9 Selection on Correlated Characters

The breeder’s equation \((R=h^2S)\) is best suited for plant and animal breeding where the parents can be chosen based on very specific traits. 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 not only had deeper beaks, they also differed in several other respects compared to the base population of finches before the drought. The surviving birds also had larger overall body mass, larger wing length, larger beak width and larger beak length. Was selection targeted specifically at beak depth, or was general size the primary determinant of survival? How can we determine the actual target of selection? In addition, those traits are all 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 for several characters when selection is operating simultaneously on the suite of traits.

In other cases, traits that increase one component of fitness (such as survival) may decrease another (such as reproduction). Natural selection will reflect the net effect of various combinations of traits and their various costs and benefits to the organism.

9.1 Fitness functions and selection gradients

We’ll start with breeder’s equation (eq. 8.1) and use the definition of heritability from equation 8.2: \(R = h^2S\) or \(R = \frac{V_A}{V_P} S\). That can then be rearranged to yield \(R = \frac{V_A}{V_P} S\).

This last format is useful because it turns out that the quantity \(S/V_p\) is the slope of a regression of relative fitness on the trait (Fig. 9.1):

\[
\frac{w_i}{W} = a + bX_i
\]

where \(w\) is a measure of fitness and \(X_i\) is the phenotype of the \(i\)th individual, \(a\) is an intercept and \(b\) is the slope of the regression. We call that slope \((b)\) the “directional selection gradient”. Positive selection gradients indicate directional selection for larger trait values, negative slopes indicate selection for smaller trait values. If the slope is zero then there is no selection, i.e. no relationship between the phenotype and relative fitness. Notice that figure 9.1 is slightly different from the fitness graphs in Section 8.7 because it uses the relative fitness \(\frac{w_i}{W}\), instead of absolute fitness for the dependent variable.

Figure 9.1 Fitness function for beak size of Galapagos finches during the drought of 1977. The slope of his line \((b)\) is a measure of the selection gradient for beak depth. In this case \(b=0.4..\)
Using the selection gradient \( b \) the breeder’s equation can be rewritten as:

\[
R = V_a \cdot b
\]

Equation 9.1 was popularized by Russell Lande and is sometimes known as the “Lande Equation”. For example, Figure 9.1 shows the 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 they 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. On that graph the slope is \( b=0.4 \).

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

- In nature there is often not an all-or-none distinction between the selected parents and the unselected adults. Different individuals just have different degrees of reproductive success.
- It is easy to calculate this regression for other measures of fitness besides survival (e.g. fecundity).
- It is straightforward to extend this approach to examine simultaneous selection on multiple characters.
- The fitness function graph provides a visual understanding of how fitness depends on the phenotype.

### 9.1.1 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 the relative fitness of a particular individual, \( \frac{w_i}{W} \).

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 equation 9.2 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.

9.2 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 similarity 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 (Fig. 9.2a). In the second graph there is a positive genetic covariance between beak depth and beak width (Fig 9.2b). 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 when two characters are genetically correlated.

9.3 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.
Total Response = Response to direct selection on this trait + Response to indirect selection acting on other correlated traits

As we saw in eq. 9.2, the response to direct selection will be proportional to the additive genetic variance for that same trait. In addition that character may also change through indirect response to selection on another trait. The indirect response to selection on trait 2 will be proportional to the additive genetic covariance between traits 1 and 2. So the total response of character 1 to simultaneous selection on both traits is

\[ R_1 = V_{A,1} \cdot b_1 + COV_{A,12} \cdot b_2 \]  
\[ \text{eq. 9.3} \]

As before \( V_{A,1} \) is the additive variance for character 1, \( COV_{A,12} \) is the additive genetic covariance between the two traits, and \( b_1 \) and \( b_2 \) are the selection gradients on each trait.

