A Quick Refresher of Basic Matrix Algebra

- Matrices and vectors and given in **boldface** type. Usually, uppercase is a matrix, lower case a vector (a matrix with only one row or column).

\[ A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}, \quad v = \begin{pmatrix} e \\ f \end{pmatrix} \]

- The **Transpose** of a matrix switches the rows and columns.

\[ A^T = \begin{pmatrix} a & c \\ b & d \end{pmatrix}, \quad v^T = \begin{pmatrix} e & f \end{pmatrix} \]

- **Matrix Multiplication**

Matrix and a vector,

\[ Av = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} e \\ f \end{pmatrix} = \begin{pmatrix} a \cdot e + b \cdot f \\ c \cdot e + d \cdot f \end{pmatrix} \]

example:

\[
\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix} \begin{pmatrix} 5 \\ 6 \end{pmatrix} = \begin{pmatrix} 17 \\ 39 \end{pmatrix}
\]

Two matrices

\[ B = \begin{pmatrix} e & f \\ g & h \end{pmatrix} \]

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

\[ BA = \begin{pmatrix} e & f \\ g & h \end{pmatrix} \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} ea + fc & eb + fd \\ ga + hc & gb + hd \end{pmatrix} \]

example:

\[
\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix} \begin{pmatrix} 4 & 3 \\ 6 & 2 \end{pmatrix} = \begin{pmatrix} 16 & 7 \\ 36 & 17 \end{pmatrix}
\]

\[
\begin{pmatrix} 4 & 3 \\ 6 & 2 \end{pmatrix} \begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix} = \begin{pmatrix} 13 & 20 \\ 12 & 20 \end{pmatrix}
\]

- Note the order of multiplication matters! Usually \( AB \neq BA \)

- **The Identity Matrix** \( I \).

\[ I = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \]

\( I \) serves a role akin to one in matrix multiplication, as

\[ IA = AI = A \]

- **The Inverse of a matrix, \( A^{-1} \)**

\[ A^{-1}A = AA^{-1} = I \]

This serves the role of division in matrix multiplication.
Here

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

for $A = \begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix}$, $A^{-1} = \frac{1}{-2} \begin{pmatrix} 4 & -2 \\ -3 & 15 \end{pmatrix} = \begin{pmatrix} -2 & 1 \\ 1.5 & -0.5 \end{pmatrix}$

- Note that if $ad - bc$ (the determinant of $A$) is zero, then $A^{-1}$ does not exist and the matrix is said to be singular.

- Suppose we wish to solve $Ax = v$ for the vector $x$ of unknowns, e.g.,

$$Ax = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} e \\ f \end{pmatrix}$$

Premultiply both sides by the inverse of $A$,

$$A^{-1}Ax = A^{-1}v$$

where

$$A^{-1}Ax = Ix = x$$

giving the solution as

$$x = A^{-1}v$$

**Correlated Characters**

- Phenotypic correlations
- Genetic correlations

$$\sigma(z_1, z_2) = \sigma(G_1, G_2) + \sigma(E_1, E_2)$$

Shared environmental effects are expected, as traits are developed in the same individual

Genetic correlations can be due either to linkage (in which case they are transient and decay over time) or pleiotropy (the genes effecting more than one trait)

**Estimating Genetic Covariances**

- It is the additive genetic covariance $= \sigma(A_1, A_2)$, the covariance between the breeding values of the two traits in an individual, that is of interest.

- The phenotypic covariance between the value of trait $i$ in a parent and trait $j$ in its offspring is just

$$\sigma(z_i(\text{parent}), z_j(\text{offspring})) = \frac{\sigma(A_1, A_2)}{2}$$

- The expected slope of the regression of trait $i$ in the midparent on trait $j$ in the offspring is

$$b_{z_i, z_j} = \frac{\sigma(A_1, A_j)}{\sigma^2(z_i)}$$
Selection on the Vector of Means

Let \( \mu \) be the vector of character means, \( \mu^* \) the means after selection, and \( s \) the vector of directional selection differentials,

\[
\mu = \begin{pmatrix} \mu_1 \\ \mu_2 \\ \vdots \\ \mu_n \end{pmatrix}, \quad s = \begin{pmatrix} \mu_1^* - \mu_1 \\ \mu_2^* - \mu_2 \\ \vdots \\ \mu_n^* - \mu_n \end{pmatrix} = \begin{pmatrix} S_1 \\ S_2 \\ \vdots \\ S_n \end{pmatrix}
\]

The elements of the vector \( s \) are the covariances between trait values and relative fitness,

\[
s = \sigma(z, w) = \begin{pmatrix} \sigma(z_1, w) \\ \sigma(z_2, w) \\ \vdots \\ \sigma(z_n, w) \end{pmatrix}
\]

The directional selection gradient is now a vector,

\[
\beta = P^{-1} \sigma(z, w) = P^{-1} s
\]

- \( P \) is the phenotypic variance-covariance matrix,
  \[
P_{ij} = \sigma(z_i, z_j)
\]
- The elements of \( \beta \) are the slopes for a multivariate linear regression of trait value on relative fitness,
  \[
w(z) = 1 + \sum_{j=1}^{n} \beta_j (z_j - \mu_j) = 1 + \beta^T (z - \mu)
\]
- \( \beta_j \) is called a **partial regression coefficient**.
- A one unit change in trait \( i \) while holding all the other traits constant changes fitness by \( \beta_i \)
- \( \beta_i \) measures the amount of **direct selection** on trait \( i \)
- Note that the mean of a trait can change simply by direction selection on a phenotypically correlated trait. Since \( s = P\beta \),
  \[
s_i = \sum_{j=1}^{n} \beta_j P_{ij} = \beta_i P_{ii} + \sum_{j \neq i}^{n} \beta_j P_{ij}
\]
Thus, the directional selection differential confounds both direct selection on the trait and indirect selection from selection on phenotypically correlated traits.

