

**Lecture 5. Age- and stage-structured models: Leslie-Lefkovich Models.**

## Reading:

Gotelli, 2001, A Primer of Ecology, Chapter 3, pages 49-80.

Noon, B. R. and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441-464 *in* D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: Populations. Elsevier Applied Science, New York, New York, USA.

## Optional:

Lande, R. 1991. Population dynamics and extinction in heterogeneous environments: the Northern Spotted Owl. Pages 566-580 *in* C. M. Perrins, J-D. Lebreton, and G. J. M. Hirons, eds. Bird Population Studies, Oxford, New York, New York, USA.

Define age structure dynamics in terms of difference equations.

$N_{i,t}$  is population at time  $t$  of age class  $i$

Time  $t$  is start of biological year, or the time of reproduction.

With  $k$  age classes, the maximum age an animal can attain is  $k$ , so that the survival rate of animals  $k$  years old is 0.

Only females are considered in the following example.

The modeler must define the anniversary date of the population census. For the following equations, the animal is incremented in age (i.e., mortality takes place), then reproduces. The population census is after the birth-pulse. Define  $f_i$  as the number of young produced by animals of age  $i$  and  $s_i$  as survival rate of animals of age  $i$  to end of the year. Animals just born are in the  $N_0$  age class.

Survival to next age class

$$N_{1,t+1} = N_{0,t} \times s_0$$

$$N_{2,t+1} = N_{1,t} \times s_1$$

$$N_{3,t+1} = N_{2,t} \times s_2$$

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$$N_{k,t+1} = N_{k-1,t} \times s_{k-1}$$

Reproduction

$$N_{0,t+1} = N_{1,t+1} \times f_1 + N_{2,t+1} \times f_2 + \dots + N_{k,t+1} \times f_k$$

However, we do not want the equations to refer to the  $t + 1$  populations, but rather the  $t$  populations. Therefore, we must substitute the survival equations into the reproduction equation:

$$N_{0,t+1} = N_{0,t} \times s_0 \times f_1 + N_{1,t} \times s_1 \times f_2 + \dots + N_{k-1,t} \times s_{k-1} \times f_k$$

Now, construct the Leslie (1945, 1948) matrix (also known as a projection matrix or transition matrix) based on the above difference equations.

$$\underline{N}_{t+1} = \underline{L} \times \underline{N}_t$$

$$\underline{N}_{t+1} = \begin{bmatrix} s_0 f_1 & s_1 f_2 & \cdots & s_{k-1} f_k & 0 \\ s_0 & 0 & 0 & \cdots & 0 \\ 0 & s_1 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & s_{k-1} & 0 \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_k \end{bmatrix}$$

In the following equations, reproduction takes place, then mortality. The census of the population is before the birth-pulse. The definitions of the  $f_i$  and  $s_i$  remain the same as the after birth-pulse model. However, the interpretation of the  $N_i$  changes slightly, because now the population sizes are just prior to reproduction. Hence, there are no newly born animals in this model corresponding to the  $N_0$  of the after birth-pulse model. Rather,  $N_i$  corresponds to animals 2 days younger than in the previous model. That is,  $N_1$  in the after birth-pulse model was the population of animals aged 1 year + a day. Now, in the before birth-pulse model,  $N_1$  is the population of animals aged 1 year - a day, i.e., just before they reach their first birthday. As a result, the  $N_0$  age class is no longer being modeled directly, although the survival rate of animals from birth to 1 year of age ( $s_0$ ) is still in the model.

Survival to next age class

$$N_{2,t+1} = N_{1,t} \times s_1$$

$$N_{3,t+1} = N_{2,t} \times s_2$$

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$$N_{k,t+1} = N_{k-1,t} \times s_k$$

Reproduction

$$N_{1,t+1} = N_{1,t} \times f_1 \times s_0 + N_{2,t} \times f_2 \times s_0 + \dots + N_{k,t} \times f_k \times s_0$$

Construct the Leslie matrix.

$$\underline{N}_{t+1} = \underline{L} \times \underline{N}_t$$

$$\underline{N}_{t+1} = \begin{bmatrix} f_1 s_0 & f_2 s_0 & f_3 s_0 & \cdots & f_k s_0 \\ s_1 & 0 & 0 & \cdots & 0 \\ 0 & s_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & s_k & 0 \end{bmatrix} \times \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_k \end{bmatrix}_t$$

Carefully note the differences in the 2 Leslie matrices. In the after birth-pulse matrix, the top row contains the survival rates of the reproducing animals. In the before birth-pulse matrix, the top row contains the survival rate of new born animals to 1 year of age. The most common mistake with application of the Leslie notation is that the presenter confuses order of the birth and death process. Noon and Saur (1992) discuss how to configure the matrix for use of estimates of survival and reproduction from a population.

