delta \sigma_A^2(t)$$

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

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,

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

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Application: Egg Weight in Ducks

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

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

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

$\text{Var}(A) = 0.6 \cdot 52.7 = 31.6$. If selection stops, $\text{Var}(A)$ is expected to increase to $31.6 + 3.2 = 34.8$

$\text{Var}(z)$ should increase to 55.9, giving $h^2 = 0.62$

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Specific models of selection-induced changes in variances

Proportional reduction model:

$$\sigma_{z^*}^2 = (1 - \kappa) \sigma_z^2$$

constant fraction κ of variance removed

$$\delta(\sigma_z^2) = \sigma_{z^*}^2 - \sigma_z^2 = -\kappa \sigma_z^2$$

Bulmer equation simplifies to

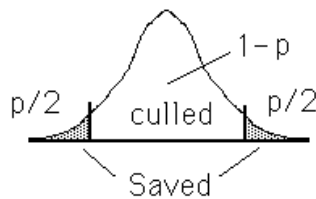
$$\begin{aligned} d(t+1) &= \frac{d(t)}{2} - \frac{\kappa}{2} h^2(t) \sigma_A^2(t) \\ &= \frac{d(t)}{2} - \frac{\kappa}{2} \frac{[\sigma_a^2 + d(t)]^2}{\sigma_z^2 + d(t)} \end{aligned}$$

Closed-form solution to equilibrium h^2

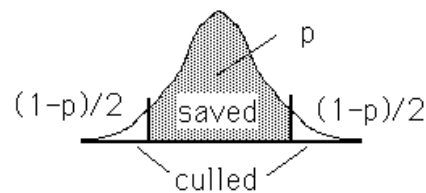
$$\tilde{h}^2 = \frac{-1 + \sqrt{1 + 4h^2(1 - h^2)\kappa}}{2\kappa(1 - h^2)}$$

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Disruptive Selection



Stabilizing Selection



Directional Truncation Selection: Uppermost (or lowermost) p saved

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

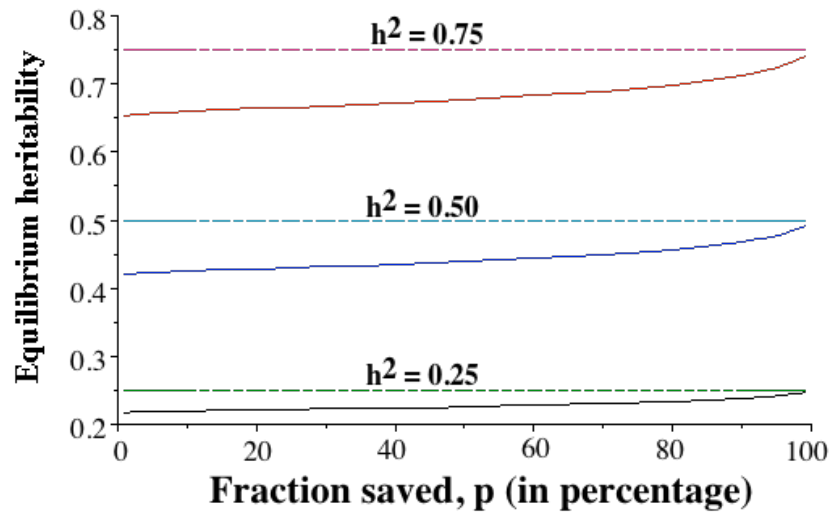
Stabilizing Truncation Selection: Middle fraction p of the distribution saved

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

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

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

Equilibrium h^2 under direction truncation selection



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Directional truncation selection

$$\kappa = \bar{\tau} (\bar{\tau} - z_{[1-p]})$$

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,

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

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

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

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

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

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

Response declines from an initial value of $R = 1.4 \cdot 0.5 \cdot 10 = 7$ to an 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.

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Multivariate Selection

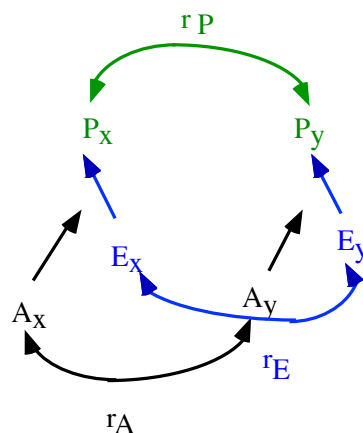
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Genetic vs. Phenotypic correlations

- Within an individual, trait values can be positively or negatively correlated,
 - height and weight -- positively correlated
 - Weight and lifespan -- negatively correlated
- Such phenotypic correlations can be directly measured,
 - r_p denotes the phenotypic correlation
- Phenotypic correlations arise because genetic and/or environmental values within an individual are correlated.