You end up with a system of equations describing the response of each character to selection:

\[ R_1 = V_{A,1} \cdot b_1 + COV_{A,12} \cdot b_2 \]
\[ R_2 = COV_{A,12} \cdot b_1 + V_{A,2} \cdot b_2 \]
\[ \text{eqns. 9.4} \]

What would this set of equations look like for three traits?

9.4 Matrix notation:

Those equations quickly become messy to write out in long form if there are more than two or three traits because you need to include covariance terms for all possible pairs of traits.

This system of equations 9.4 can be written much more compactly in matrix form:

\[
\begin{bmatrix}
R_1 \\
R_2
\end{bmatrix} =
\begin{bmatrix}
V_{A,1} & COV_{A,12} \\
COV_{A,12} & V_{A,2}
\end{bmatrix}
\begin{bmatrix}
b_1 \\
b_2
\end{bmatrix}
\]

or simply

\[ R = Gb \]  
\[ \text{eq. 9.5} \]

In equation 9.5 the boldface characters indicate that they refer to matrices and vectors. \( R \) is a column vector showing the response in each character, \( b \) is now a column vector of regression coefficients (i.e. selection gradients), and \( G \) 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. Because of the way matrix operations are defined, equations 9.4 and 9.5 are exactly the same, just written in different formats.

See Appendix A for a brief refresher on matrix notation and how to multiply matrices.
**Warmup Example:** Let's imagine that there are two genetically correlated traits. The first trait is not under selection but second trait is. Therefore the partial regression coefficients are $b_1 = 0$ for trait 1 and $b_2 = +2$ for trait 2. Let the additive variance be $V_a=10$ for trait 1 and $V_a=2.5$ for trait 2, and assume the covariance between them is $COV_a=5$. What will be the net response to selection? Substituting those values into equations 9.4, we get

$$R_1 = 10 \cdot 0 + 5 \cdot 2 = 10$$
$$R_2 = 5 \cdot 0 + 2.5 \cdot 2 = 5$$

or in matrix form as in eq 9.5:

$$\begin{bmatrix} R_1 \\ R_2 \end{bmatrix} = \begin{bmatrix} 10 & 5 \\ 5 & 2.5 \end{bmatrix} \begin{bmatrix} 0 \\ 2 \end{bmatrix}.$$ 

so $\mathbf{R} = \begin{bmatrix} 10 \\ 5 \end{bmatrix}$

There is a response of +10 units 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 experienced positive selection.

Notice also that equations 9.4 and 9.5 give exactly the same results. That is because they are *exactly the same equations* in different formats.

For another example, let's imagine there is now 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 9.5, we get

$$\begin{bmatrix} R_1 \\ R_2 \end{bmatrix} = \begin{bmatrix} 10 & 5 \\ 5 & 2.5 \end{bmatrix} \begin{bmatrix} -1 \\ 2 \end{bmatrix}.$$ 

What is the expected response for this pattern of selection?

$$R_1 = \underline{\hspace{2cm}}$$

$$R_2 = \underline{\hspace{2cm}}$$

In this case we predict that there will be no change in either trait. Even though there was direct selection on both traits, there was no net response. Any directional selection on trait 1 it was balanced by indirect selection acting through trait 2. Similarly the response in trait 2 was offset by the conflicting selection acting through trait 1.’
9.5 How fast will plants be able to adapt to changing climate? Evolution in the partridge pea, *Chamaecrista fasciculata*.

The increase in atmospheric concentrations of greenhouse gases is causing a general increase in global mean temperatures. As the Earth warms plants will experience new environments. One prediction is that in the next 50 years the climate of Minnesota will become similar to the current climate in Kansas and Oklahoma. How fast will plants be able to adapt to those new conditions?

Julie Etterson, then a graduate student at the University of Minnesota, chose to study a particular prairie plant and its evolutionary potential to respond to climate change. She chose the partridge pea, an annual legume that is common in the Midwestern prairies. Her approach was to examine the growth of plants from Minnesota when they were planted in more southern parts of the range. The idea was that those southern sites were similar to what Minnesota might experience in the next few decades. In order to project the possible future evolution of those plants she first needed to measure the genetic variation for several traits. She also measured the fitness functions to determine the pattern of selection on those traits under the warmer climatic regime.

