

# Notes on Fitness Sensitivities

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## Videos

1. [Calculating fitness sensitivities.](#)

## 1 Introduction

### 1.1 Population Growth with Age Structure

We start with a simple example. Assume that we have an organism with two age-classes. Then the population is now described by the following model:

$$n_1(t+1) = f_1 n_1(t) + f_2 n_2(t) \quad (1)$$

$$n_2(t+1) = p_1 n_1 \quad (2)$$

where  $n_1$  is the number in stage 1.  $n_2$  is the number in stage 2,  $f_1$  is the fertility of stage 1 individuals,  $f_2$  is the fertility of stage 2 individuals, and  $p_1$  is the survivals of 1's to age class 2.

The question we wish to answer: Is there a unique exponential growth rate for such a population analogous to the unstructured case? Imagine you start with a total population size ( $N(0) = n_1(0) + n_2(0)$ ) of 10. What will the population look like in one time step? If there are 10 ones and zero twos, then we have

$$n_1(1) = 10f_1 \quad (3)$$

$$n_2(1) = 10p_1. \quad (4)$$

However, if there are zero ones and 10 twos, then we have a very different situation:

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$$n_1(1) = 10f_2 \quad (5)$$

$$n_2(1) = 0. \quad (6)$$

These two populations can only increase at the same rate in the degenerate case where  $f_1 = f_2$  and  $p_1 = 0$ . The solution to this apparent paradox is that a structured population will grow geometrically only when the ratios between the different classes of the population remain constant. In the age-structured case, we call this the *stable age distribution* and in the state-structured case, we call it the stable stage distribution.

The two sets of equations represented in equations 4 or 6 can be represented in the compact notation of matrices and the rules for working with them derived from linear algebra.

First, some definitions. A *matrix* is a rectangular array of numbers. We typically represent matrices by bold face upper-case letters. We indicate an element of a matrix by the lower case letter in plain face, indexed by subscripted row followed by column numbers:

$$\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}.$$

$a_{12}$  therefore represents the element from the first row and second column of matrix  $\mathbf{A}$

A vector is simply a list of numbers. Vectors are typically bold face lower-case letters and elements are indexed by their position in the vector with a subscripted number. Vectors can come as either row or column vectors.

$$\mathbf{n}(t) = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}.$$

A scalar is a single number:  $\lambda = 1.05$ .

## 1.2 The Leslie Matrix

The *Leslie matrix* is a special matrix for demography and population biology. It is referred to as a Leslie Matrix after its inventor Sir Paul Leslie (Leslie 1945, 1948). A Leslie matrix contains: (1) age-specific fertilities along the first row, (2) age-specific survival probabilities along the subdiagonal, and (3) zeros everywhere else. Here is an example of a  $5 \times 5$  Leslie matrix:

$$\mathbf{A} = \begin{bmatrix} 0 & F_2 & F_3 & F_4 & F_5 \\ P_1 & 0 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 & 0 \\ 0 & 0 & P_3 & 0 & 0 \\ 0 & 0 & 0 & P_4 & 0 \end{bmatrix} \quad (7)$$

The Leslie matrix is a special case of a *projection matrix* for an age-classified population. With age-structure, the only transitions that can happen are from one age to the next and from adult ages back to the first age class. Can you imagine a projection matrix structured by something other than age?

### 1.3 The Life Cycle Diagram

It is useful to think of the matrix entries in a life-cycle manner. The entry  $a_{ij}$  is the transition probability of going from (st)age  $j$  to (st)age  $i$ .<sup>1</sup>

$$a_{ij} = a_{i \leftarrow j}. \quad (8)$$

We formalize this life-cycle approach by noting the linkages between the projection matrix and the life-cycle graph. A life-cycle graph is a digraph (or directed graph) composed two things: (1) nodes, which represent the states (ages, stages, subgroups, localities, etc.) and (2) edges, which represent transitions between states. Figure 1 presents a simple age-structured life cycle with five ages and reproduction in age classes 2-5.