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The phenotypic values between traits x and y within an individual are correlated



Correlations between the breeding values of x and y within the individual can generate a phenotypic correlation

Likewise, the environmental values for the two traits within the individual could also be correlated

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Genetic & Environmental Correlations

- r_A = correlation in breeding values (the **genetic correlation**) can arise from
 - pleiotropic effects of loci on both traits
 - linkage disequilibrium, which decays over time
- r_E = correlation in environmental values
 - includes non-additive genetic effects (e.g., D, I)
 - arises from exposure of the two traits to the same individual environment

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The relative contributions of genetic and environmental correlations to the phenotypic correlation

$$r_P = r_A h_X h_Y + r_E \sqrt{(1 - h_X^2)(1 - h_Y^2)}$$

If heritability values are high for both traits, then the correlation in breeding values dominates the phenotypic correlation

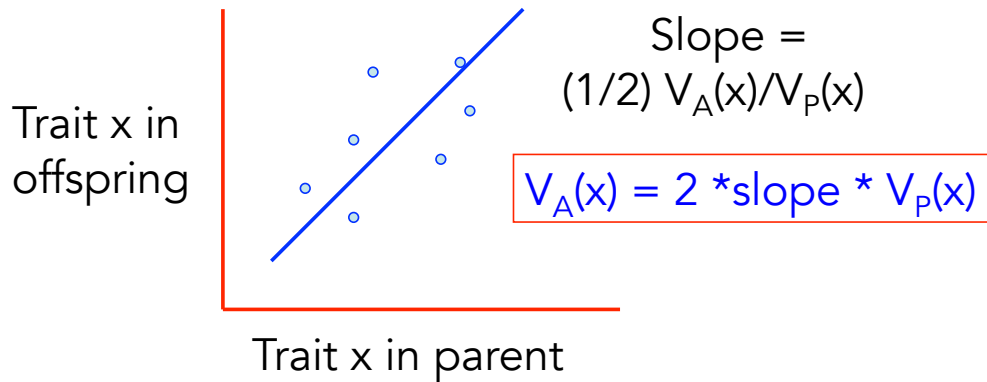
If heritability values in EITHER trait are low, then the correlation in environmental values dominates the phenotypic correlation

In practice, phenotypic and genetic correlations often have the same sign and are of similar magnitude, but this is not always the case

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Estimating Genetic Correlations

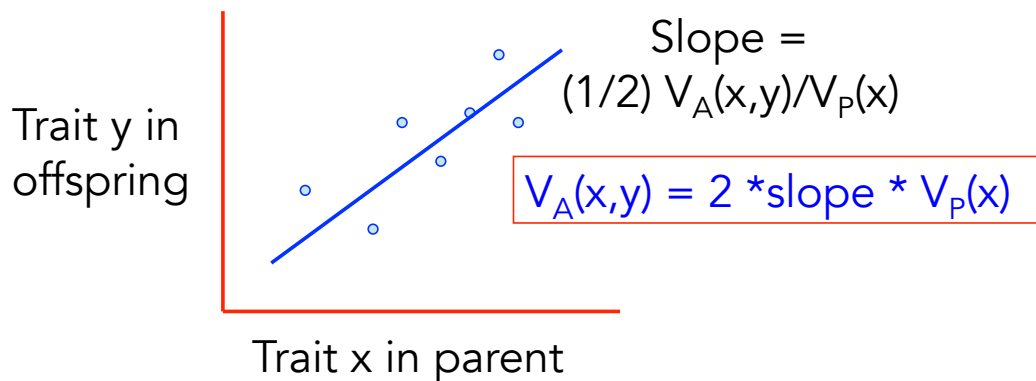
Recall that we estimated V_A from the regression of trait x in the parent on trait x in the offspring,



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Estimating Genetic Correlations

Similarly, we can estimate $V_A(x,y)$, the covariance in the breeding values for traits x and y , by the regression of trait x in the parent and trait y in the offspring



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Thus, one estimator of $V_A(x,y)$ is

