Selection on Correlated Characters (notes only)

The breeder’s equation is best suited for plant and animal breeding where specific traits can be selected. In natural populations selection is rarely directed at a single trait. Survival and fecundity will depend on many aspects of an organism’s morphology, life history, and behavior simultaneously. For the Galapagos finches, survivors differed in several respects compared to the base population of finches before the drought. In addition to having larger beak depth, surviving birds had larger overall body mass, larger wing length, larger beak width and larger beak length. Was selection targeted specifically at beak shape, or was general size the primary determinant of survival?

In addition, body size and beak size are genetically correlated, so selection on one trait can result in a change in the other. Here we will see how to disentangle selection and response several characters when selection is operating simultaneously on the suite of traits.

Fitness Functions

We’ll start by rearranging the breeder’s equation a bit:

\[ R = h^2 S = \frac{V_A}{V_p} S = \frac{S}{V_p} \]

That last format is useful because it turns out that the quantity \( S/V_p \) is the slope of the regression of relative fitness on the trait (i.e. the fitness function). In calculating the fitness function, it is important to use relative fitness, defined as fitness relative to the population mean fitness: \( \frac{w_i}{\bar{w}} \). So, using \( b \) to indicate the slope of the fitness function, the breeder’s equation can be rewritten as:

eq. 1 \[ R = V_A \cdot b \]

Here is a fitness function for beak depth of the Galapagos finches during the 1977 drought. In this graph, birds with a beak depth of about 9.5 mm have a relative fitness of 1.0, which means that have average survival. Relative fitness is greater than 1.0 for birds with bigger beaks, and less than 1.0 for birds with smaller beaks.

There are several advantages for measuring selection from the slope of this regression instead of calculating the selection differential.

1. This graph provides a visual understanding of how fitness depends on the phenotype.
2. It is easy to calculate this regression for other measures of fitness besides survival (e.g. fecundity).
3. It is straightforward to extend this to examine simultaneous selection on multiple characters.

**Selection on more than one trait:** Remember that the general regression equation

\[ y = a + bx \]

has a slope, b, and an intercept, a. With a multiple regression, the dependent variable is predicted from two different independent variables simultaneously. There are then two partial regression coefficients, \( b_1 \) and \( b_2 \), that reflect the dependence on each of the two factors. Therefore the equation used to estimate simultaneous selection on two traits is

\[
  w = a + b_1 z_1 + b_2 z_2
\]

where once again \( w \) is relative fitness \( \frac{w_i}{\bar{w}} \).

The partial regression coefficient \( b_1 \) measures the strength of selection on trait 1, holding trait 2 constant. Similarly \( b_2 \) measures the strength of selection on trait 2, holding trait 1 constant. That makes this a convenient way to separate the relative contribution of several traits to the total variation in fitness.

What would the equation look like for measuring selection on three traits?

For now we won’t worry about exactly how those slopes are computed, and just say that there are many computer programs that will do it for you.

The coefficients \( b \) are usually called the **directional selection gradients**.

**Genetic Correlations among Characters**

A particular gene will often have effects on several different traits, a process known as **pleiotropy**. Because several traits often share part of the same underlying genetic architecture, they may be genetically correlated. Previously we showed how the total variation in a trait can be partitioned into genetic and environmental variance components. The total covariance between two traits can also be partitioned into genetic and environmental covariances. And just as the additive genetic variance is responsible for the similarity of parents and offspring, the additive genetic covariance structure determines the correlated inheritance of several traits.

**Measuring genetic covariances.** Just as the genetic variance is measured by the covariance among relatives, genetic covariances are also measured by the similarity among relatives. The only difference is that we’ll follow **two different** traits, for example beak depth in parents vs. beak width in offspring. As we have seen before, there is
significant additive genetic variance for beak depth, so parents with larger than average beaks have offspring with larger than average beaks. In the second graph there is a positive genetic covariance between beak depth and beak width. Parents with deeper than average beaks produce offspring with wider than average beaks (in addition to being deeper).

As we’ll see next, selection on one trait can result in a response in the other.

