Lecture 02
# Selection on Multiple Traits

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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.

The phenotypic values between traits *x* and *y* within an individual are correlated
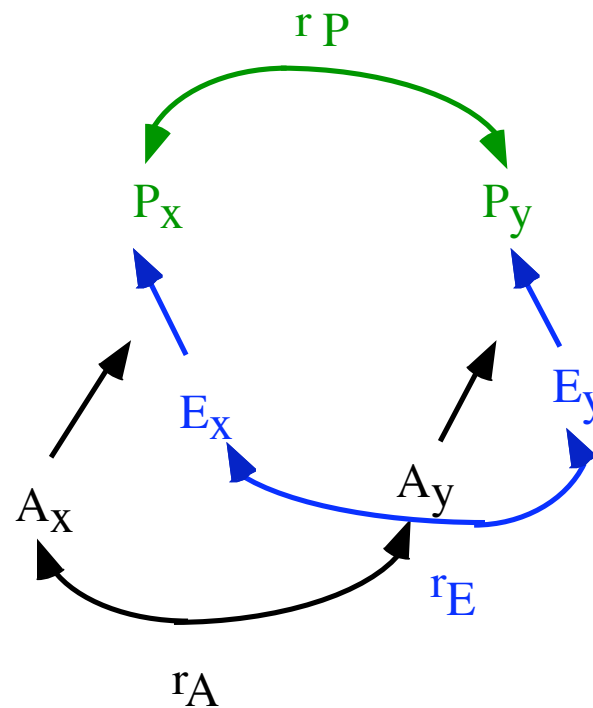
Correlations between the breeding values of x and y within the individual can generate a phenotypic correlation

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

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 corrrelation

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,

Trait x in offspring

Slope =
$(1/2)\ V_A(x)/V_P(x)$

$V_A(x) = 2*slope*V_P(x)$
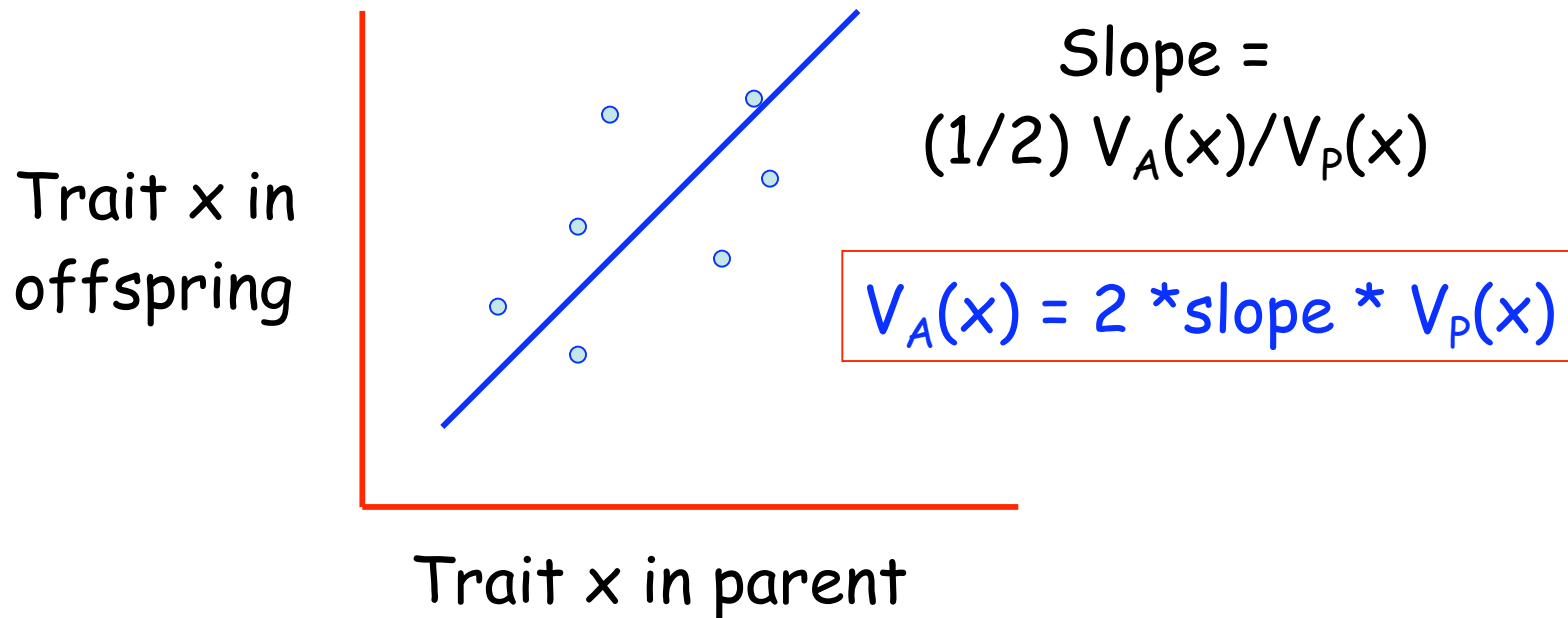
Trait x in parent