$$V_A(x,y) = \frac{2 * b_{y|x} * V_P(x) + 2 * b_{x|y} * V_P(y)}{2}$$

giving

$$V_A(x,y) = b_{y|x} V_P(x) + b_{x|y} V_P(y)$$

Put another way,

$$\text{Cov}(x_O, y_P) = \text{Cov}(y_O, x_P) = (1/2)\text{Cov}(A_x, A_y)$$

$$\text{Cov}(x_O, x_P) = (1/2) V_A(x) = (1/2)\text{Cov}(A_x, A_x)$$

$$\text{Cov}(y_O, y_P) = (1/2) V_A(y) = (1/2)\text{Cov}(A_y, A_y)$$

Likewise, for half-sibs,

$$\text{Cov}(x_{HS}, y_{HS}) = (1/4) \text{Cov}(A_x, A_y)$$

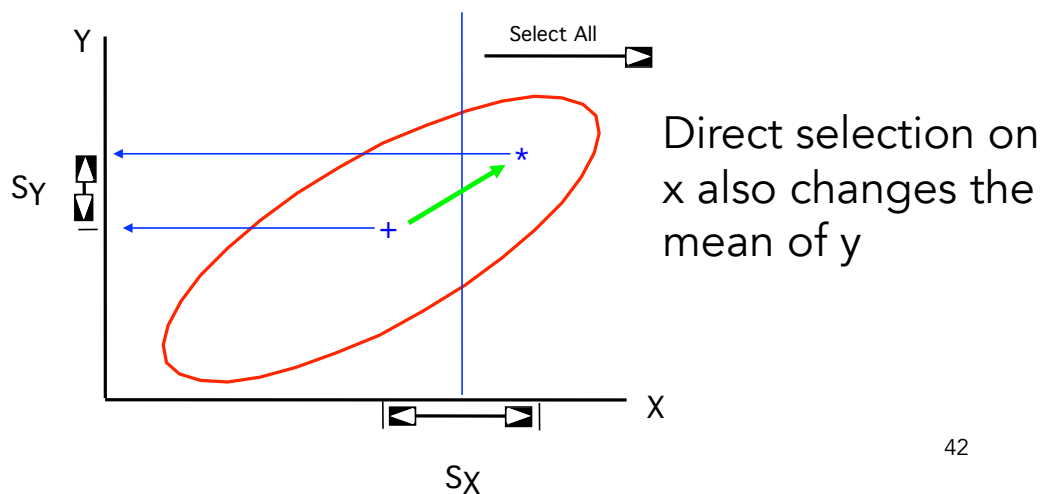
$$\text{Cov}(x_{HS}, x_{HS}) = (1/4) \text{Cov}(A_x, A_x) = (1/4) V_A(x)$$

$$\text{Cov}(y_{HS}, y_{HS}) = (1/4) \text{Cov}(A_y, A_y) = (1/4) V_A(y)$$

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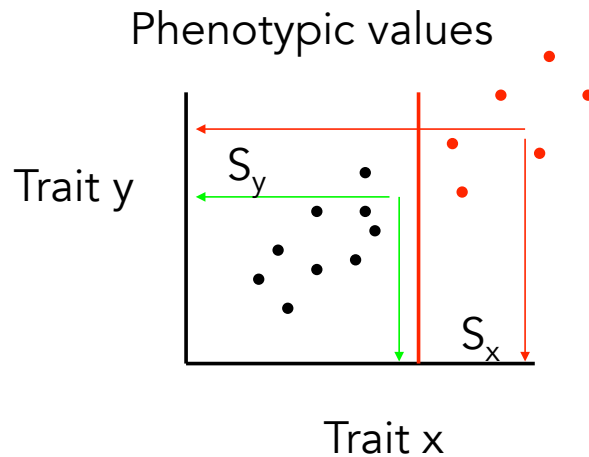
Correlated Response to Selection

Direct selection of a character can cause a within-generation change in the mean of a phenotypically correlated character.



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Phenotypic correlations induce **within-generation changes**



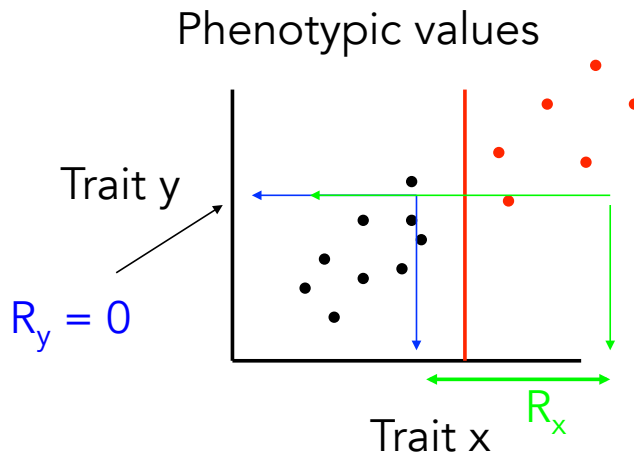
For there to be a **between-generation change**, the **breeding values must be correlated**. Such a change is called a **correlated response to selection**

