one organism ≠ one phenotypic trait

Multivariate Quantitative Genetics

Image of complex phenotypes

Fungus beetle
Bolithotherus cornutus

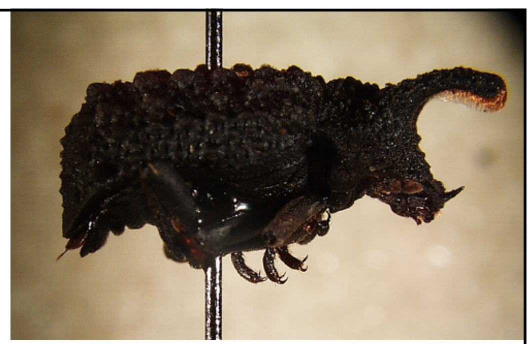


TABLE 6.1 *Estimates of total and direct selection in fungus beetles and Darwin's finches*

	Total selection (*S*)
Fungus beetles	
Elytra	0.38**
Horn	0.49***
Weight	0.39**

Multiple Regression

$$y = a + bx$$

$$y = a + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4 + ... + b_nx_n$$

Multivariate Linear Fitness Equation

$$w = a + \beta_1x_1 + \beta_2x_2 + \beta_3x_3 + \beta_4x_4 + ... + \beta_nx_n$$

a: baseline fitness
β: directional selection gradients

Fungus beetle
Bolithotherus cornutus

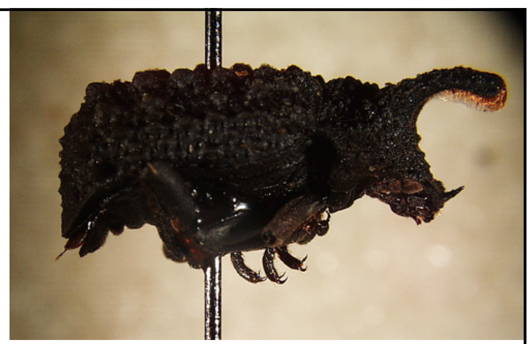
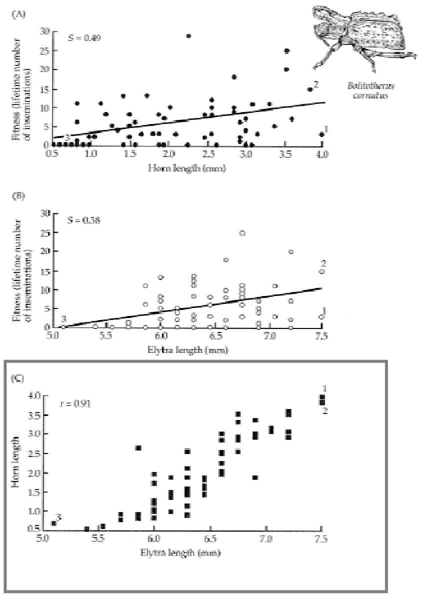


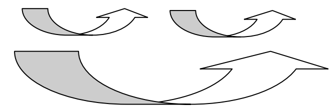
TABLE 6.1 *Estimates of total and direct selection in fungus beetles and Darwin's finches*

	Total selection (S)	Direct selection (β)
Fungus beetles		
Elytra	0.38**	–0.33
Horn	0.49***	0.94**
Weight	0.39**	–0.16

Linear Fitness Function:
Directional Selection



$$w = a + \beta_1(Elytra) + \beta_2(Horn) + \beta_3(Weight)$$



Correlations
(not independent traits)

$$\beta_1 = \beta_{Elytra} = -0.31$$

$$\beta_2 = \beta_{Horn} = 0.94**$$

$$\beta_3 = \beta_{Weight} = -0.16$$

The Multivariate "Breeder's Equation"

$$\Delta \bar{z} = \frac{G}{P} S = h^2 S = G\beta$$

Univariate breeder's equation

$$\mathbf{\Delta \bar{z} = G P^{-1} S = G \beta}$$

Multivariate "breeder's equation"

Russell Lande and **Stevan J. Arnold**. 1983. The measurement of selection on correlated characters. *Evolution* 37/6, 1210-1226.

The Multivariate "Breeder's Equation"

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\boldsymbol{\beta}$$

Genetic covariances

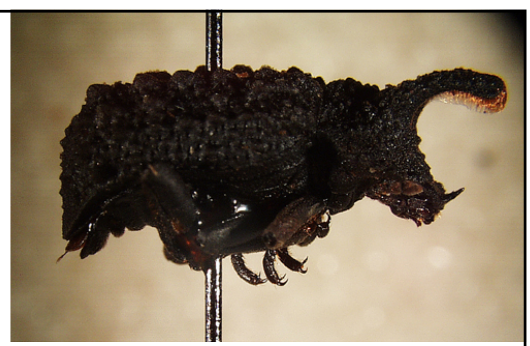
$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \\ \Delta\bar{z}_3 \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} & G_{13} \\ G_{21} & G_{22} & G_{23} \\ G_{31} & G_{32} & G_{33} \end{pmatrix} \begin{pmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{pmatrix}$$