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

Trait y in offspring

Trait x in parent

Slope =
$(1/2) \, V_A(x,y)/V_P(x)$

$V_A(x,y) = 2 \, *slope \, * \, V_P(x)$
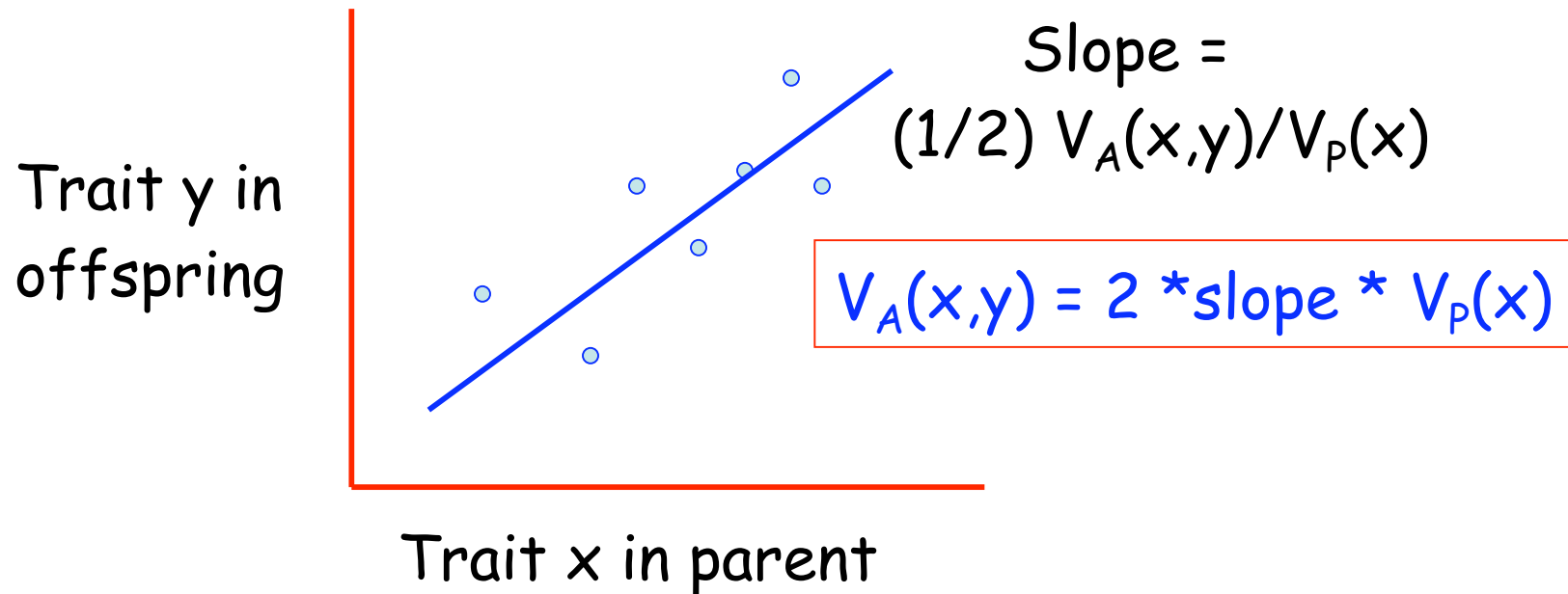
Thus, one estimator of $V_A(x,y)$ is