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Example

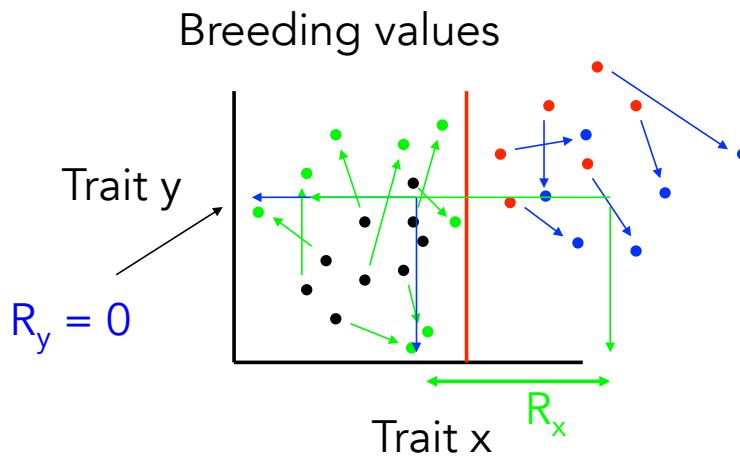
- Suppose h^2 trait x = 0.5, h^2 trait y = 0.3
- Select on trait one to give $S_x = 10$
 - Expected response is $R_x = 5$
- Suppose $\text{Cov}(t_x, t_y) = 0.5$, then $S_y = 5$
- What is the response in trait 2?
 - is it $CR_y = 0.3 \cdot 5 = 1.5$. NO!
 - Could be positive, negative, or zero
 - Depends on the Genetic correlation between traits x and y. Why??

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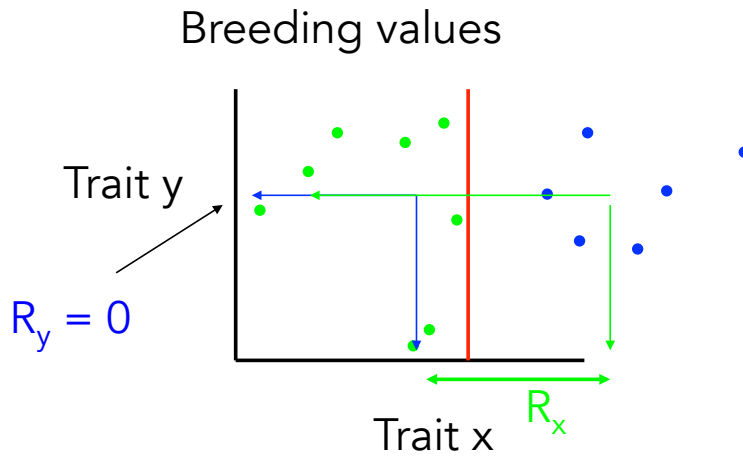


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Phenotypic values are misleading, what we want are the breeding values for each of the selected individuals. Each arrow takes an individual's phenotypic value into its actual breeding value.



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Predicting the correlated response

The change in character y in response to selection on x is the regression of the breeding value of y on the breeding value of x ,

where

$$A_y = b_{A_y|A_x} A_x$$

$$b_{A_y|A_x} = \frac{\text{Cov}(A_x, A_y)}{\text{Var}(A_x)} = r_A \frac{\sigma(A_y)}{\sigma(A_x)}$$

If R_x denotes the direct response to selection on x , CR_y denotes the correlated response in y , with

$$CR_y = b_{A_y|A_x} R_x$$

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We can rewrite $CR_y = b_{Ay|Ax} R_x$ as follows

First, note that $R_x = h_x^2 S_x = i_x h_x \sigma_A(x)$

↑
Recall that $i_x = S_x / \sigma_P(x)$
(x) is the selection intensity on x

Since $b_{Ay|Ax} = r_A \sigma_A(x) / \sigma_A(y)$,

We have $CR_y = b_{Ay|Ax} R_x = r_A \sigma_A(y) h_x i_x$

Substituting $\sigma_A(y) = h_y \sigma_P(y)$ gives our final result:

$$CR_y = i_x h_x h_y r_A \sigma_P(y)$$

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$$CR_y = i_x h_x h_y r_A \sigma_P(y)$$

Noting that we can also express the direct response as $R_x = i_x h_x^2 \sigma_P(x)$

shows that $h_x h_y r_A$ in the corrected response plays the same role as h_x^2 does in the direct response. As a result, $h_x h_y r_A$ is often called the **co-heritability**

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Direct vs. Indirect Response

We can change the mean of x via a direct response R_x or an indirect response CR_x due to selection on y

$$\frac{CR_x}{R_x} = \frac{i_Y r_A \sigma_{AX} h_Y}{i_X h_X \sigma_{AX}} = \frac{i_Y r_A h_Y}{i_X h_X}$$

Hence, indirect selection gives a large response when

$$i_Y r_A h_Y > i_X h_X$$

- The selection intensity is much greater for y than x . This would be true if y were measurable in both sexes but x measurable in only one sex.
- Character y has a greater heritability than x , and the genetic correlation between x and y is high. This could occur if x is difficult to measure with precision but y is not.