Vector of evolutionary change in individual traits

Genetic variance-covariance matrix (the "**G-Matrix**")

Vector of directional selection gradients

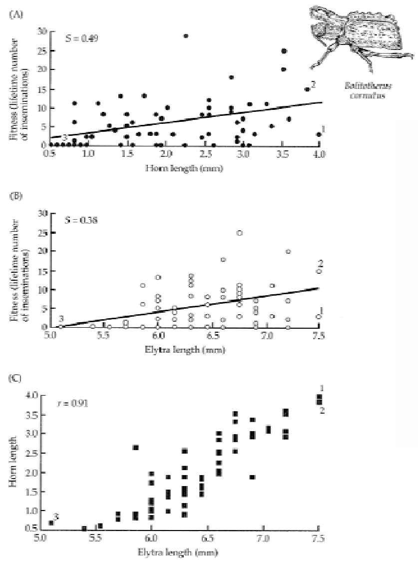
Fungus beetle
Bolithotherus cornutus

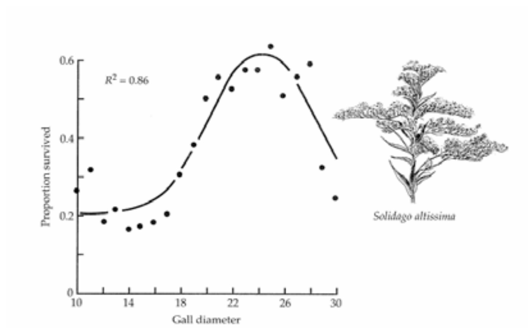


$$\begin{pmatrix} \Delta Elytra \\ \Delta Horn \\ \Delta Weight \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} & G_{13} \\ G_{21} & G_{22} & G_{23} \\ G_{31} & G_{32} & G_{33} \end{pmatrix} \begin{pmatrix} -0.31 \\ 0.94 \\ -0.16 \end{pmatrix}$$

Linear Fitness Function:
Directional Selection

Non-Linear Fitness Function:
Non-linear/stabilizing Selection





$w = a + \beta_1 z_1 + \beta_2 z_2 + ... + \beta_n z_n$

??????????

Multivariate *Quadratic* Fitness Equation

$$w = a + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_t x_t + \frac{1}{2}\gamma_1 {x_1}^2 + \frac{1}{2}\gamma_2 {x_2}^2 + ... + \frac{1}{2}\gamma_t {x_t}^2$$

Linear component

Non-linear (quadratic) component

The non-linear selection gradient does not directly affect the change in the phenotypic mean from one generation to the next ($\Delta\bar{z}$).
But it affect the genetic co-/variances.

Matrix Algebra

Dimensionality

r x c matrix (row x column)
(n x m matrix)

3 x 1 matrix = column vector $\begin{pmatrix} 3 \\ 1 \\ 6 \end{pmatrix}$

1 x 3 matrix = row vector $\begin{pmatrix} 1 & 7 & 3 \end{pmatrix}$

3 x 3 matrix („square matrix“) $\begin{pmatrix} 2 & 5 & 1 \\ 6 & 3 & 2 \\ 6 & 9 & 2 \end{pmatrix}$

Matrix Algebra

Matrix addition/subtraction

$$\begin{pmatrix} 2 & 5 & 1 \\ 6 & 3 & 2 \\ 6 & 9 & 2 \end{pmatrix} + \begin{pmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 1 \end{pmatrix} = \begin{pmatrix} 3 & 6 & 2 \\ 7 & 4 & 3 \\ 7 & 10 & 3 \end{pmatrix}$$

$$\begin{pmatrix} 2 & 5 & 1 \\ 6 & 3 & 2 \\ 6 & 9 & 2 \end{pmatrix} - \begin{pmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 1 \end{pmatrix} = \begin{pmatrix} 1 & 4 & 0 \\ 5 & 2 & 1 \\ 5 & 8 & 1 \end{pmatrix}$$

Matrix Algebra

Matrix multiplication

Multiplication by a scalar

$$2 \times \begin{pmatrix} 2 & 5 & 1 \\ 6 & 3 & 2 \\ 6 & 9 & 2 \end{pmatrix} = \begin{pmatrix} 4 & 10 & 2 \\ 12 & 6 & 4 \\ 12 & 18 & 4 \end{pmatrix}$$

Matrix-multiplication: the dot-product

$$\begin{pmatrix} 1 & 2 \\ 4 & 3 \end{pmatrix} \times \begin{pmatrix} 2 & 1 \\ 3 & 5 \end{pmatrix} = \begin{pmatrix} 1\times2+2\times3 & 1\times1+2\times5 \\ 4\times2+3\times3 & 4\times1+3\times5 \end{pmatrix}$$