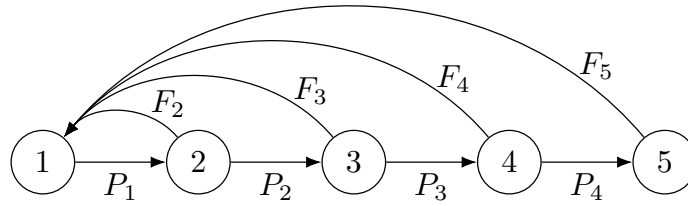


Figure 1: Life cycle diagram corresponding to the Leslie matrix of equation 7.

There are a number of desirable properties of demographic projection matrices. These properties are required for all the important results that we will discuss to apply. Every demographic matrix is non-negative (all its entries are greater than or equal to zero). In general, we are only interested in non-negative matrices since all survival probabilities and fertility rates must be non-negative. Indeed, any rate of interest in demography must be positive. We have seen that it is important for the elements of a structured population model to come to some sort of stable distribution. However, not all population models do this. Fortunately, the conditions that allow a population to converge to its stable age distribution are simple and the use of the life cycle graph greatly facilitates determining if the conditions do indeed apply. In order for a population to converge on its stable population structure, it must be *irreducible*. A matrix is irreducible if and only if there is a path between every node and every other node in the life cycle graph. Irreducibility is necessary but not sufficient for stability. The second, sufficient condition is called *primitivity*. An irreducible non-negative matrix is primitive if all its elements become positive when raised to sufficiently high powers. A matrix is primitive if the greatest common divisor of all loops in the corresponding life-cycle graph is 1.

Figures 2 and 3 show two examples of reducible life cycles that will not converge to stable distributions.

Figure 4 presents an imprimitive life cycle. Reproduction only occurs in the even ages. This causes bulges in the age pyramid that never get evened out. Consequently, the population never converges to a stable age distribution.

<sup>1</sup>The column-to-row convention of the Leslie Matrix is transposed from the convention commonly found in sociological applications (e.g., social mobility matrices).

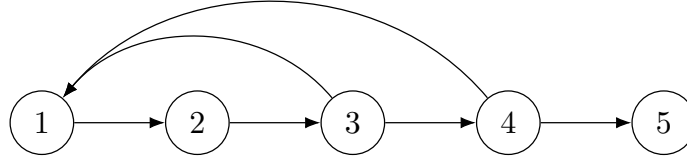


Figure 2: A reducible life cycle.

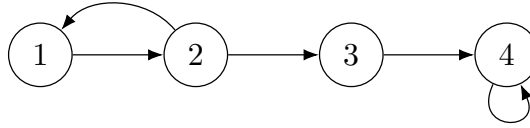


Figure 3: A weird reducible life cycle.

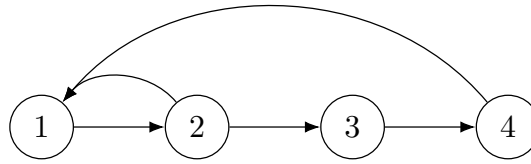


Figure 4: An imprimitive life cycle.

Two ways of insuring that a life cycle will be primitive are: (1) having two consecutive age classes in which reproduction occurs or (2) having a life cycle with a self loop. A life cycle with a self-loop is illustrated in figure 5.

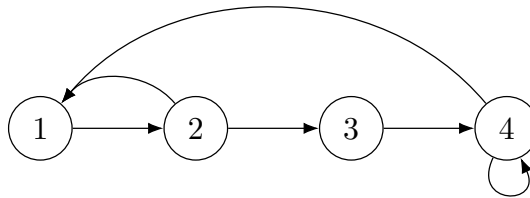


Figure 5: Life cycles with self loops are primitive.

## 1.4 Growth of Structured Populations

Having redefined the population model in matrix form, we can write it in a more compact notation of matrix algebra:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \tag{9}$$

Let's now assume that there is a solution to the exponential growth model in a structured population. Write the population model as:

$$\mathbf{A}\mathbf{n} = \lambda\mathbf{n} \quad (10)$$

Now solve for  $\lambda$ . The rules of linear algebra make this a little trickier than just dividing both sides by  $\mathbf{n}$ . Here are the steps we need:

$$\mathbf{A}\mathbf{n} - \lambda\mathbf{n} = 0 \quad (11)$$

$$\mathbf{A}\mathbf{n} - \lambda\mathbf{I}\mathbf{n} = 0 \quad (12)$$

$$(\mathbf{A} - \lambda\mathbf{I})\mathbf{n} = 0 \quad (13)$$

$\mathbf{I}$  is an identity matrix of the same rank as  $\mathbf{A}$  (ones along the diagonal, zeros elsewhere)

