OLM 4.4. Sensitivity and elasticity

Ch4.4 introduced the notions of sensitivity and elasticity of the growth rate towards the vital rates in the transition matrix. This OLM demonstrates the basic results Eqs. (4.19-20), which connects sensitivity/elasticity to the equilibrium population distribution and to the vector of reproductive values. The latter one is introduced in TBox 4.4 and important here. We use the concise vector-matrix notation more freely here, than in Ch4Struct and in the previous OLMs.

The growth rate λ of a population is determined by individual (genetic) traits and the environment through the vital rates, i.e., the a_{ij} elements of the PPM. Therefore it is essential to understand how the growth potential depends on the vital rates. We constrain changes to small ones, for these can be linearly approximated by the derivatives of λ, as functions of vital rates a_{ij} (see the concept of linearization in Figure 1.2). We have to know this dependence both in the absolute and in a relative sense – the former will be referred to as *sensitivity*, the latter as *elasticity*.

Sticking to our notations $\boldsymbol{v}^{\mathrm{T}}$ and $\boldsymbol{w}$ are the left and right eigenvectors belonging to λ, the leading eigenvalue of the transition matrix $\boldsymbol{A}$. Recall the definition of the eigenvalue from Eq. (4.10):

$$\boldsymbol{A}\boldsymbol{w} = \lambda \boldsymbol{w} \tag{4.4.1}$$

Take the partial derivatives of both sides! (The rules of differentiation for scalar functions apply for vectors and matrices as well; the derivative of a vector/matrix is the vector/matrix composed of the derivatives of its elements). It yields

$$\boldsymbol{A}\frac{\partial \boldsymbol{w}}{\partial a_{ij}} + \frac{\partial \boldsymbol{A}}{\partial a_{ij}}\boldsymbol{w} = \lambda \frac{\partial \boldsymbol{w}}{\partial a_{ij}} + \frac{\partial \lambda}{\partial a_{ij}}\boldsymbol{w}. \tag{4.4.2}$$

Multiply both sides with the row vector of reproductive values ($\boldsymbol{v}^{\mathrm{T}}$) from the left:

$$\boldsymbol{v}^{\mathrm{T}}\boldsymbol{A}\frac{\partial \boldsymbol{w}}{\partial a_{ij}} + \boldsymbol{v}^{\mathrm{T}}\frac{\partial \boldsymbol{A}}{\partial a_{ij}}\boldsymbol{w} = \lambda \boldsymbol{v}^{\mathrm{T}}\frac{\partial \boldsymbol{w}}{\partial a_{ij}} + \frac{\partial \lambda}{\partial a_{ij}}\boldsymbol{v}^{\mathrm{T}}\boldsymbol{w}. \tag{4.4.3}$$

The first terms on the two sides of the equation are equal by the definition of the left eigenvector, so they are omitted. The elements of the $\frac{\partial \boldsymbol{A}}{\partial a_{ij}}$ matrix are all zero except for the (i,j) element which is 1, therefore

$$\boldsymbol{v}^{\mathrm{T}}\frac{\partial \boldsymbol{A}}{\partial a_{ij}}\boldsymbol{w} = v_i w_j. \tag{4.4.4}$$

Substituting this to Eq. (4.4.3) yields the sensitivity of λ to vital rate a_{ij} as

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\boldsymbol{v}^{\mathrm{T}} \boldsymbol{w}}. \qquad (4.4.5)$$

This result has a very straightforward intuitive interpretation: the vital rate a_{ij} belonging to the $j \rightarrow i$ transition has a strong effect on the growth rate of the population if a) a considerable fraction of the population is in the initial *i*-state *j*, (i.e., w_j is large) and b) the target *i*-state (*i*) has a large reproductive value v_i so that it makes a high contribution to future population size.

Having calculated the sensitivity of λ to changes in the vital rates and applying the chain-rule of differentiation one can determine the sensitivity of λ to lower-level parameters, i.e., to those which affect the vital rates directly:

$$\frac{\partial \lambda}{\partial x} = \sum_{i,j} \frac{\partial a_{ij}}{\partial x} s_{ij} = \frac{1}{\boldsymbol{v}^{\mathrm{T}} \boldsymbol{w}} \boldsymbol{v}^{\mathrm{T}} \frac{\partial \boldsymbol{A}}{\partial x} \boldsymbol{w} \qquad (4.4.6)$$

This equation is to be interpreted in a way similar to the previous result.

If we want to know the proportional effects of the vital rates on population growth rate, then we need to use elasticities (e_{ij}) instead of sensitivities (s_{ij}):

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{a_{ij}}{\lambda} s_{ij} \qquad (4.4.7)$$

This specifies the proportional change of λ in response to proportional change in the vital rate a_{ij}. The sum of the elasticities for all vital rates is 1:

$$\sum_i \sum_j e_{ij} = \frac{1}{\lambda \boldsymbol{v}^{\mathrm{T}} \boldsymbol{w}} \sum_i \sum_j v_i a_{ij} w_j = \frac{\boldsymbol{v}^{\mathrm{T}} \boldsymbol{A} \boldsymbol{w}}{\lambda \boldsymbol{v}^{\mathrm{T}} \boldsymbol{w}} = \frac{\lambda \boldsymbol{v}^{\mathrm{T}} \boldsymbol{w}}{\lambda \boldsymbol{v}^{\mathrm{T}} \boldsymbol{w}} = 1. \qquad (4.4.8)$$

It is easy to see why this needs to be true: increasing all the elements of the matrix by 1% means increasing the matrix and thus also its eigenvalues by 1%. This amounts to elasticities adding up to 1.

This rule enables the expression of relative importance for each i-state transition in percentages: We may say that a certain vital rate determines the growth rate of the population in 34%, if the corresponding elasticity has a value of 0.34. It is important to remember, however, that sensitivity and elasticity is based on linearisation; therefore in case of non-linear functions they describe only the effects of small changes accurately. Figure 4.19 on page 65 shows a case when the deviation of the functions from linearity is small.