Suppose

\[
s = \begin{pmatrix} 1 \\ 1 \end{pmatrix}
\]

If

\[
P = \begin{pmatrix} 4 & 0 \\ 0 & 8 \end{pmatrix}, \quad \text{then} \quad \beta = \begin{pmatrix} 0.25 \\ 0.125 \end{pmatrix}
\]
Direct selection on both traits, stronger on trait 1.

However, if
\[ P = \begin{pmatrix} 4 & 4 \\ 4 & 8 \end{pmatrix}, \quad \text{then} \quad \beta = \begin{pmatrix} 0.25 \\ 0 \end{pmatrix} \]

Direct selection on trait 1, none on trait 2.

• Using \( \beta \) removes the effect of phenotypic correlations.

• \( \beta \) is the gradient of mean fitness,
\[ \beta = \frac{1}{W} \begin{pmatrix} \frac{\partial W(\mu)}{\partial \mu_1} \\ \frac{\partial W(\mu)}{\partial \mu_2} \\ \vdots \\ \frac{\partial W(\mu)}{\partial \mu_n} \end{pmatrix} \]

\( \beta \) is the vector this points in the direction of steepest ascent on the mean fitness– i.e., the direction the means should move to most rapidly increase mean fitness.

• Hence, optimal change is to move the means along the vector \( \beta \)

• Genetic correlations cause the response to selection to depart from this optional direction, as the vector of response to selection in the mean is given by
\[ R = G\beta = GP^{-1}s \]

where \( G \) is the matrix of additive genetic variances and covariances, \( G_{ij} = \sigma(A_i, A_j) \).

• Note that \( GP^{-1} \) is the multivariate analog to \( h^2 \), and \( G\beta \) is the multivariate analog of \( \sigma^2_A \beta \).

• Selection response involves direct response plus indirect response due to selection on genetically correlated characters,
\[ R_i = \sum_{j=1}^{n} \beta_j G_{ij} = \beta_i G_{ii} + \sum_{j \neq i} \beta_j G_{ij} \]

Examples:
\[ \beta = \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \quad G = \begin{pmatrix} 4 & 0 \\ 0 & 8 \end{pmatrix}, \quad R = \begin{pmatrix} 4 \\ 8 \end{pmatrix} \]
for \( G = \begin{pmatrix} 4 & -4 \\ -4 & 8 \end{pmatrix}, \quad R = \begin{pmatrix} 0 \\ 4 \end{pmatrix} \)

**Selection on the Covariance Matrix**

- The quadratic selection differential is now a matrix
  \[
  C = \sigma[w, (z - \mu)(z - \mu)^T] = P^* - P + ss^T
  \]

- Diagonal \((C_{ii})\) elements means selection on the mean of trait \(i\), off-diagonal elements \((C_{ij})\) to selection on the phneotypic covariance between traits \(i\) and \(j\)
  \[
  C_{ij} = \sigma[w, (z_i - \mu_z_i)(z_j - \mu_z_j)]
  \]

- Directional selection reduces the variance and alters the covariances,
  \[
  P^*_{ij} - P_{ij} = -s_is_j
  \]

- The quadratic selection gradient is now a matrix,
  \[
  \gamma = P^{-1} \sigma[w, (z - \mu)(z - \mu)^T] P^{-1} = P^{-1} C P^{-1}
  \]

- The elements of \(\gamma\) correspond to coefficients in the quadratic multivariate regression of trait value on relative fitness,
  \[
  w(z) = a + \sum_{j=1}^n b_j z_j + \frac{1}{2} \sum_{j=1}^n \sum_{k=1}^n \gamma_{jk} (z_j - \mu_j)(z_k - \mu_k)
  \]
  \[
  = a + \beta^T z + \frac{1}{2} (z - \mu)^T \gamma (z - \mu)
  \]

If the distribution of the vector \(z\) of character values is multivariate normal,

\[
 w(z) = a + \beta^T z + \frac{1}{2} (z - \mu)^T \gamma (z - \mu)
\]

- Changes in \(C_{ij}\) occur from both direct selection and indirect selection from correlated characters.
Solving for $C$ by post- and pre-multiplying $\gamma$ by $P$ gives $C = P \gamma P$, or

$$C_{ij} = \sum_{k=1}^{n} \sum_{\ell=1}^{n} \gamma_{k\ell} P_{ik} P_{\ell j}$$

$$G^* - G = G(\gamma - \beta \beta^T)G = -\delta \mu \delta \mu^T + G \gamma G$$

- The within-generation change in the covariance matrix is given by

$$G^*_{ij} - G_{ij} = -\Delta \mu_i \cdot \Delta \mu_j + \sum_{k=1}^{n} \sum_{\ell=1}^{n} \gamma_{k\ell} G_{ik} G_{\ell j}$$

Thus the within-generation change in the additive genetic variance of character $i$ is given by

$$G^*_{ii} - G_{ii} = - (\Delta \mu_i)^2 + \sum_{k=1}^{n} \sum_{\ell=1}^{n} \gamma_{k\ell} G_{ik} G_{i\ell}$$