Benefits of Leslie matrix formulation

$\lambda$  = eigenvalue of  $\underline{L}$  = rate of population growth, i.e.,  $N_{t+1} = \lambda N_t$ .

Equilibrium age ratios are eigenvector of  $\underline{L}$ , i.e., ratio of  $N_1:N_2$  is the same as the ratio of the first 2 values in the eigenvector. The stable age distribution is the ratio of the various age classes to one another. These ratios are stable in a Leslie matrix projection, regardless of the value of  $\lambda$ . For  $\lambda = 1$ , the age distribution is termed stationary, because the population is stationary.

Ease of presentation (if you know matrix algebra!)

Construction of a spreadsheet model from this formulation:

Provides a simple, available alternative to model a population.

Ratio of  $N_{t+1}/N_t$  after a few generations provides  $\lambda$ .

Ratio of age classes is equivalent to eigenvector after a few generations.

Interpretation of age ratios measured in a population: Because the projection matrix generates a stable age distribution after effects of initial population size are depreciated, age ratios tell you nothing about increase or decrease of a population.

"To sum up: age ratios cannot be interpreted without a knowledge of rate of increase, and if we have an estimate of this rate we do not need age ratios."

Caughley (1974).

Example of eigenvalue calculation:

$$\underline{L} = \begin{bmatrix} f_0 s_0 & f_1 s_0 \\ s_1 & 0 \end{bmatrix}$$

Eigenvalues are values of  $\lambda$  that solve

$$0 = \det(\underline{L} - \lambda I)$$

where  $I$  is the identity matrix.

$$0 = \det \left[ \begin{bmatrix} f_0 s_0 & f_1 s_0 \\ s_1 & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix} \right]$$

$$0 = \det \left[ \begin{bmatrix} f_0 s_0 - \lambda & f_1 s_0 \\ s_1 & -\lambda \end{bmatrix} \right]$$

$$0 = -\lambda f_0 s_0 + \lambda^2 - f_1 s_0 s_1$$

$$0 = \lambda^2 - (f_0 s_0) \lambda - (f_1 s_0 s_1)$$

Remember that for the polynomial  $ax^2 + bx + c$ , the roots are

$$\frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

Thus, the roots of the characteristic equation are

$$\frac{f_0 s_0 + \sqrt{f_0^2 s_0^2 + 4f_1 s_0 s_1}}{2}$$

and

$$\frac{f_0 s_0 - \sqrt{f_0^2 s_0^2 + 4f_1 s_0 s_1}}{2}$$

with the first root (+) the largest value, or dominant eigenvalue. Typically, the analytical eigenvalues are seldom used, and only the

numerical value provided. Computing the eigenvalues of a matrix is a standard numerical analysis problem.

The basic Leslie Matrix formulation is limited because only density-independent population growth with just births and deaths is modeled. The following examples (all with the census before the birth-pulse) are some approaches to extend the basic formulation to incorporate additional population processes.

Exponential growth is what the above examples portray, i.e., all rates are density independent. The matrix can be modified to make  $f_i$  and  $s_i$  functions of the total population size,  $N_t$ . Another possibility is to make some age-specific parameters density-dependent only on the size of a specific age class. In both cases, if these functions are linear relationships, then logistic population growth results. In the following example, assume that  $N_t$  is the sum of the population sizes for all the age classes. Then, replace survival for the first age class with the function

$$s_0(N_t) = \beta_0 + \beta_1 N_t$$

so that survival of this age class is now density-dependent. The matrix would look like the following.

$$\frac{N}{t+1} = \begin{bmatrix} f_0(\beta_0 - \beta_1 N_t) & f_1(\beta_0 - \beta_1 N_t) & f_2(\beta_0 - \beta_1 N_t) & \cdots & f_k(\beta_0 - \beta_1 N_t) \\ s_1 & 0 & 0 & \cdots & 0 \\ 0 & s_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & s_k & 0 \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_k \end{bmatrix}_t$$

Only density-dependence in this one age class is needed to produce logistic growth. For discussion, what is the value of  $\lambda$  for  $t \rightarrow \infty$ ? Would density-dependence in just one of the  $f_i$  also result in density-dependent population growth? Hint: if you set a parameter to zero, and  $\lambda$  remains greater than 1, what is the impact on population growth of making the parameter density-dependent?