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Matrices

$$\mathbf{A} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \quad \mathbf{B} = \begin{pmatrix} e & f \\ g & h \end{pmatrix} \quad \mathbf{C} = \begin{pmatrix} i \\ j \end{pmatrix}$$

Dimensions given by rows x columns ($r \times c$)

The identity matrix \mathbf{I} , $\mathbf{I}_{2 \times 2} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$

Matrix Multiplication

$$\mathbf{AB} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} e & f \\ g & h \end{pmatrix}$$
$$= \begin{pmatrix} ae + bg & af + bh \\ ce + dg & cf + dh \end{pmatrix}$$

In order to multiply two matrices, they must conform

$$A_{r \times c} B_{c \times k} = C_{r \times k}$$

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Matrix Multiplication

$$\mathbf{A} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \quad \mathbf{B} = \begin{pmatrix} e & f \\ g & h \end{pmatrix} \quad \mathbf{C} = \begin{pmatrix} i \\ j \end{pmatrix}$$

$$\mathbf{BA} = \begin{pmatrix} ae + cf & eb + df \\ ga + ch & gd + dh \end{pmatrix} \quad \mathbf{AC} = \begin{pmatrix} ai + bj \\ ci + dj \end{pmatrix}$$

The **identity matrix I** serves the role of one in matrix multiplication: $\mathbf{AI} = \mathbf{A}$, $\mathbf{IA} = \mathbf{A}$


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The Inverse Matrix, A^{-1}

For a square matrix A , define the **Inverse** of A , A^{-1} , as the matrix satisfying

$$A^{-1}A = AA^{-1} = I$$

For $A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$ $A^{-1} = \frac{1}{ad-bc} \begin{pmatrix} d & -b \\ -c & a \end{pmatrix}$



If this quantity (the determinant) is zero, the inverse does not exist.

The inverse serves the role of division in matrix multiplication

Suppose we are trying to solve the system $Ax = c$ for x .

$$A^{-1}Ax = A^{-1}c. \text{ Note that } A^{-1}Ax = Ix = x, \text{ giving } x = A^{-1}c$$

The Multivariate Breeders' Equation

Suppose we are interested in the vector \mathbf{R} of Responses when selection occurs on n correlated traits

Let \mathbf{S} be the vector of selection differentials.

In the univariate case, the relationship between \mathbf{R} and \mathbf{S} was the Breeders' Equation, $\mathbf{R} = h^2\mathbf{S}$

What is the multivariate version of this?

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$$\mathbf{S} = \begin{pmatrix} S_1 \\ S_2 \\ \vdots \\ S_n \end{pmatrix} \quad \mathbf{R} = \begin{pmatrix} R_1 \\ R_2 \\ \vdots \\ R_n \end{pmatrix}$$

$$\mathbf{P} = \begin{pmatrix} \sigma^2(z_2) & \sigma(z_1, z_2) \\ \sigma(z_1, z_2) & \sigma^2(z_2) \end{pmatrix}$$

$$\mathbf{G} = \begin{pmatrix} \sigma^2(A_2) & \sigma(A_1, A_2) \\ \sigma(A_1, A_2) & \sigma^2(A_2) \end{pmatrix}$$

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The multivariate breeder's equation

$$R = G P^{-1} S$$

$$R = h^2 S = (V_A / V_P) S$$

Natural parallels with univariate breeder's equation

$P^{-1} S = \beta$ is called the **selection gradient** and measures the amount of direct selection on a character

The gradient version of the breeder's equation is given by $R = G \beta$. This is often called the Lande Equation (after Russ Lande)

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Sources of within-generation change in the mean

Since $\beta = P^{-1} S$, $S = P \beta$, giving the j-th element as

$$S_j = \sigma^2(P_j) \beta_j + \sum_{i \neq j} \sigma(P_j, P_i) \beta_i$$

Change in mean from direct selection on trait j
Change in mean from phenotypically correlated characters under direct selection

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Within-generation change in the mean

$$S_j = \sigma^2(P_j) \beta_j + \sum_{i \neq j} \sigma(P_j, P_i) \beta_i$$

Response in the mean

Between-generation
change (response)
in trait j

Indirect response
from genetically
correlated
characters under
direct selection

$$R_j = \sigma^2(A_j) \beta_j + \sum_{i \neq j} \sigma(A_j, A_i) \beta_i$$

Response from direct
selection on trait j

Correlated response

Direct response

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Example in **R**

Consider three of these traits, z_1 = oil content, z_2 = protein content, and z_3 = yield. For these characters, Brim et al. estimated the covariance matrices as

$$P = \begin{pmatrix} 287.5 & 477.4 & 1266 \\ 477.4 & 935 & 2303 \\ 1266 & 2303 & 5951 \end{pmatrix}, \quad G = \begin{pmatrix} 128.7 & 160.6 & 492.5 \\ 160.6 & 254.6 & 707.7 \\ 492.5 & 707.7 & 2103 \end{pmatrix}$$

Suppose you observed a within-generation change of -10 for oil, 10 for protein, and 100 for yield.