It's a fact of linear algebra, that the solution to equation 10 exists only if the determinant of the matrix  $(\mathbf{A}\mathbf{n} - \lambda\mathbf{I})$  is zero. For the  $2 \times 2$  case of equation 10, the determinant is simple. For any  $2 \times 2$  matrix the determinant is given by:

$$\det \begin{bmatrix} a & b \\ c & d \end{bmatrix} = ad - bc$$

Determinants of matrices of larger rank are, necessarily, more complex.

So, using our fact of linear algebra, we can proceed with the calculation:

$$(\mathbf{A} - \lambda\mathbf{I}) = \begin{bmatrix} f_1 & f_2 \\ p_1 & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix} = \begin{bmatrix} f_1 - \lambda & f_2 \\ p_1 & -\lambda \end{bmatrix}$$

$$\det(\mathbf{A} - \lambda\mathbf{I}) = -(f_1 - \lambda)\lambda - f_2p_1$$

$$\lambda^2 - f_1\lambda - f_2p_1 = 0$$

Use the quadratic equation to solve for  $\lambda$ :

$$\frac{-f_1 \pm \sqrt{f_1^2 - 4f_2p_1}}{2f_1}$$

We can use a numerical example to make this more concrete. Define:

$$\mathbf{A} = \begin{bmatrix} 1.5 & 2 \\ 0.5 & 0 \end{bmatrix} \quad (14)$$

$$\det(\mathbf{A} - \lambda\mathbf{I}) = \begin{bmatrix} 1.5 - \lambda & 2 \\ 0.5 & -\lambda \end{bmatrix}$$

$$\lambda^2 - 1.5\lambda - 1 = 0$$

$$(\lambda - 2)(\lambda + 0.5) = 0$$

Matrix  $\mathbf{A}$  has two roots:  $\lambda = 2$  and  $\lambda = -0.5$ . These roots are known as the *eigenvalues* of matrix  $\mathbf{A}$ . One of these eigenvalues is the growth rate of the population, but which one? For this  $2 \times 2$  example, there are two roots. For larger matrices, there are more. In fact, there are always as many eigenvalues as there are rows (or columns since we are dealing with square matrices) in the matrix. One could imagine this getting a bit hairy. Thankfully, a handy theorem from linear algebra, known as the Perron-Frobenius theorem, tells us that a square non-negative matrix that is irreducible and primitive will have a single eigenvalue which is positive, real, and strictly greater than all the others. Our matrix 14 fulfills these criteria, so we may conclude that the growth rate of this population is  $\lambda = 2$ . This is reassuring since a negative growth rate is an idea that's a little hard to fathom – at least for the moment.<sup>2</sup>

We began this chapter with the statement that for an age-structured population to grow geometrically, it must maintain constant ratios between its age classes. There is a special vector that goes hand-in-hand with the eigenvalue called, strangely enough, an *eigenvector*. Let's keep up with our example. Remember that the eigenvalues of this model are  $\lambda = 2$  and  $\lambda = -0.5$ . That means that we can write our model as:

$$\mathbf{A} = \begin{bmatrix} 1.5 & 2 \\ 0.5 & 0 \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \end{bmatrix} = \begin{bmatrix} 2n_1 \\ 2n_2 \end{bmatrix} \quad (15)$$

We now solve this system to two equations and find that  $n_1 = 4n_2$  is a solution. That is, if there are four times the number of stage ones as there are stage twos, the population will grow geometrically.

## 1.5 Projection, The Simplest Form of Analysis

Most demographers use matrices primarily for projection of populations into the future. Projection is in fact the simplest form of analysis of a population model. When you make a projection, you ask the question: “How big will the population be if the following rates apply for the next  $t$  years?” Your projection will only apply to the specific assumptions you build into it, but it may nonetheless yield more general, qualitative insight.