Etterson planted seeds of the partridge pea into the field in three locations (Minnesota, Kansas, and Oklahoma). We’ll concentrate only on her results from Oklahoma, the warmest site.

During the season she returned to each plant and measured three traits: the timing of reproduction (RS), the number of leaves (LN), and the leaf area (SLA). Then, at the end of the season she counted the number of seeds produced by each plant (i.e. its fitness) and computed the fitness function for the three traits as in equation 9.2.

Write out the version of equation 9.2 that she would have used to measure selection. What are the X variables? What is the Y variable?
Here are the selection gradients that she found for the Oklahoma site:

\[ b_{RS} = +0.03 \]
\[ b_{LN} = +0.33 \]
\[ b_{SLA} = -0.18 \]

What do those tell you about the direction of selection on leaf number? What does it tell you about selection on leaf area?

Fitness was highest for plants with slightly faster reproduction, more leaves, and thicker leaves (i.e. smaller leaf area per gram of leaf tissue).

She measured the genetic variance by examining the similarity among relatives. Instead of parent-offspring regressions she used the similarity among siblings from many sets of crosses but the principles are similar. By setting up a number of controlled crosses in the greenhouse she was able to produce full siblings (that share both parents) as well as half-siblings (that have only the pollen donor in common). Etterson could then use those different degrees of genetic relatedness to determine the genetic components of variance and covariance for each trait.

Here are the additive genetic components of variance (Va) for each of the three traits:

\[ V_{RS} = 38.2 \]
\[ V_{LN} = 1.58 \]
\[ V_{SLA} = 0.085 \]

And here are the additive genetic covariances for each pair of traits (COVa):

\[ \text{Cov}_{RS,LN} = -10.1 \]
\[ \text{Cov}_{RS,SLA} = -12.8 \]
\[ \text{Cov}_{LN,SLA} = 1.16 \]

In words, what does her measurement of \( \text{Cov}_{RS,LN} \) tell you? _____

Let’s look first at leaf number by itself.

Using equation 9.1 and her estimates of Va and b, what is the predicted response to selection on leaf number at the Oklahoma site?

\[ R_{LN} = \]
Now let's look at the pair of traits Leaf Number and Leaf Area.

From her estimates of $b_{LN}$ and $b_{SLA}$ we see that selection favors an increase in leaf number and a decrease in leaf area. But the covariance between them is positive. An increase in leaf number will also indirectly increase leaf area (opposite to its selection gradient). Similarly, selection to decrease leaf area would also indirectly decrease leaf number, (again, opposite to the direct selection on leaf number).

What is the predicted joint response to selection for the two traits Leaf Number and Specific Leaf Area? (hint: you’ll need two equations as in 9.4). How does that compare to your result when you look at leaf number alone?

$$R_{LN} = \quad \text{______________}$$

$$R_{SLA}= \quad \text{______________}$$

The simultaneous selection on both characters in opposite directions constrains the evolutionary response of each, so they are not able to adapt as quickly as you might predict from looking each trait by itself.

Figure 9.3 shows why the selection response is so slow. In that figure the points show the “breeding values” of hypothetidal plants from this population, which is a way to visualize the genetic variation. There is additive genetic variation in both leaf number and leaf area. The positive covariance between them means that high breeding values for leaf number also have high values for leaf area.

The arrow shows the direction of selection, which favors an increase in leaf number and a decrease in leaf area. Because the direction of selection is almost perpendicular to the major axis of genetic variation there will be relatively little response to selection.