What is **R**? What is the nature of selection on each trait?

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Enter G, P, and S

```
> P<-matrix(c(287.5,477.4,1266,477.4,935,2303,1266,2303,5951),nrow=3)
> P
      [,1] [,2] [,3]
[1,] 287.5 477.4 1266
[2,] 477.4 935.0 2303
[3,] 1266.0 2303.0 5951
> G<-matrix(c(128.7,160.6,492.5,160.6,254.6,707.7,492.5,707.7,2103),nrow=3)
> G
      [,1] [,2] [,3]
[1,] 128.7 160.6 492.5
[2,] 160.6 254.6 707.7
[3,] 492.5 707.7 2103.0
> S<-matrix(c(-10,10,100),nrow=3)
> S
      [,1]
[1,] -10
[2,] 10
[3,] 100
```

$$R = G P^{-1} S$$

```
> G %*% solve(P) %*% S
      [,1]
[1,] -13.57729
[2,] 12.28425
[3,] 65.14172
```

13.6 decrease in oil
12.3 increase in protein
65.1 increase in yield

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S versus β : Observed change versus targets of Selection, $\beta = P^{-1} S$, $S = P \beta$,

$$S_j = \sigma^2(P_j) \beta_j + \sum_{i \neq j} \sigma(P_j, P_i) \beta_i$$

```
> solve(P) %*% S
      [,1]
[1,] -2.708160
[2,] -1.431750
[3,] 1.147009
```



```
> S
      [,1]
[1,] -10
[2,] 10
[3,] 100
```

β : targets of selection

S: observed within-generation change

Observe a within-generation increase in protein, but the actual selection was to decrease it.

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Quantifying Multivariate Constraints to Response

Is there genetic variation in the direction of selection?

Consider the following \mathbf{G} and $\boldsymbol{\beta}$:

$$\mathbf{G} = \begin{pmatrix} 10 & 20 \\ 20 & 40 \end{pmatrix}, \quad \boldsymbol{\beta} = \begin{pmatrix} 2 \\ -1 \end{pmatrix}$$

Taken one trait at a time, we might expect $R_i = G_{ii}\beta_i$

Giving $R_1 = 20$, $R_2 = -40$.

What is the actual response?

$$\mathbf{R} = \mathbf{G}\boldsymbol{\beta} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

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Constraints Imposed by Genetic Correlations

While $\boldsymbol{\beta}$ is the directional optimally favored by selection, the actual response is dragged off this direction, with $\mathbf{R} = \mathbf{G}\boldsymbol{\beta}$.

Example: Suppose

$$\mathbf{S} = \begin{pmatrix} 10 \\ -10 \end{pmatrix}, \quad \mathbf{P} = \begin{pmatrix} 20 & -10 \\ -10 & 40 \end{pmatrix}, \quad \mathbf{G} = \begin{pmatrix} 20 & 5 \\ 5 & 10 \end{pmatrix}$$

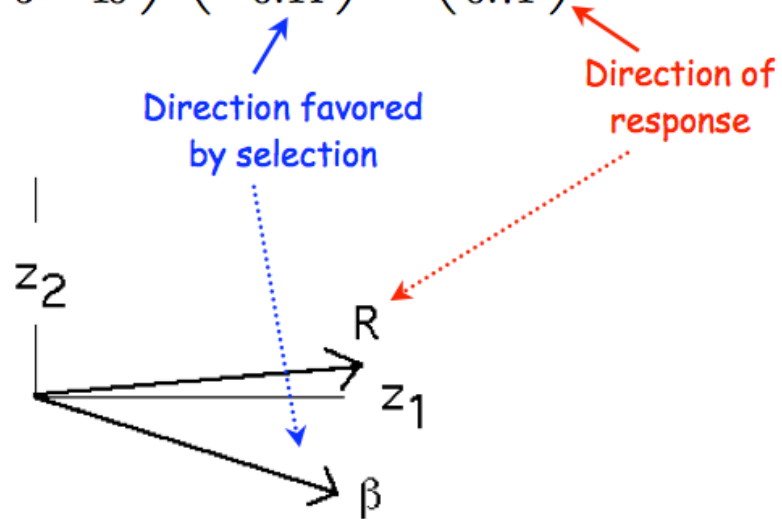
What is the true nature of selection on the two traits?

$$\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{S} = \mathbf{P}^{-1} \begin{pmatrix} 10 \\ -10 \end{pmatrix} = \begin{pmatrix} 0.43 \\ -0.14 \end{pmatrix}$$

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What does the actual response look like?

$$\mathbf{R} = \mathbf{G}\boldsymbol{\beta} = \begin{pmatrix} 20 & 5 \\ 5 & 10 \end{pmatrix} \begin{pmatrix} 0.43 \\ -0.14 \end{pmatrix} = \begin{pmatrix} 7.86 \\ 0.71 \end{pmatrix}$$



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Extra stuff

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Time for a short diversion: The Geometry of a matrix

A vector is a geometric object, leading from the origin to a specific point in n-space.