Consider the plot in figure 6 of a population that does not start off in its stable age distribution. Even though the rates remain constant, the population oscillates around its general upward trajectory. If we let it run long enough, the oscillations dampen and we see the straight line on semilog axes, indicating geometric increase.

### 1.5.1 Fun facts about Eigenvalues

The Perron-Frobenius Theorem guarantees that one eigenvalue will be real, positive and absolutely greater than all others. This is called the *dominant eigenvalue* of the projection matrix. The dominant eigenvalue of the projection matrix is the asymptotic growth rate of the population described by that matrix. The dominant eigenvalue of the projection matrix is also the fitness

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<sup>2</sup>Note that the eigenvalues are the multiplicative growth rates. A declining population will not have a negative multiplicative growth rate. It will have a growth rate  $1 > \lambda > 0$ .

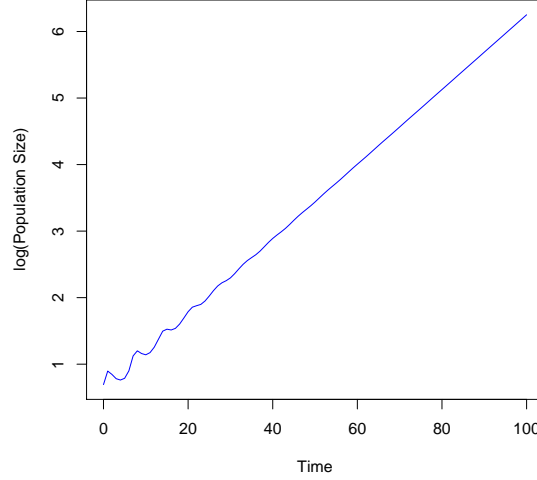


Figure 6: Projection of a population that does not start out in its stable age distribution.

measure of choice for age-structured populations.  $\log(\lambda) = r$ . That is, the natural logarithm of the dominant eigenvalue gives the annual rate of increase of the population. By calculating the eigenvalues of a projection matrix, you get lots of other important information.

## 1.6 Left Eigenvectors of the Projection Matrix

In matrix algebra, multiplication is not commutative,  $\mathbf{AB} \neq \mathbf{BA}$ . Thus, the left eigenvector of a matrix is distinct from the right eigenvector:

$$\mathbf{v}^* \mathbf{A} = \lambda \mathbf{v}^*, \quad (16)$$

where the asterisk denotes the complex-conjugate transpose

Define  $\mathbf{U}$  as a matrix of eigenvectors where each column  $i$  is the  $i$ th eigenvector of  $\mathbf{A}$ , and  $\mathbf{\Lambda}$  as a matrix with the eigenvalues of  $\mathbf{A}$  along the diagonal and zeros elsewhere, we have

$$\mathbf{AU} = \mathbf{U}\mathbf{\Lambda} \quad (17)$$

$$\mathbf{\Lambda} = \mathbf{U}^{-1}\mathbf{AU} \quad (18)$$

$$\mathbf{U}^{-1}\mathbf{A} = \mathbf{\Lambda}\mathbf{U}^{-1} \quad (19)$$

Equation 19 is the matrix formula for an eigensystem (Equation 16), suggesting that the rows of  $\mathbf{U}^{-1}$  must be the left eigenvectors of  $\mathbf{A}$ .

The left eigenvector, corresponding to the dominant eigenvalue, of a demographic projection matrix has a particular interpretation. It represents the age-specific *reproductive value* of the population. The reproductive value of the  $i$ th age class is the expected contribution of individuals

age  $i$  to the population in the distant future. This is an important concept in evolutionary biology which will be taken up repeatedly.

## 1.7 Spectral Decomposition of the Projection Matrix

We will now expand upon what we mean by reproductive value being the contribution to the population in the distant future. Suppose we are given an initial population vector,  $\mathbf{n}(0)$ . We can write  $\mathbf{n}(0)$  as a linear combination of the right eigenvectors,  $\mathbf{u}_i$  of the projection matrix  $\mathbf{A}$ .

$$\mathbf{n}(0) = c_1 \mathbf{u}_1 + c_2 \mathbf{u}_2 + \cdots + c_k \mathbf{u}_k$$

where the  $c_i$  are a set of coefficients.