Figure 9.3. The direction of selection (arrow) is almost perpendicular to the major axis of genetic covariation between leaf number and leaf area.
9.6 **Tradeoffs can constrain evolutionary response.**

It is often true that genetic correlations among traits impose constraints on the simultaneous response to selection on those characters. There are many kinds of tradeoffs that are commonly observed, for example, seed size vs. seed number, longevity vs. fecundity, survival vs. growth, etc. Often they arise because limited resources can be allocated to one function or another, but not both. For example, the ideal individual would live forever, grow fast, and produce lots of offspring. But there are always tradeoffs—the same resources can’t be used for both growth of the parent and investment in offspring, so selection for alleles that increase growth rate necessarily decreases reproduction (and vice versa). Thus the net result of evolution is often a compromise between those conflicting demands.

9.7 **Your turn:**

Etterson also planted seeds from the same Minnesota population in Kansas, where the climate difference is slightly less extreme. As before, she measured the genetic variances and covariances and estimated the selection gradient for each of the three traits. What is the predicted response to selection at the Kansas site? How does the simultaneous selection on the three traits compare with the predicted response for each trait separately?

In Kansas,

\[
G = \begin{bmatrix}
0.88 & -8.85 & -67.7 \\
-8.85 & 1.06 & 4.04 \\
-67.7 & 4.04 & 0.075
\end{bmatrix}
\quad b = \begin{bmatrix}
0.03 \\
0.45 \\
-0.06
\end{bmatrix}
\]

for the three traits RS, LN, and SLA.
Appendix A: Very short introduction to matrices

Let’s start with a generic set of equations predicting a set of Y’s (Y_1 – Y_3) from a set of X variables (X_1 to X_3). The coefficients a_{ij} describe the effect of X_j on Y_i.

\[
\begin{align*}
Y_1 &= a_{11} X_1 + a_{12} X_2 + a_{13} X_3 \\
Y_2 &= a_{21} X_1 + a_{22} X_2 + a_{23} X_3 \\
Y_3 &= a_{31} X_1 + a_{32} X_2 + a_{33} X_3
\end{align*}
\text{eqns. A1}
\]

Written this way you can see that there is a clear structure to the set of equations. All of the X variables line up in columns and the coefficients \( a \) are numbered according to their row and column.

We can rewrite that in matrix form by collecting the \( a \) coefficients together in one matrix and the X variables in another, and the Y variables in a third.

\[
\begin{bmatrix}
Y_1 \\
Y_2 \\
Y_3
\end{bmatrix}, \quad
\begin{bmatrix}
a_{11} & a_{12} & a_{13} \\
a_{21} & a_{22} & a_{23} \\
a_{31} & a_{32} & a_{33}
\end{bmatrix}, \quad
\begin{bmatrix}
X_1 \\
X_2 \\
X_3
\end{bmatrix}
\]

Now the set of equations A1 can be re-written as simply

\[
Y = AX
\]

By convention, boldface symbols are used to represents matrices and vectors.

That translation from the format of equations A1 to equation A2 works because there are defined rules for multiplying matrices and vectors.

**General rules for multiplying matrices**

Assume there is a matrix A with \( k \) rows and \( m \) columns, and a matrix B with \( m \) rows and \( n \) columns. The product of those two matrices will have dimensions \( k \times n \).

In symbols, we can write that as \( Y_{k\times n} = A_{k\times m} B_{m\times n} \).

To find the element \( Y_{ij} \), you sum the products of the elements in row i of A and the corresponding elements of column j of B.

\[
Y_{ij} = \sum_k a_{ik} B_{kj}
\]

Here is a numerical example: A is now a 4x3 matrix, B is a 3x2 matrix and the result Y will have 4 rows and 2 columns. To find \( Y_{ij} \) we will sum the products of the elements of row i in A and column j in B. As an example let’s look at element \( Y_{21} \) which is highlighted in bold in the following example.