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

giving

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

Put another way,

$$Cov(x_O,y_P) = Cov(y_O,x_P) = (1/2)Cov(A_x,A_y)$$
$$Cov(x_O,x_P) = (1/2) V_A(x) = (1/2)Cov(A_x, A_x)$$
$$Cov(y_O,y_P) = (1/2) V_A(y) = (1/2)Cov(A_y, A_y)$$

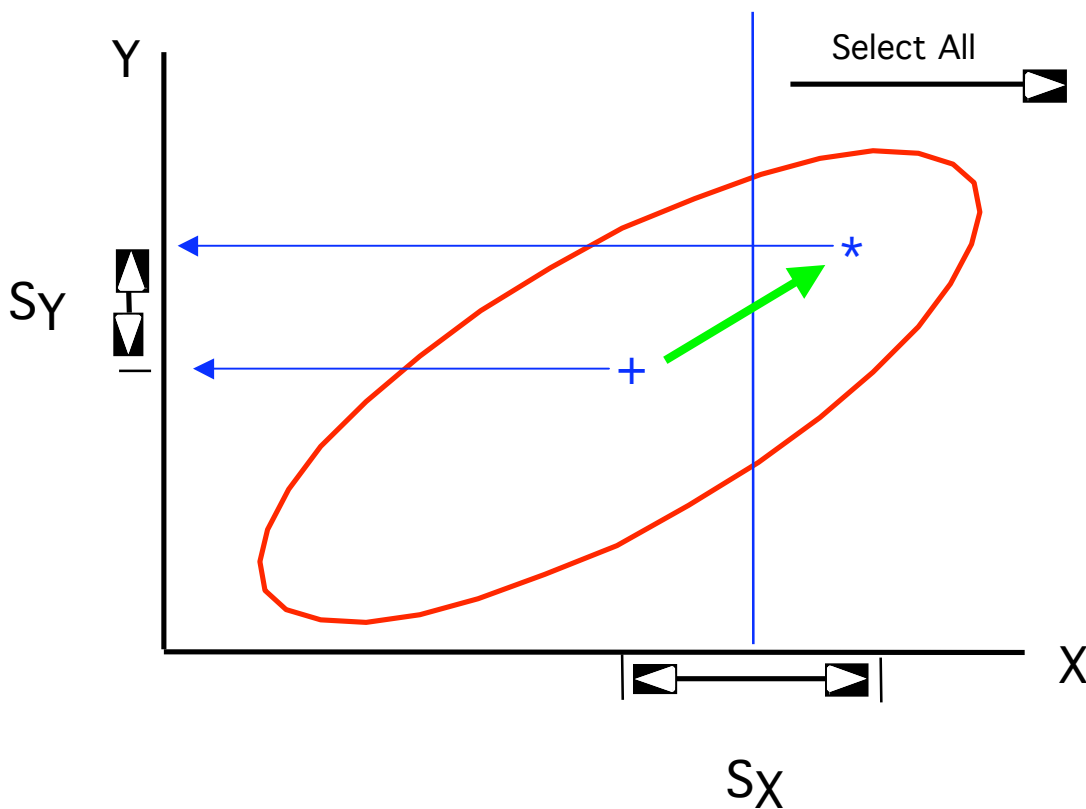Likewise, for half-sibs,

$$Cov(x_{HS},y_{HS}) = (1/4) Cov(A_x,A_y)$$
$$Cov(x_{HS},x_{HS}) = (1/4) Cov(A_x,A_x) = (1/4) V_A(x)$$
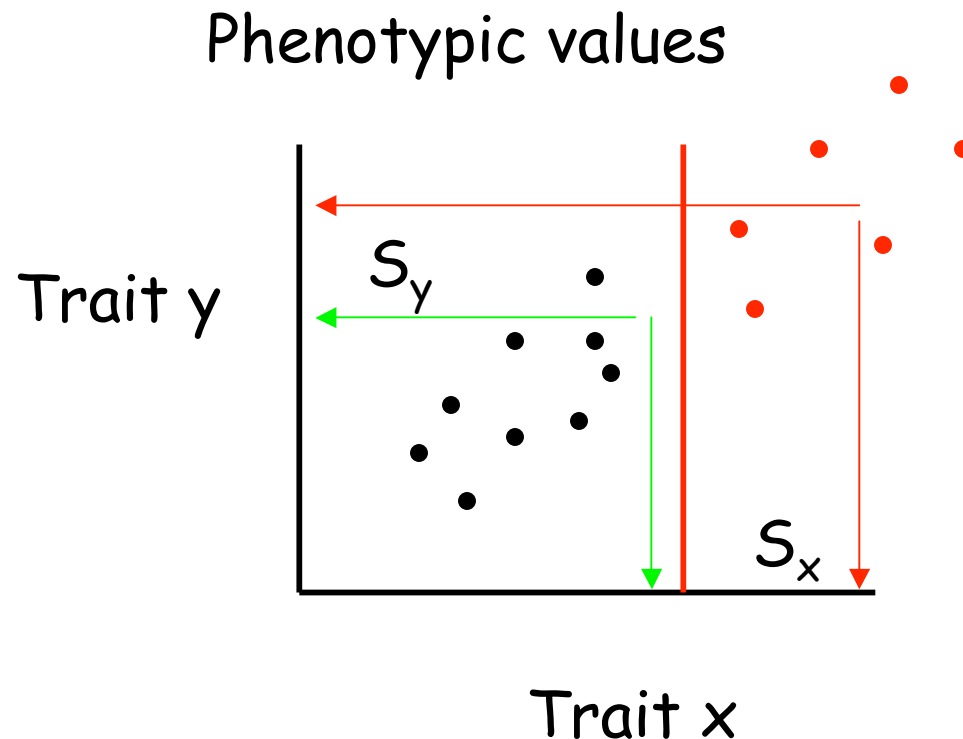$$Cov(y_{HS},y_{HS}) = (1/4) Cov(A_y,A_y) = (1/4) V_A(y)$$