Immigration is precluded, i.e., the population is closed to immigrants. However, an extension to the Leslie matrix is to include immigration with the following technique, where  $I_i$  is the number of immigrants of age  $i$ .

$$\underline{N}_{t+1} = \begin{bmatrix} f_0 s_0 & f_1 s_0 & f_2 s_0 & \cdots & f_k s_0 \\ s_1 & 0 & 0 & \cdots & 0 \\ 0 & s_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & s_k & 0 \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_k \end{bmatrix}_t + \begin{bmatrix} I_0 \\ I_1 \\ I_2 \\ \vdots \\ I_k \end{bmatrix}_t$$

Emigration can be considered part of the death process, but this is rather ad hoc.

A more sophisticated approach is to treat the survival entries as survival minus emigration, as shown in the following example, where the  $e_i$  values are the emigration rate for animals of age  $i$ .

$$\underline{N}_{t+1} = \begin{bmatrix} f_0(s_0 - e_0) & f_1(s_0 - e_0) & f_2(s_0 - e_0) & \cdots & f_k s_0 \\ (s_1 - e_1) & 0 & 0 & \cdots & 0 \\ 0 & (s_2 - e_2) & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & (s_k - e_k) & 0 \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_k \end{bmatrix}_t$$

Harvest can be treated either as an absolute loss from the population, such as

$$\underline{N}_{t+1} = \begin{bmatrix} f_0 s_0 & f_1 s_0 & f_2 s_0 & \cdots & f_k s_0 \\ s_1 & 0 & 0 & \cdots & 0 \\ 0 & s_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & s_k & 0 \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_k \end{bmatrix}_t - \begin{bmatrix} H_0 \\ H_1 \\ H_2 \\ \vdots \\ H_k \end{bmatrix}_t$$

where the  $H_i$  values are the number of animals harvested of each age class. Another approach is more like the emigration example above, where a harvest rate ( $h_i$ ) is applied to each age class such as the following.

$$\underline{N}_{t+1} = \begin{bmatrix} f_0(s_0 - h_0) & f_1(s_0 - h_0) & f_2(s_0 - h_0) & \cdots & f_k s_0 \\ (s_1 - h_1) & 0 & 0 & \cdots & 0 \\ 0 & (s_2 - h_2) & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & (s_k - h_k) & 0 \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_k \end{bmatrix}_t$$

Environmental stochasticity can be incorporated into a Leslie matrix by making the parameters random variables. Also, demographic stochasticity can be included by applying the rates are random processes. Thus, instead of multiplying by the survival rate of  $s_1$ , a binomial process is applied to the update from  $N_1$  to  $N_2$ . A similar strategy can be used for fecundity rates.

Another common extension is to allow the last age class to continue to survive and reproduce at constant rates. This is accomplished by setting the survival rate for the maximum age in population in the lower-right corner of the matrix (Lefkovich 1965, Usher 1966). Hence the label: "corner trick".

$$\underline{N}_{t+1} = \begin{bmatrix} s_0 f_0 & s_1 f_1 & s_2 f_2 & s_3 f_3 & s_4 f_4 \\ s_0 & 0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 \\ 0 & 0 & s_2 & 0 & 0 \\ 0 & 0 & 0 & s_3 & s_4 \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}_t$$

In this matrix, the maximum age animals do not suffer 0 survival, but persist with probability  $s_4$ . The implication is that there is no senescence in the population, i.e., that older animals continue to perform the same in terms of reproduction and survival. Depending on the proportion of the population in this age class, the assumption of no senescence may be invalid. For example, Ericsson et al. (2001) demonstrated that female moose (*Alces alces*) showed senescence in reproduction (i.e., litter size) from about 12 yr of age. Further evidence of senescence was a decrease in parental care during summer (expressed as increased offspring mortality) with the mother's age. A compensating mechanism for senescence may come with heavy harvest, in that few animals achieve an age whereby senescence is exhibited.

Instead of treating the population values as ages, these values can be treated as stages of a population life cycle. Stage-structured population models were developed by Usher (1966, 1969) with stage meaning the stage of development, i.e., insect instars.  $N_{i,t}$  now represents the number of animals of stage  $i$ , not age  $i$ . Then, animals can remain in the same stage, or be advanced to the next stage, or even advanced more than one stage. The following matrix is an example from a stage-structured population for loggerhead sea turtles (*Caretta caretta*) from Crouse et al. (1987). Seven life stages were considered: 1) eggs and hatchlings (<1 year), 2) small juveniles (1-7 years), 3) large juveniles (8-15 years), 4) subadults (16-21 years), 5) novice breeders (22 years), 6) first-year

emigrants (23 years), and 7) mature breeders (>23 years).

