I. Where do genetic constraints fit into the framework we have developed?

The only way genetic constraints can be manifested in our current framework is as limited or absent additive genetic variance.

How else could genetic constraints be manifested in the real world?

What if selection acts on multiple traits?

II. Derivation of the multivariate "breeder's" equation

i. We saw in Lecture #2 that the mean phenotype in the next generation can be written as:

$$\bar{z}' = \int z^o w(z^p)\phi(z^p)dz^p \qquad (1)$$

ii. Taking a slightly different approach than in Lecture #2, we re-write (1) as:

$$= \overline{z^o w^p}$$

$$= Cov[z^o, w^p] + \overline{z^o} \overline{w^p}$$

Because $\overline{w^p} = 1$, this can be simplified to:

$$= Cov[z^o, w^p] + \overline{z^o} \qquad (2)$$

And the change in mean phenotype over a single generation given by:

$$\Delta\bar{z} = Cov[z^o, w^p] + \overline{z^o} - \overline{z^p} \qquad (3)$$

iii. Assuming the expected phenotype of offspring is equal to the expected phenotype of their parents, $\overline{z^o} = \overline{z^p}$ and (3) becomes:

$$\Delta\bar{z} = Cov[z^o, w^p] \qquad (4)$$

iv. Now, to understand the evolution of multivariate phenotypes, we decompose total relative fitness in the parental generation into the contributions made by individual traits:

$$w^p = w_0 + \beta_1 z_1^p + \beta_2 z_2^p + \cdots + \beta_n z_n^p \qquad (5)$$

and substitute (5) into (4), yielding:

$$\Delta\bar{z_i} = Cov\left[z_i^o, w_0 + \beta_1 z_1^p + \beta_2 z_2^p + \cdots + \beta_n z_n^p\right]$$

$$\Delta\bar{z} = Cov\left[z_i^o, w_0\right] + Cov\left[z_i^o, \beta_1 z_1^p\right] + Cov\left[z_i^o, \beta_2 z_2^p\right] + \cdots + Cov\left[z_i^o, \beta_n z_n^p\right]$$

which equals:

$$\Delta\bar{z}_i = \sum_j \beta_j Cov[z_i^o, z_j^p] \qquad (6)$$

Assuming breeding values remain unchanged from parent to offspring, the covariance terms in (6) are simply the additive genetic variances and covariances showing that (6) is the multivariate breeder's equation which is generally written as:

$$\Delta\bar{z} = \mathbf{G}\boldsymbol{\beta} \qquad (7)$$

where $\bar{z}$ is a vector of trait means defining the multivariate phenotype of the population, $\boldsymbol{\beta}$ is a vector of selection gradients, and $\mathbf{G}$ is the additive genetic variance covariance matrix.

III. Understanding the multivariate "breeder's" equation

What does equation (6) look like if we expand it?

Expanding (6) for insight yields:

$$\begin{bmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \\ \vdots \\ \Delta\bar{z}_n \end{bmatrix} = \begin{bmatrix} G_{11} & G_{12} & \vdots & G_{1n} \\ G_{21} & G_{22} & \vdots & G_{21} \\ \vdots & \vdots & \vdots & \vdots \\ G_{n1} & G_{n2} & \vdots & G_{nn} \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \\ \vdots \\ \beta_n \end{bmatrix}$$

Remembering linear algebra ("rows into columns") this yields:

$$\Delta\bar{z}_1 = G_{11}\beta_1 + G_{12}\beta_2 + \cdots + G_{1n}\beta_n$$

$$\Delta\bar{z}_2 = G_{21}\beta_1 + G_{22}\beta_2 + \cdots + G_{2n}\beta_n$$

$$\vdots$$

$$\Delta\bar{z}_n = G_{n1}\beta_1 + G_{n2}\beta_2 + \cdots + G_{nn}\beta_n$$

*What do these equations suggest about the nature of genetic constraints?*

Which components of the G matrix comprise the genetic constraints?