Correlated Response to Selection

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

Direct selection on x also changes the mean of y

Phenotypic correlations induce within-generation changes

Phenotypic values

Trait y

S_y

S_x

Trait x

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

Phenotypic values

Trait y

$R_y = 0$

Trait x

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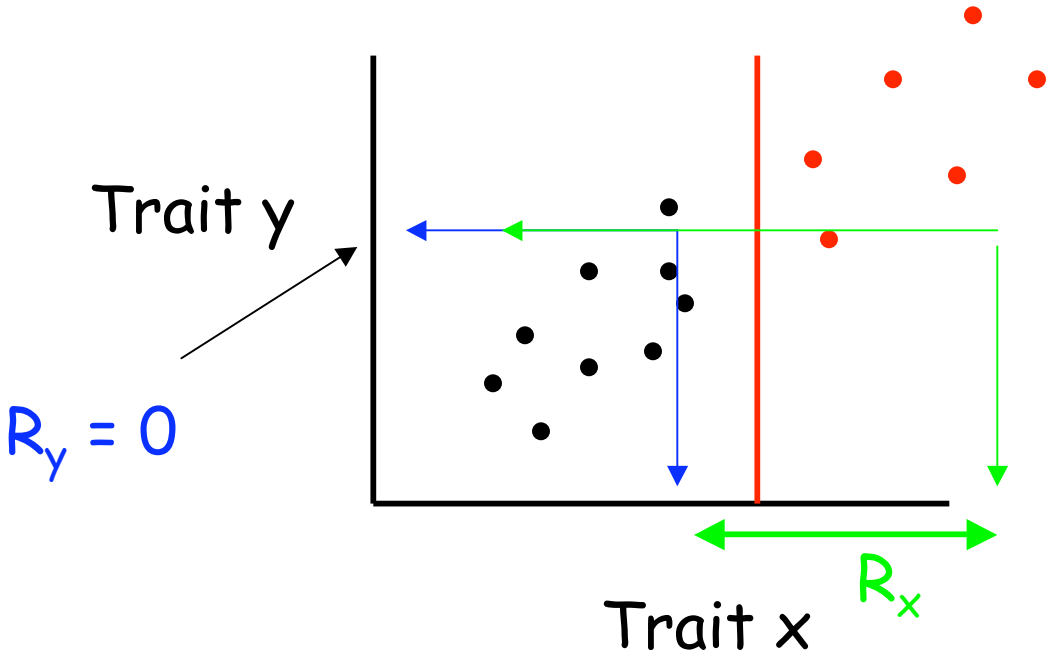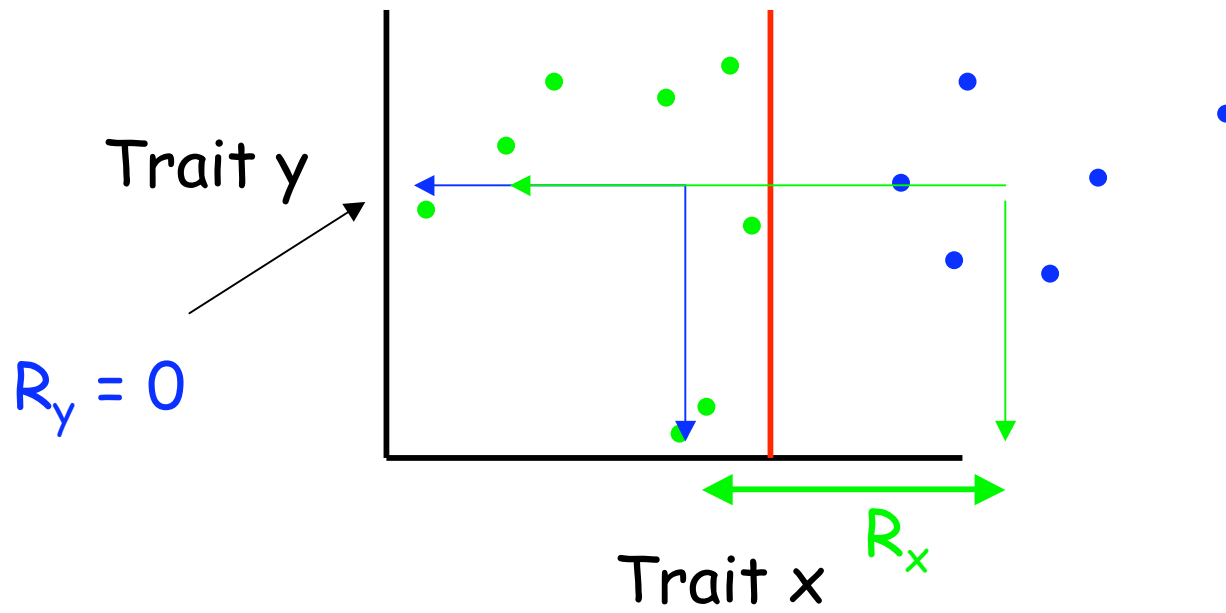
Phenotypic values are misleading, what we want are the breeding values for each of the selected individuals. Each arrow takes an individual's phenotypic value into its actual breeding value.