Hence, a vector has a length and a direction.

We can thus change a vector by both rotation and scaling

The length (or norm) of a vector \mathbf{x} is denoted by $\|\mathbf{x}\|$

$$\|\mathbf{x}\| = \sqrt{x_1^2 + x_2^2 + \cdots + x_n^2} = \sqrt{\mathbf{x}^T \mathbf{x}}$$

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The (Euclidean) distance between two vectors \mathbf{x} and \mathbf{y} (of the same dimension) is

$$\|\mathbf{x}-\mathbf{y}\|^2 = \sum_{i=1}^n (x_i - y_i)^2 = (\mathbf{x}-\mathbf{y})^T (\mathbf{x}-\mathbf{y}) = (\mathbf{y}-\mathbf{x})^T (\mathbf{y}-\mathbf{x})$$

The angle θ between two vectors provides a measure for how they differ.

If two vectors satisfy $\mathbf{x} = a\mathbf{y}$ (for a constant a), then they point in the same direction, i.e., $\theta = 0$ (Note that $a < 0$ simply reflects the vector about the origin)

Vectors at right angles to each other, $\theta = 90^\circ$ or 270° are said to be orthogonal. If they have unit length as well, they are further said to be orthonormal.

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Matrices Describe Vector transformations

Matrix multiplication results in a **rotation** and a **scaling** of a vector

The action of multiplying a vector x by a matrix A generates a new vector $y = Ax$, that has different dimension from x unless A is square.

Thus A describes a **transformation** of the original coordinate system of x into a new coordinate system.

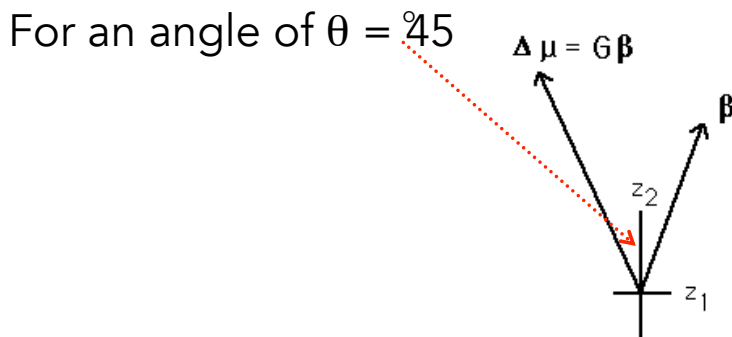
Example: Consider the following G and β :

$$\mathbf{G} = \begin{pmatrix} 4 & -2 \\ -2 & 2 \end{pmatrix} \quad \beta = \begin{pmatrix} 1 \\ 3 \end{pmatrix}, \quad \mathbf{R} = \mathbf{G}\beta = \begin{pmatrix} -2 \\ 4 \end{pmatrix} \quad 71$$

The resulting angle between R and β is given by

$$\cos \theta = \frac{\beta^T \mathbf{R}}{|\mathbf{R}| |\beta|} = \frac{1}{\sqrt{2}}$$

For an angle of $\theta = 45^\circ$



Eigenvalues and Eigenvectors

The **eigenvalues** and their associated **eigenvectors** fully describe the geometry of a matrix.

Eigenvalues describe how the original coordinate axes are **scaled** in the new coordinate systems

Eigenvectors describe how the original coordinate axes are **rotated** in the new coordinate systems

For a square matrix A , any vector y that satisfies $Ay = \lambda y$ for some scalar λ is said to be an **eigenvector** of A and λ its associated **eigenvalue**.

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Note that if y is an eigenvector, then so is $a*y$ for any scalar a , as $Ay = \lambda y$.