\[
\begin{bmatrix}
22 & 28 \\
49 & 64 \\
76 & 100 \\
103 & 136
\end{bmatrix} = \begin{bmatrix}
1 & 2 & 3 \\
4 & 5 & 6 \\
7 & 8 & 9 \\
10 & 11 & 12
\end{bmatrix} \begin{bmatrix}
1 & 2 \\
3 & 4 \\
5 & 6
\end{bmatrix}
\]
The element in the second row and first column of \( Y \) \((Y_{21})\) is the sum of the products of elements in the second row of \( A \) and the first column of \( B \): 
\[
Y_{21} = A_{21}B_{11} + A_{22}B_{21} + A_{23}B_{31} \text{ or } Y_{21} = 4 \cdot 1 + 5 \cdot 3 + 6 \cdot 5 = 49.
\]
Similarly, the element in the third row and second column of \( Y \), will be the sum of the products of elements in the third row of \( A \) and the second column of \( B \): 
\[
Y_{32} = A_{31}B_{12} + A_{32}B_{22} + A_{33}B_{32} = 7 \cdot 1 + 8 \cdot 2 + 9 \cdot 3 = 50.
\]

Often one of the matrices will have a single row or column, but the general procedure is exactly the same. If matrix \( B \) has only a single column then \( Y \) will also have only a single column. But just as before, the element in the third row and first column of \( Y \) will be the sum of the products of the elements in the third row of \( A \) and the first column of \( B \).

\[
\begin{bmatrix}
. \\
. \\
50 \\
. \\
\end{bmatrix}
\begin{bmatrix}
1 & 2 & 3 \\
4 & 5 & 6 \\
7 & 8 & 9 \\
10 & 11 & 12 \\
\end{bmatrix}
\begin{bmatrix}
1 \\
2 \\
3 \\
\end{bmatrix}
\]

\[
7 \cdot 1 + 8 \cdot 2 + 9 \cdot 3 = 50.
\]

What are the other three elements of \( Y \) in this example? ______________

Notice that the dimensions must be compatible. To multiply matrices, the number of columns of the first matrix must equal the number of rows of the second. The result will have the same number of rows as the first matrix and the same number of columns as the second. Therefore \( A_{4 \times 3} B_{3 \times 1} \) is valid because the number of columns of \( A \) and rows of \( B \) match. The reverse (\( B_{3 \times 1} A_{4 \times 3} \)) is not allowed.
Answers

p 2. For three traits,  
\[ w = a + b_1z_1 + b_2z_2 + b_3z_3 \]

p 5.  
\[ R_1 = 10 \cdot -1 + 5 \cdot 2 = 0 \]
\[ R_2 = 5 \cdot -1 + 2.5 \cdot 2 = 0 \]

p 6. Let \( s \) be the number of seeds produced by each plant (her measure of fitness). The phenotypes she measured were reproductive stage, leaf number and leaf area (RS, LN, and SLA). So relative fitness (the \( Y \) variable) will be  
\[ w_i = \frac{s}{a} \]
and her version of equation 9.2 will be  
\[ w_i = a + b_1RS_i + b_2LN_i + b_3SLA_i. \]

p 7. Selection on leaf number if positive and selection on leaf area is negative. That means that plants with many small leaves have higher relative fitness.

\( \text{COV}_{RS, LN} = -10.1 \) means that there is a negative genetic covariance between reproductive stage and leaf number. Alleles that increase leaf number decrease reproductive stage and vice versa.

The additive genetic variance for leaf number is 1.58, and the selection gradient is 0.33, so the response is  
\[ R_{LN} = V_A \cdot b = 1.58 \cdot 0.33 = 0.52 \]

p 8. For simultaneous selection on leaf number and leaf area,
\[ R_{LN} = (1.58 \cdot 0.33) + (1.16 \cdot -0.18) = 0.31 \]
\[ R_{SLA} = (1.16 \cdot 0.33) + (0.085 \cdot -0.18) = 0.36 \]

p 9. In Kansas the predicted response is  
\[ R_{-} = \begin{bmatrix} 0.005 \\ 0.005 \\ -0.001 \end{bmatrix} \]

p 11.  
\[ R_{-} = \begin{bmatrix} 0.005 \\ 0.005 \\ -0.001 \end{bmatrix} \]