*What is direct vs. indirect selection?*

IV. What do these equations tell us about multivariate adaptation?

Let's gain insight by looking at a concrete example with two traits and a single bivariate phenotypic optimum
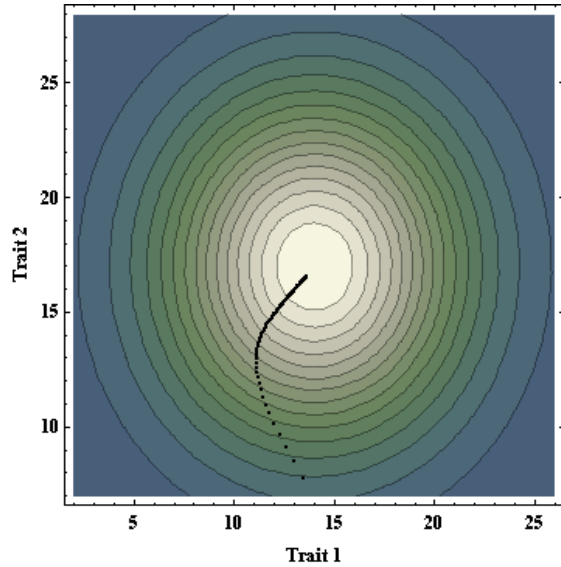
i. Assume fitness is defined by the surface below where blue is low fitness and white is high fitness:
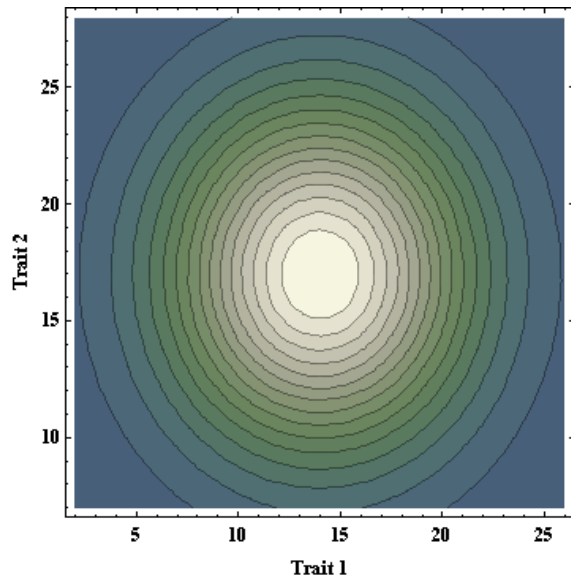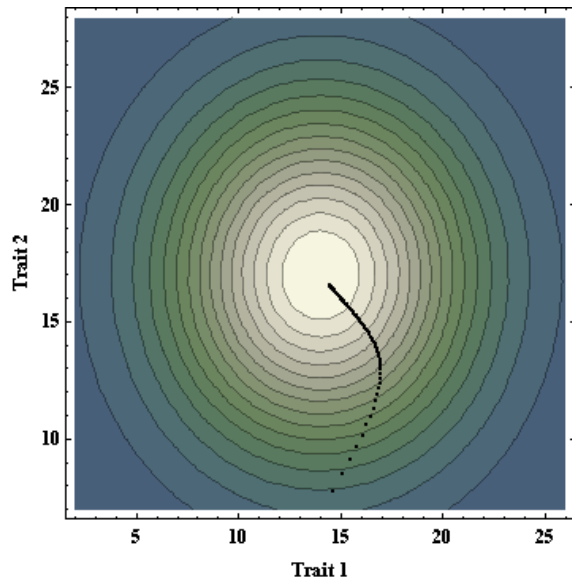

ii. How would evolution proceed if the two traits were uncorrelated?
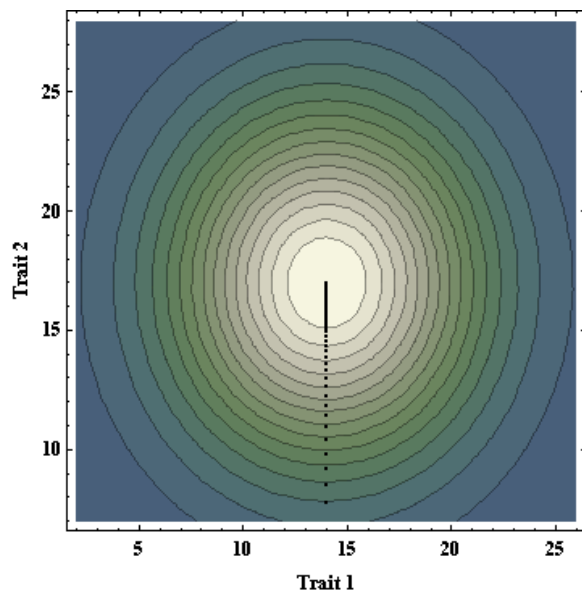
iii. How would this outcome/dynamic be altered if the traits were negatively correlated?

iv. How would this outcome/dynamic be altered if the traits were positively correlated?

Conclusion: At least for cases where selection is relatively weak, genetic correlations alter the rate and trajectory of adaptation but do not change the final evolutionary outcome.

V. How can we use this framework to study multivariate selection, adaptation, and constraint in the wild?

In our derivation we partitioned selection into its direct and indirect components using:

$$w = w_0 + \beta_1 z_1 + \beta_2 z_2 + \cdots + \beta_n z_n \qquad (4)$$

What does the form of this equation suggest about a potential methodology for estimating the selection gradients?

Step by Step guidelines for using *Multiple regression* as a methodology for estimating direct and indirect selection in the wild:

i. Transform absolute fitness to relative fitness

ii. Standardize trait data. Specifically, transform each individual phenotype to units of standard deviations: $z_j = \frac{z_j - \bar{z}}{\sigma_z}$. This transformation is done within each trait such that selection gradients can be meaningfully compared across traits that may be measured in different units.

iii. Perform a multiple regression with the traits as predictors and relative fitness as the response (i.e., equation (4)).

iv. The estimates for the selection gradients returned by the multiple regression will be the best possible estimates whether the regression assumptions are satisfied or not. However, the statistical significance of these estimates may be invalid if the assumptions are violated. In these cases, an alternative approach is required in order to establish significance. One such possibility is bootstrapping.

For more details, see (Lande and Arnold 1983)

Warning:

Do not transform relative fitness. This may be tempting as fitness data does not generally conform to the assumptions of multiple regression, but transforming the fitness data will yield evolutionarily meaningless results. In contrast, it is possible to transform the trait data as long as you recognize that your evolutionary predictions are then in terms of the transformed trait and that you must have performed the same transform on the data used to estimate the G-matrix.

VI. Estimating the G-matrix

This can be accomplished in many ways, but all involve complicated breeding designs and statistical techniques. If you are interested in finding more information on how G-matrices are estimated, check out the following references:

(Lande and Arnold 1983; Falconer and Mackay 1996; Lynch and Walsh 1998)

VII. References

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to Quantitative Genetics. Longman, Burnt Mill, Harlow, Essex, England.
Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210-1226.
Lynch, M., and B. Walsh. 1998. Genetics and the analysis of quantitative traits. Sinaur Associates, Inc., Sunderland.