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 127 & 4 & 80 \\ 0.6747 & 0.7370 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.0486 & 0.6611 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.0147 & 0.6907 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.0518 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.8091 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.8091 & 0.8089 \end{bmatrix}$$

Reproduction is from the last 3 stages only, with fecundity rates being 127, 4, and 80 each year, respectively. At stage 2, for example, the probability of surviving and remaining in the stage from one year to the next is 0.7370, whereas the probability of advancing to stage 3 is 0.0486. The annual survival rate of stage 2 animals is  $0.7370 + 0.0486 = 0.7856$ , so  $1 - 0.7856$  is the annual mortality rate. For this matrix,  $\lambda = 0.9450$ , so the population is expected to decline. A modification of this model was used by Crowder et al. (1994) to evaluate turtle excluder devices on trawl fisheries of the southeastern US.

Variance of  $\lambda$  as a function of the variance of the entries in the projection matrix is given by this Taylor series approximation (Delta method):

$$\sigma_{\lambda}^2 = \sum_i \sum_j \left( \frac{\partial \lambda}{\partial \pi_i} \right) \left( \frac{\partial \lambda}{\partial \pi_j} \right) \sigma_{ij}$$

where variance of  $\lambda$  is expressed as the partial of  $\lambda$  with respect to parameters  $\pi_i$  and  $\pi_j$  (entries in the matrix). The  $\pi_i$  and  $\pi_j$  are not cell values, but rather correspond to the basic parameters used to create the cell values. For example,  $\pi_1$  might correspond to  $f_1$ ,  $\pi_2$  to  $f_2$ ,  $\pi_3$  to  $s_1$ , etc. Covariance of  $\pi_i$  and  $\pi_j$  is  $\sigma_{ij}$ . The sensitivity of  $\lambda$  is the partial of  $\lambda$  with respect to parameter  $\pi_i$ .  $\sigma_{ij}$  and  $\sigma_{ii}$  may represent just process variation, just sampling variation, or a combination of both. For determining minimum viable population size, you want  $\sigma_{ij}$  to just represent process variation. To estimate the sampling variation of  $\lambda$ , you want  $\sigma_{ij}$  to just represent sampling variation. Lande (1991) uses this procedure with northern spotted owls, also discussed by Caswell (2001). Gross (2002) describes how to allocate effort in data collection to minimize the sampling variance of  $\lambda$ .

Sensitivity analysis for the mathematically challenged. To determine relative sensitivity of  $\lambda$  with respect to  $s_1$ :



- 1) compute  $\lambda$  with the given value of  $s_1$ ,
- 2) compute  $\lambda_\Delta$  with the value  $s_1 + \Delta$ , where  $\Delta$  is some small value compared to  $s_1$ ,
- 3) compute the sensitivity of  $\lambda$  with respect to  $s_1$  as

$$\frac{\Delta\lambda}{\Delta s_1} = \frac{\lambda_\Delta - \lambda}{\Delta}$$

This approach is equivalent to computing numerical partial derivatives, and as  $\Delta$  approaches zero, the resulting sensitivity value approaches  $\frac{\partial\lambda}{\partial s_1}$ . This procedure

is relatively easy to perform in a spreadsheet. In general, projection matrix models demonstrate that the adult survival rate (particularly the parameter(s) in the lower right corner) is the most sensitive parameter, whereas reproductive rates and juvenile survival have the same sensitivity with  $\lambda$  being less sensitive to them.

A common misconception is that the most sensitive parameters are the most important for the persistence of the population. As we will see later, the variation of a parameter across time, space, and individuals affects persistence, and is unrelated to sensitivity. However, even though the concepts of parameter sensitivity and process variance are unrelated, most populations do show a relationship. This is because parameters to which  $\lambda$  is highly sensitive probably do not have a large process variance because if this is the case, the population would likely go extinct.

A nifty use of the Leslie matrix is demonstrated by McGraw and Caswell (1996), where they define individual fitness as the dominant eigenvalue of an individual's Leslie matrix. Thus, reproduction for the individual is the actual number of offspring produced, and the survival rate for the individual is 1 until the animal dies, when it is zero. The dominant eigenvalue of the matrix is then the animal's fitness.

A general reference on projection matrices is Manly (1990). A mathematical treatment is given in Caswell (1989, 2001).

Laboratory Exercise 4: Quattro spreadsheet with age-structured population.

### Literature Cited

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