Because of this, we typically take eigenvectors to be scaled to have unit length (their norm = 1)

An **eigenvalue** λ of A satisfies the equation $\det(A - \lambda I) = 0$, where \det = determinant

For an n -dimensional square matrix, this yields an n -degree polynomial in λ and hence up to n unique roots

Two nice features:

$\det(A) = \prod_i \lambda_i$ The determinant is the product of the eigenvalues

$\text{trace}(A) = \sum_i \lambda_i$. The **trace** (sum of the diagonal elements) is the sum of the eigenvalues

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Note that $\det(A) = 0$ if and only if at least one eigenvalue = 0

For symmetric matrices (such as covariance matrices) the resulting n eigenvectors are mutually orthogonal, and we can factor A into its spectral decomposition,

$$\mathbf{A} = \lambda_1 \mathbf{e}_1 \mathbf{e}_1^T + \lambda_2 \mathbf{e}_2 \mathbf{e}_2^T + \cdots + \lambda_n \mathbf{e}_n \mathbf{e}_n^T$$

Hence, we can write the product of any vector x and A as

$$\begin{aligned} \mathbf{A}x &= \lambda_1 \mathbf{e}_1 \mathbf{e}_1^T x + \lambda_2 \mathbf{e}_2 \mathbf{e}_2^T x + \cdots + \lambda_n \mathbf{e}_n \mathbf{e}_n^T x \\ &= \lambda_1 \text{Proj}(x \text{ on } \mathbf{e}_1) + \lambda_2 \text{Proj}(x \text{ on } \mathbf{e}_2) + \cdots + \lambda_n \text{Proj}(x \text{ on } \mathbf{e}_n) \end{aligned}$$

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Example: Let's reconsider a previous G matrix

$$\begin{aligned} |\mathbf{G} - \lambda \mathbf{I}| &= \left| \begin{pmatrix} 4 - \lambda & -2 \\ -2 & 2 - \lambda \end{pmatrix} \right| \\ &= (4 - \lambda)(2 - \lambda) - (-2)^2 = \lambda^2 - 6\lambda + 4 = 0 \end{aligned}$$

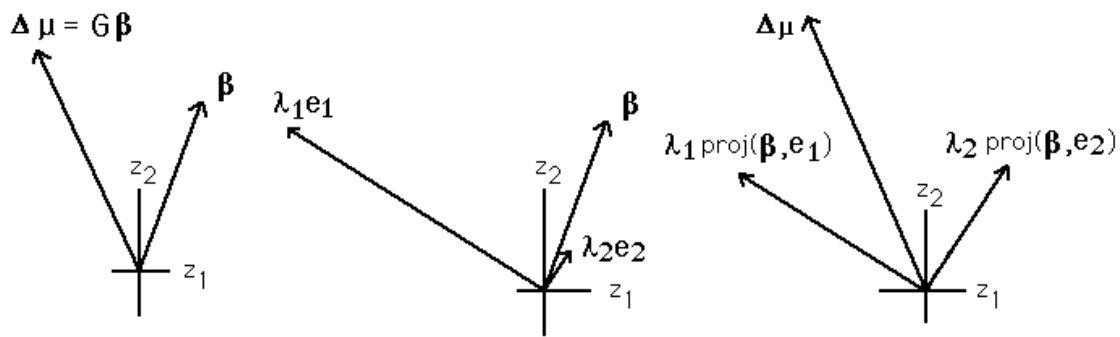
The solutions are

$$\lambda_1 = 3 + \sqrt{5} \simeq 5.236 \quad \lambda_2 = 3 - \sqrt{5} \simeq 0.764$$

The corresponding eigenvectors become

$$\mathbf{e}_1 \simeq \begin{pmatrix} -0.851 \\ 0.526 \end{pmatrix} \quad \mathbf{e}_2 \simeq \begin{pmatrix} 0.526 \\ 0.851 \end{pmatrix}$$

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Even though β points in a direction very close of e_2 , because most of the variation is accounted for by e_1 , **its projection is this dimension yields a much longer vector**. The sum of these two projections yields the selection response R .

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Realized Selection Gradients

Suppose we observe a difference in the vector of means for two populations, $R = \mu_1 - \mu_2$.

If we are willing to assume they both have a common G matrix that has remained constant over time, then we can estimate the nature and amount of selection generating this difference by

$$\beta = G^{-1} R$$

Example: You are looking at oil content (z_1) and yield (z_2) in two populations of soybeans. Population a has $\mu_1 = 20$ and $\mu_2 = 30$, while for Pop 2, $\mu_1 = 10$ and $\mu_2 = 35$.

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Here

$$\mathbf{R} = \begin{pmatrix} 20 & -10 \\ 30 & -35 \end{pmatrix} = \begin{pmatrix} 10 \\ -5 \end{pmatrix}$$

Suppose the variance-covariance matrix has been stable and equal in both populations, with

$$\mathbf{G} = \begin{pmatrix} 20 & -10 \\ -10 & 40 \end{pmatrix}$$

The amount of selection on both traits to obtain this response is

$$\boldsymbol{\beta} = \begin{pmatrix} 20 & -10 \\ -10 & 40 \end{pmatrix}^{-1} \begin{pmatrix} 10 \\ -5 \end{pmatrix} = \begin{pmatrix} 0.5 \\ 0 \end{pmatrix}$$

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More extra stuff

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

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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.

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