We can collect the eigenvectors into a matrix where each column  $i$  is simply the  $i$ th eigenvector and the coefficients into a vector and re-write this equation as:

$$\mathbf{n}(0) = \mathbf{U} \mathbf{c}.$$

From this it is clear that  $\mathbf{c} = \mathbf{U}^{-1} \mathbf{n}(0)$ .  $\mathbf{U}^{-1}$  is just the matrix of left eigenvectors (or their complex conjugate transpose), so  $c_i = \mathbf{v}_i^* \mathbf{n}(0)$ .

Project the initial population vector  $\mathbf{n}(0)$  forward by multiplying it by the projection matrix  $\mathbf{A}$ :

$$\begin{aligned} \mathbf{n}(1) &= \mathbf{A} \mathbf{n}(0) \\ &= \sum_i c_i \mathbf{A} \mathbf{u}_i \\ &= \sum_i c_i \lambda_i \mathbf{u}_i \end{aligned}$$

Multiply again!

$$\begin{aligned} \mathbf{n}(2) &= \mathbf{A} \mathbf{n}(1) \\ &= \sum_i c_i \lambda_i \mathbf{A} \mathbf{u}_i \\ &= \sum_i c_i \lambda_i^2 \mathbf{u}_i \end{aligned}$$

We could keep going, but at this point it isn't hard to believe that the following holds:

$$\mathbf{n}(t) = \sum_i c_i \lambda_i^t \mathbf{u}_i \tag{20}$$

This is equivalent to:

$$\mathbf{n}(t) = \sum_i \lambda_i^t \mathbf{u}_i \mathbf{v}_i^* \mathbf{n}(0) \tag{21}$$



Equation 21 is known as the **Spectral Decomposition** of the projection matrix  $\mathbf{A}$

It is instructive to compare this to the solution for population growth in an unstructured (i.e., scalar) population, characterized by a geometric rate of increase  $a$ :

$$N(t+1) = aN(t)$$

$$N(t) = N(0)a^t$$

For the scalar case, the solution is exponential. For a  $k$ -dimensional matrix, this solution means that the population size at time  $t$  is a weighted sum of  $k$  exponentials. While both depend on the initial conditions, the  $k$ -dimensional case weights the initial population vector by the reproductive values of the  $k$  classes.

## 1.8 Matrix Perturbations

This derivation follows Caswell (2001). We start from the general matrix population model:

$$\mathbf{A}\mathbf{u} = \lambda\mathbf{u} \quad (22)$$

Now we perturb the system

$$(\mathbf{A} + d\mathbf{A})(\mathbf{u} + d\mathbf{u}) = (\lambda + d\lambda)(\mathbf{u} + d\mathbf{u}) \quad (23)$$

Multiply all the products and discard the second-order terms such as  $(d\mathbf{A})(d\mathbf{u})$

$$\mathbf{A}\mathbf{u} + \mathbf{A}(d\mathbf{u}) + (d\mathbf{A})\mathbf{u} = \lambda\mathbf{u} + \lambda(d\mathbf{u}) + (d\lambda)\mathbf{u}. \quad (24)$$

Simplify this to yield

$$\mathbf{A}(d\mathbf{u}) + (d\mathbf{A})\mathbf{u} = \lambda(d\mathbf{u}) + (d\lambda)\mathbf{u}. \quad (25)$$

Multiply both sides by  $\mathbf{v}^*$  to get

$$\mathbf{v}^*\mathbf{A}(d\mathbf{u}) + \mathbf{v}^*(d\mathbf{A})\mathbf{u} = \lambda\mathbf{v}^*(d\mathbf{u}) + \mathbf{v}^*(d\lambda)\mathbf{u}. \quad (26)$$

From the definition of a left eigenvector, we know that the first term on the left-hand side is the same as the first term on the right-hand side. Similarly, because the right and left eigenvectors are scaled so that  $\langle \mathbf{w}, \mathbf{v} \rangle = 1$ , the last term simplifies to  $d\lambda$ . We are left with

$$\mathbf{v}^*d\mathbf{A}\mathbf{u} = d\lambda. \quad (27)$$

When we do a perturbation analysis, we typically only change a single element of  $\mathbf{A}$ . Thus the basic formula for the sensitivity of the dominant eigenvalue to a small change in element  $a_{ij}$  is

$$\frac{\partial \lambda}{\partial a_{ij}} = v_i u_j. \quad (28)$$

In other words, the sensitivity of fitness to a small change in projection matrix element  $a_{ij}$  is simply the  $i$ th element of the left eigenvector weighted by the proportion of the stable population in the  $j$ th class (assuming vectors have been normed such that  $\langle \mathbf{v}, \mathbf{u} \rangle = 1$ ).