Breeding values

Trait y

$R_y = 0$

R_x

Trait x

Breeding values

Trait y

$R_y = 0$

R_x

Trait x

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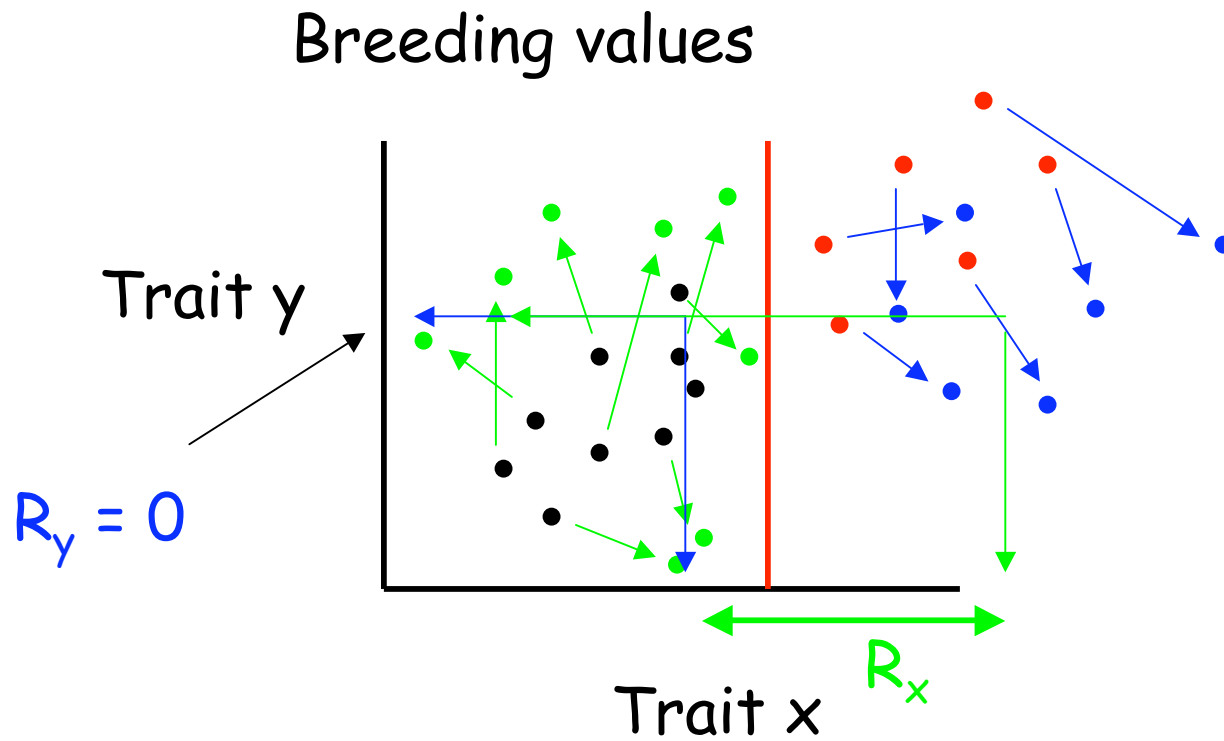
Predicting the correlated response

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,

$$A_y = b_{Ay|Ax} \, A_x$$

where

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

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

$$CR_y = b_{Ay|Ax} \, R_x$$

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

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

$\uparrow$

Recall that $i_x = S_x/\sigma_P (x)$ 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:

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

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

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

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 precison but y is not.

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G x E

The same trait measured over two (or more) environments can be considered as two (or more) correlated traits.

If the genetic correlation $|\rho| = 1$ across environments and the genetic variance of the trait is the same in both environments, then no G x E

However, if $|\rho| < 1$, and/or Var(A) of the trait varies over environments, then G x E present

Hence, dealing with G x E is a *multiple-trait problem*

Participatory breeding

The environment where a crop line is developed may be different from where it is grown

An especially important example of this is participatory breeding, wherein subsistence farmers are involved in the field traits.