Direct and indirect selection

The Multivariate "Breeder's Equation"

Genetic covariances

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \\ \Delta\bar{z}_3 \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} & G_{13} \\ G_{21} & G_{22} & G_{23} \\ G_{31} & G_{32} & G_{33} \end{pmatrix} \begin{pmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{pmatrix}$$

Vector of evolutionary change in individual traits

Genetic variance-covariance matrix (the "**G-Matrix**")

Vector of directional selection gradients

The Multivariate "Breeder's Equation"

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \\ \Delta\bar{z}_3 \end{pmatrix} = \begin{pmatrix} G_{11} & G_{12} & G_{13} \\ G_{21} & G_{22} & G_{23} \\ G_{31} & G_{32} & G_{33} \end{pmatrix} \begin{pmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{pmatrix}$$

Indirect selection

$$\Delta\bar{z}_1 = G_{11}\beta_1 + G_{12}\beta_2 + G_{13}\beta_3$$

$$\Delta\bar{z}_2 = G_{21}\beta_1 + G_{22}\beta_2 + G_{23}\beta_3$$

$$\Delta\bar{z}_3 = G_{31}\beta_1 + G_{32}\beta_2 + G_{33}\beta_3$$

The way back to univariate

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \\ \Delta\bar{z}_3 \end{pmatrix} = \begin{pmatrix} G_{11} & 0 & 0 \\ 0 & G_{22} & 0 \\ 0 & 0 & G_{33} \end{pmatrix} \begin{pmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{pmatrix}$$

$$\Delta\bar{z}_1 = G_{11}\beta_1$$

$$\Delta\bar{z}_2 = G_{22}\beta_2$$

No indirect selection

$$\Delta\bar{z}_3 = G_{33}\beta_3$$

Exercise

Calculate Δz_1, Δz_2 and Δz_3 based on the following G-matrix and vector of directional selection gradients.

a) Make the full calculation

b) Assume independence of traits

$$\mathbf{G} = \begin{pmatrix} 2 & 0.5 & -1 \\ 0.5 & 3 & -0.5 \\ -1 & -0.5 & 1.5 \end{pmatrix} \qquad \boldsymbol{\beta} = \begin{pmatrix} -0.5 \\ 1.5 \\ -1 \end{pmatrix}$$

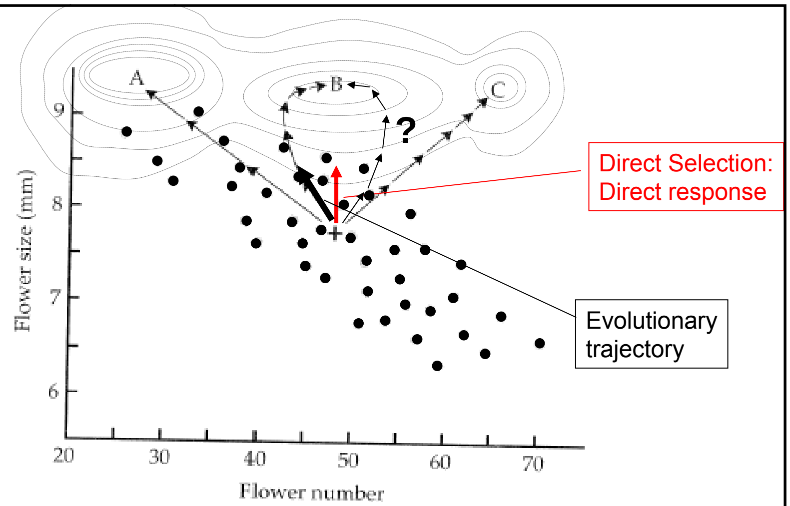


Figure 6.11 Hypothetical examples of evolutionary constraints caused by genetic correlation. The points represent breeding values; thus, the elliptical cluster of points represents a negative genetic correlation between the two traits. The cross represents the current mean for both traits in the population, and the letters A–C are three evolutionary optima. The three sets of arrows represent evolutionary trajectories to these optima; each arrow represents 50 generations.

Joint effects of signs of selection gradients and genetic correlations on evolutionary change

Gradients same sign
No genetic correlation

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

Gradients same sign
Positive genetic correlation

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix} = \begin{pmatrix} 2 \\ 2 \end{pmatrix}$$

Augmented

Gradients opposite sign
Positive genetic correlation

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix} \begin{pmatrix} 1 \\ -1 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

Constrained

Gradients same sign
Negative genetic correlation

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{pmatrix} = \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

Constrained

Gradients opposite sign
Negative genetic correlation

$$\begin{pmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{pmatrix} = \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix} \begin{pmatrix} 1 \\ -1 \end{pmatrix} = \begin{pmatrix} 2 \\ -2 \end{pmatrix}$$

Augmented