Eigenvalue Sensitivities are Linear Estimates of the Change in  $\lambda_1$ , Given a Perturbation, as illustrated in figure 7.

Hal Caswell has an open-access text on sensitivity analysis and matrix methods in demography (Caswell 2019).

## 1.9 Elasticities

Another measure of the change in a matrix given a small change in an underlying element is the eigenvalue elasticity:

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}}.$$

Elasticities are proportional sensitivities: they measure the linear change on a log scale. Given a 1% change in vital rate  $a_{ij}$  what percentage change will accompany  $\lambda$ ? This is an elasticity. A very important property of elasticities is that they sum to one:  $\sum_{i,j} e_{ij} = 1$ . As such, one can think of the elasticity of  $\lambda$  with respect to  $a_{ij}$  as measuring the proportion of the total selection on that trait. This interpretation is somewhat limited because it is conditioned on all other traits remaining constant and on the change being small.

Another interesting property of elasticities is that the summed elasticities of all outgoing transitions from a stage will be equal to the summed elasticities of all incoming transitions. In terms of the projection matrix, this means that the elasticities of all elements in column  $i$  will be equal to the summed elasticities of row  $i$ .

## 1.10 Relationship to Hamilton

The elasticities of the sub-diagonal elements of the Leslie matrix (i.e., the  $P_i$  from the life-cycle graph) are essentially the same thing that Hamilton (1966) calculates by differentiating the discrete-time Euler-Lotka equation. A major advantage of the matrix approach is the ease with which the sensitivities and elasticities can be calculated. Furthermore, the approach is easily extended to other types of structured models (i.e., not just age-structure) and to related measures such as the second derivatives of fitness, which provide an estimate the form of selection (stabilizing, directional).

Conceptually, it is illuminating to think of the force of selection on a given life-cycle transition as being simply a product of the reproductive value of the receiving stage and the fraction of the stable age distribution from the sending stage.

## 2 Eigenvalue Second Derivatives

We can measure the curvature of the fitness surface as the second derivative of  $\lambda$  with respect to traits  $a_{ij}$  and  $a_{kl}$ :