Here, the correlated response is the yield in subsistence environment given selection at a regional center, while direct response is yield when selection occurred in subsistence environment. Regional center selection works when

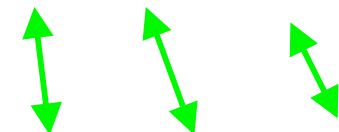$$i_Y \, r_A \, h_Y > i_X \, h_X$$

The Multivariate Breeders' Equation

Suppose we are interested in the vector R of responses when selection occurs on n correlated traits

Let S be the vector of selection differentials.

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

What is the multivariate version of this?

The multivariate breeders' equation

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

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

Natural parallels with univariate breeders 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 breeders' Equation is given by $R = G\ \beta$. This is often called the Lande Equation (after Russ Lande)

Sources of within-generation change in the mean

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

Change in mean from
phenotypically
correlated characters
under direct selection

Within-generation
change in trait j

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

Change in mean
from direct
selection on trait j

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

Direct response

Correlated response

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

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

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?

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⁻¹S

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

```
> 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

S versus β : Observed change versus targets of
Selection, β = P⁻¹ S, S = P β,

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

```
> solve(P) %*% S               > S
              [,1]                      [,1]
[1,] -2.708160           [1,]    -10
[2,] -1.431750           [2,]     10
[3,]  1.147009           [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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Constraints Imposed by
Genetic Correlations

While β is the directional optimally favored by selection, the actual response is dragged off this direction, with R = G β.

Example: Suppose

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

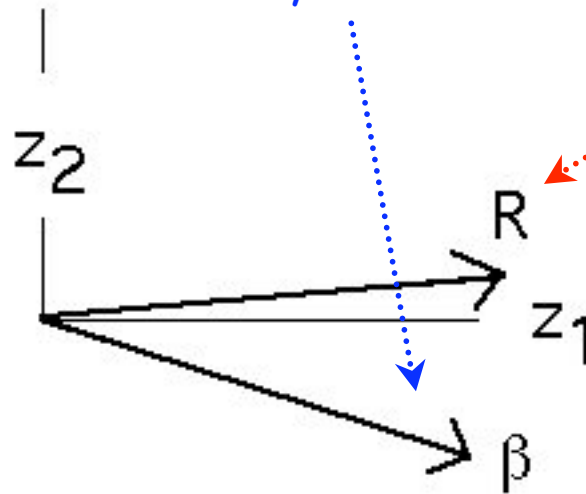What is the true nature of selection on the two traits?

$$\boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{S} = \mathbf{P} = \begin{pmatrix} 20 & -10 \\ -10 & 40 \end{pmatrix}^{-1} \begin{pmatrix} 10 \\ -10 \end{pmatrix} = \begin{pmatrix} 0.43 \\ -0.14 \end{pmatrix}$$

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What does the actual response look like?

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

Direction favored by selection

Direction of response

z_2

R

z_1

β

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.

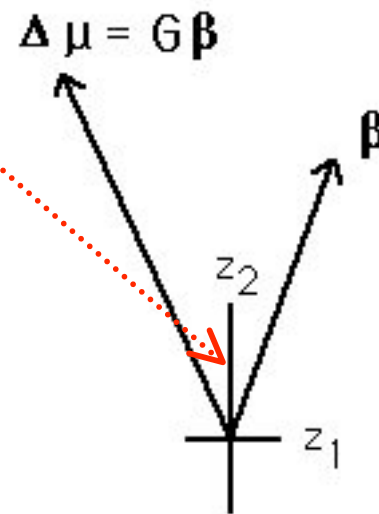Thus A describes a *transformation* of the original coordinate system of x into a new coordinate system.