**Response to selection on correlated characters**

In natural populations, where selection is acting simultaneously on several correlated characters, the total response to selection will be a combination of direct selection on a particular trait, plus indirect selection resulting from a correlated response to selection on some other trait.

\[
\text{Total Response} = \text{Response to direct selection on this trait} + \text{Response to indirect selection acting on other correlated traits}
\]

The response to direct selection will be proportional to the additive genetic variance for that trait. The response to indirect selection will be proportional to the additive genetic covariance between this trait and the other selected trait.

\[
R_1 = V_{A_1} \cdot b_1 + COV_{A_1} \cdot b_2 \\
R_2 = COV_{A_1} \cdot b_1 + V_{A_2} \cdot b_2
\]

This system of equations can be written much more compactly in matrix form:

\[
\mathbf{R} = \mathbf{G} \mathbf{b}
\]

In equation 4, \( \mathbf{R} \) is now a column vector showing the response in each character, \( \mathbf{b} \) is now a column vector of regression coefficients (i.e. selection gradients), and \( \mathbf{G} \) is the additive genetic variance-covariance matrix that has the additive genetic variance for each trait along the diagonal and additive genetic covariances in the off-diagonal elements.

\[
\begin{bmatrix}
R_1 \\
R_2
\end{bmatrix} =
\begin{bmatrix}
V_{A_1} & COV_{A_1} \\
COV_{A_1} & V_{A_2}
\end{bmatrix}
\begin{bmatrix}
b_1 \\
b_2
\end{bmatrix}
\]

What would this equation look like for three traits?
Example: Let’s imagine that there are two genetically correlated traits. One is not under selection but second trait is. Therefore the partial regression coefficients are 0 for trait 1 and +2 for trait 2. Let the additive variance be 10 for trait 1 and 20 for trait 2, and assume the covariance between them is 5. What will be the net response to selection? Substituting those values into equations 3, we get

\[
R_1 = 10 \cdot 0 + 5 \cdot 2 = 10 \\
R_2 = 5 \cdot 0 + 20 \cdot 2 = 40
\]

or in matrix form (eq 4):

\[
\begin{bmatrix} 10 \\ 40 \end{bmatrix} = \begin{bmatrix} 10 & 5 \\ 5 & 20 \end{bmatrix} \cdot \begin{bmatrix} 0 \\ 2 \end{bmatrix}
\]

There is a response in trait 1, even though there was no selection acting directly upon it. It responded because it was genetically correlated with a second trait that was under selection.

For another example, let’s imagine there is simultaneous selection on both traits. The partial regression coefficients of the fitness function are \(b_1=-1\) and \(b_2=+2\). Selection favors a decrease in the first trait and an increase in the second. As before, let the additive variance be 10 for trait 1 and 20 for trait 2, and assume the covariance between them is 5. What will be the net response to selection? Substituting those values into equations 3, we get

\[
R_1 = 10 \cdot (-1) + 5 \cdot 2 = 0 \\
R_2 = 5 \cdot (-1) + 20 \cdot 2 = 35
\]

or in matrix form:

\[
\begin{bmatrix} 0 \\ 35 \end{bmatrix} = \begin{bmatrix} 10 & 5 \\ 5 & 20 \end{bmatrix} \cdot \begin{bmatrix} -1 \\ 2 \end{bmatrix}
\]

We predict that there will be no change in trait 1, and an increase of 35 units for trait 2. Even though selection favored a decrease in trait 1, there was no net response because it was balanced by indirect selection acting through trait 2. Similarly the response in trait 2 was somewhat less than before because of the conflicting selection acting through trait 1.

Your turn:

Coltman et al. (1995) studied selection on horn size and body size in bighorn sheep in a population in Alberta, Canada. Much of the mortality among rams in that population came from hunting. Hunters preferentially took large rams, so selection favored sheep with smaller horns and smaller body size. They estimated the selection gradient as
\[ \mathbf{b} = \begin{bmatrix} -0.24 \\ -0.20 \end{bmatrix} \]. There was significant genetic variation for both traits, and the variance-covariance matrix was: \( \mathbf{G} = \begin{bmatrix} 11.95 & 4.57 \\ 4.57 & 10.01 \end{bmatrix} \). What is the predicted response to selection?

**Tradeoffs**

An important class of correlated traits are those that show negative genetic covariances, or tradeoffs. There are lots of kinds of tradeoffs that are commonly observed: seed size vs. seed number, longevity vs. fecundity, survival vs. growth, etc. Often they arise because limited resources must be allocated to one function or another, but not both. Those kinds of tradeoffs can constrain the response to selection.

\[ \begin{array}{c}
\text{The predicted response to selection in bighorn sheep horn size and body size is } \\
\mathbf{R} = \begin{bmatrix} -3.78 \\ -3.10 \end{bmatrix}.
\end{array} \]