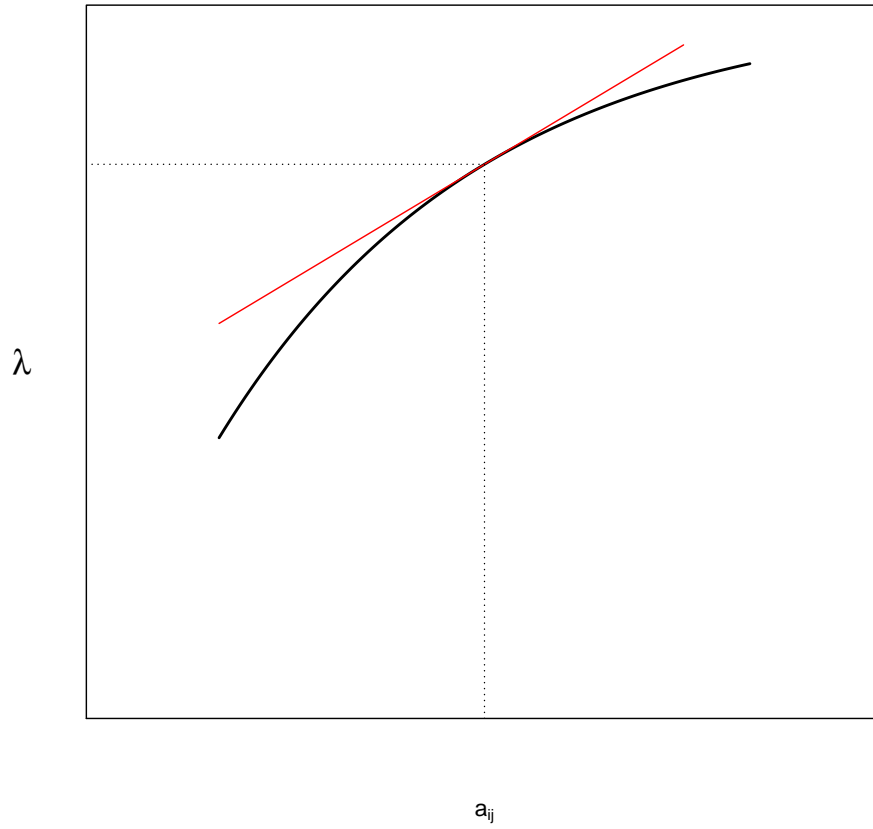


Figure 7: A fitness sensitivity is a linear approximation of the change in fitness resulting from a change in some matrix element  $a_{ij}$ . The fact that it is a linear approximation means that it is only likely to be accurate for small perturbations. The observed value of  $a_{ij}$  and the corresponding value of fitness,  $\lambda$ , are indicated by the dotted lines.

$$\frac{\partial^2 \lambda^{(1)}}{\partial a_{ij} \partial a_{kl}} = s_{il}^{(1)} \sum_{m \neq 1} \frac{s_{kj}^{(m)}}{\lambda^{(1)} - \lambda^{(m)}} + s_{kj}^{(1)} \sum_{m \neq 1} \frac{s_{il}^{(m)}}{\lambda^{(1)} - \lambda^{(m)}}, \quad (29)$$

where  $m$  is the rank of the projection matrix,  $s_{ij}^{(m)} = \partial \lambda^{(m)} / \partial a_{ij}$ , and  $\lambda^{(m)}$  is the  $m$ th eigenvalue of the projection matrix.

Caswell (1996) notes that when  $\partial^2 \lambda^{(1)} / \partial a_{ij} \partial a_{kl} < 0$ , selection is concave. This is a multivariate generalization of the idea of stabilizing selection. When the second partial derivative is greater than zero, selection is convex, the multivariate generalization of directional selection.

Another application of the eigenvalue second derivatives is calculating how elasticities will change when vital rates are perturbed – i.e., the sensitivities of the elasticities:

$$\frac{\partial e_{ij}}{\partial a_{kl}} = \frac{a_{ij}}{\lambda} \frac{\partial^2 \lambda}{\partial a_{ij} \partial a_{kl}} - \frac{a_{ij}}{\lambda^2} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}} + \frac{\delta_{ik} \delta_{jl}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \quad (30)$$

where  $\delta_{ik}$  and  $\delta_{jl}$  indicate the Kronecker delta function where  $\delta_{ik} = 1$  if  $i = k$ , otherwise  $\delta_{ik} = 0$ .

### 3 Loop Elasticities

Van Groenendaal et al. (1994) and Wardle (1998) present a method of decomposing the force of selection on the life cycle known as “loop analysis.” Loop analysis relies on a number of properties of elasticities. These properties include: (1) the sum of all elasticities is one, (2) the sum of elasticities of incoming transitions equals the sum of elasticities of outgoing transitions, and (3) all elasticities to all the transitions in a loop are the same.

To perform a loop analysis, we must first identify all the loops just as we did in section ?? . In an age-structured life cycle (and indeed in many more complexly structured life cycles) there will be many redundant arcs between loops. However, each loop will typically have a single unique arc that defines it. Because of the property that the elasticities to all transitions in a loop are equal, the value of this unique arc in the loop represents the *characteristic elasticity* of the loop. Having found the characteristic elasticity for the loop, we then simply need to multiply it by the number of arcs in the loop to arrive at the loop elasticity.

For complex life cycles, exhaustively identifying the loops present in the life cycle is not always a trivial task. Wardle (1998) describes the use of graph theory to aid in this.

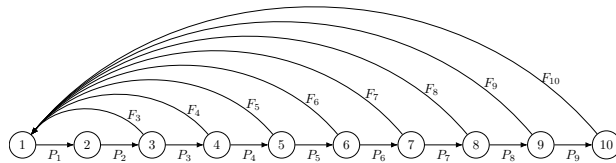


Figure 8: Life cycle graph for the Ache.