Example: Consider the following G and β:

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

The resulting angle between R and β is given by

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

For an angle of $\theta = 45°$

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 = λy for some scaler λ is said to be an eigenvector of A and λ its associated eigenvalue.

Note that if y is an eigenvector, then so is a*y
for any scaler 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:

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

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

Note that det(A) = 0 if any 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

$$\mathbf{A}\mathbf{x} = \lambda_1 \mathbf{e}_1 \mathbf{e}_1^T x + \lambda_2 \mathbf{e}_2 \mathbf{e}_2^T x + \cdots + \lambda_n \mathbf{e}_n \mathbf{e}_n^T x$$
$$= \lambda_1 \mathrm{Proj}(\mathbf{x}\,\mathrm{on}\,\mathbf{e}_1) + \lambda_2 \mathrm{Proj}(\mathbf{x}\,\mathrm{on}\,\mathbf{e}_2) + \cdots + \lambda_n \mathrm{Proj}(\mathbf{x}\,\mathrm{on}\,\mathbf{e}_n)$$

Example: Let's reconsider a previous G matrix
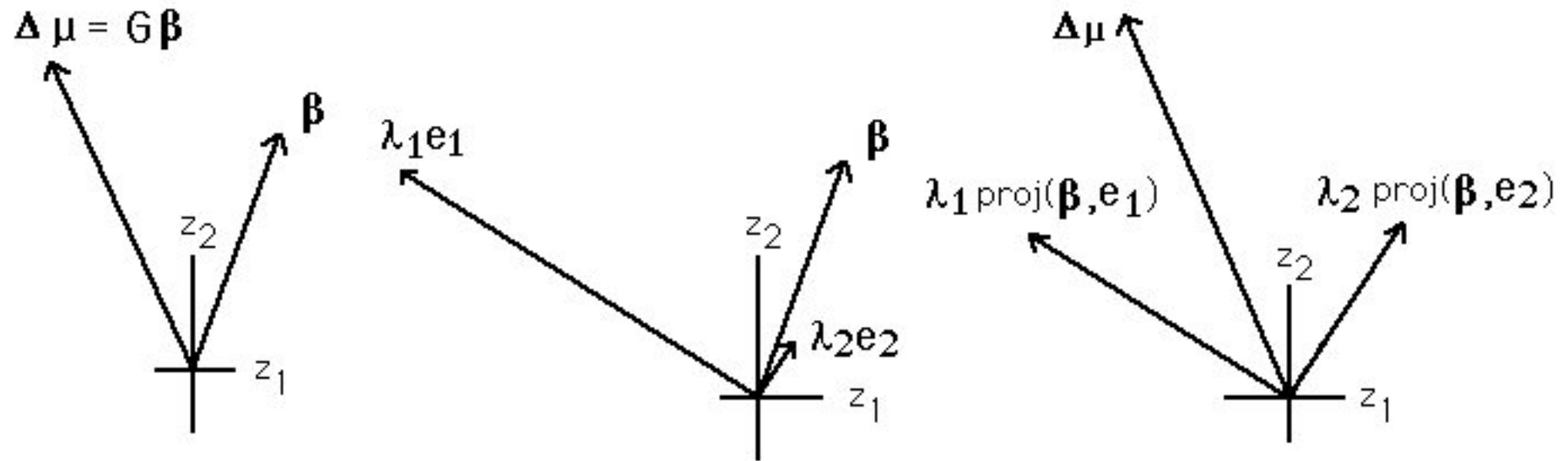
$$|\mathbf{G} - \lambda\mathbf{I}| = \left| \begin{pmatrix} 4 - \lambda & -2 \\ -2 & 2 - \lambda \end{pmatrix} \right|$$

$$= (4 - \lambda)(2 - \lambda) - (-2)^2 = \lambda^2 - 6\lambda + 4 = 0$$

The solutions are

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

The corresponding eigenvectors become

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

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.

Realized Selection Gradients

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

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 $\mu_2 = 35$.

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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