Consider the life cycle graph corresponding to the Ache projection matrix depicted in figure 8. We can calculate the elasticities of this life cycle. There are eight distinct loops. The unique arc

that defines each loop is the fertility transition contained in the loop. This will be typical of age-structured life cycles. The results of this analysis are presented in figure 9. We can compare this result to a loop analyses of four populations: Ache ([Hill and Hurtado 1996](#)), !Kung ([Howell 1979](#)), USA (U.S. Census Bureau 2005), and Venezuela 1965 ([Keyfitz and Flieger 1990](#)).

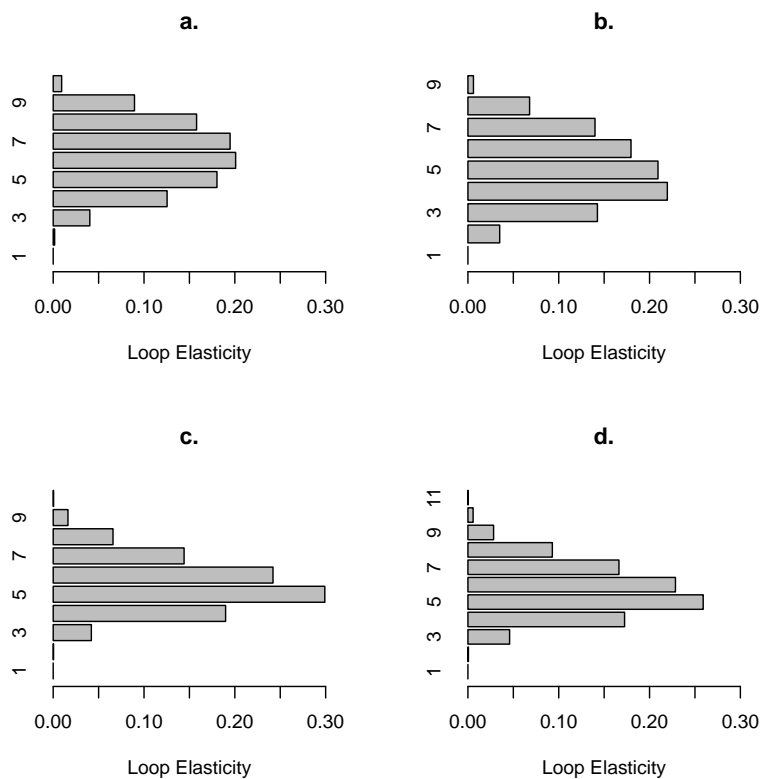


Figure 9: Loop analysis of (a) Ache, (b) !Kung, (c) USA, and (d) Venezuela (1965) life cycles.

## References

- Caswell, H. (1996). [Second derivatives of population growth rate: Calculation and applications](#). *Ecology* 77(3), 870–879.
- Caswell, H. (2001). *Matrix population models: Formulation and analysis* (2nd ed.). Sunderland, MA: Sinauer.
- Caswell, H. (2019). [Sensitivity Analysis: Matrix Methods in Demography and Ecology](#). Demographic Research Monographs (A Series of the Max Planck Institute for Demographic Research). Cham, Switzerland: Springer.

- Hamilton, W. D. (1966). [The moulding of senescence by natural selection](#). *Journal of Theoretical Biology* 12, 12–45.
- Hill, K. and A. M. Hurtado (1996). *Ache life history*. New York: Aldine De Gruyter.
- Howell, N. (1979). *The demography of the Dobe !Kung*. New York: Academic Press.
- Keyfitz, N. and W. Flieger (1990). *World population growth and aging: Demographic trends in the late twentieth century*. Chicago: University of Chicago Press.
- Van Groenendael, J., H. De Kroon, S. Kalisz, and S. Tuljapurkar (1994). [Loop analysis: Evaluating life history pathways in population projection matrices](#). *Ecology* 75(8), 2410–2415.
- Wardle, G. M. (1998). [A graph theory approach to demographic loop analysis](#). *Ecology* 79(7), 2539–2549.