Age-Structured Population Models

We have studied a number of population models this semester, but all have combined all members of the population in a single group. We know that reproduction and survival depend highly upon age, so better population models include some age-structure in the model. The simplest age-structured model is the Leslie Model, named after Patrick H. Leslie (1900-1974), and was developed in the 1940s. This is a discrete population model, in which the population of one sex (usually females) is divided into discrete age classes. The population is closed to migration and only considers births and deaths amongst the ages classes or life stages. The population, $\mathbf{X}_n$, is represented by a vector, which varies discretely with time. This model provides a valuable tool for studying the growth of a population and determining the relative size of each of the age classes.

The Leslie model is written:

$$\mathbf{X}_{n+1} = L\mathbf{X}_n,$$

where L is the Leslie matrix and $\mathbf{X}_n = [x_1, x_2, ..., x_m]_n^T$ is the population vector at time n divided into m age classes. If we let b_i be the per capita birth rate of the i^{th} class into the first class, and s_i be the survival rate of individuals of class i at time n into class $i+1$ at time $n+1$, then the Leslie matrix takes the form:

$$L = \begin{pmatrix} b_1 & b_2 & b_3 & \cdots & b_m \\ s_1 & 0 & 0 & \cdots & 0 \\ 0 & s_2 & \ddots & & \vdots \\ \vdots & \ddots & \ddots & 0 & 0 \\ 0 & \cdots & 0 & s_{m-1} & s_m \end{pmatrix},$$

where $s_m = 0$ if there older classes not considered in the population or all the population dies after class m. The survival $s_m \neq 0$, if the oldest class includes all the oldest individuals past the age class of $m-1$.

Analysis of the Leslie Model

To analyze the behavior of this discrete dynamical model, we find the eigenvalues and eigenvectors of L. If there is a single dominant eigenvalue, λ_1, with associated eigenvector (normalized), ξ_1, then asymptotically the population grows like

$$\mathbf{X}_n \simeq c_1 \lambda_1^n \xi_1.$$

It follows that the population grows or decays much like a Malthusian growth model with the exponential growth, λ_1 and the age classes having a distribution of ξ_1.

Example of U. S. Population Growth

A study of the female population in the U. S. (ref?) showed that if the population was divided into three groups of 20 years each, so that x_1 represents females age 0-20, x_2 represents females age 20-40, and x_3 represents females age 40-60, then a Leslie model for the dynamics of these age classes in the U. S. is given by:

$$\begin{pmatrix} x_1(n+1) \\ x_2(n+1) \\ x_3(n+1) \end{pmatrix} = \begin{pmatrix} 0.4271 & 0.8498 & 0.1273 \\ 0.9924 & 0 & 0 \\ 0 & 0.9826 & 0 \end{pmatrix} \begin{pmatrix} x_1(n) \\ x_2(n) \\ x_3(n) \end{pmatrix}.$$

This matrix shows that the typical female age 0-20 produces 0.4271 female offspring in a twenty year period. The typical 20-40 year old females produce the most female offspring (peak fertility) with a per capita rate of 0.8498, while the females age 40-60 have significantly fewer female offspring at only 0.1273 per woman in those older years. Survival rate to successive classes is very high with 0-20 year olds having a 99.24% chance of making it into the 20-40 age group, and the 20-40 year olds having a 98.26% chance of surviving into the 40-60 year old age class.

The eigenvalues of this Leslie matrix are $\lambda_1 = 1.2093$, $\lambda_2 = -0.6155$, and $\lambda_3 = -0.1668$. From this information, we readily see that the population growth is approximately 21% in a twenty year period, which is similar to the Malthusian growth rate that we obtained earlier for the U. S. population from the census data in the latter part of the 20^{th} century. The normalized eigenvector associated with λ_1 is

$$\xi_1 = \begin{pmatrix} 0.4020 \\ 0.3299 \\ 0.2681 \end{pmatrix},$$

which shows that the current distribution of females should be approximately 40.2% in the 0-20 age group, 33% in the 20-40 age group, and 26.8% in the 40-60 age group.

Example of Loggerhead Turtles

An article by Crowder *et al* (1994) used a modified version of the Leslie matrix model to predict the impact of turtle excluder devices on the populations of loggerhead sea turtles. (More to be written in this section in the future.)

Nonlinear Semelparous Leslie Models

The general nonlinear Leslie model has the form:

$$\mathbf{x}(n+1) = P(\mathbf{x}(n))\mathbf{x}(n),$$

where n is the discrete time interval, $\mathbf{x}$ is an m-vector, and $P(\mathbf{x}) = F(\mathbf{x}) + T(\mathbf{x})$ with the fertility matrix F and transition matrix T given by:

$$F(\mathbf{x}) = \begin{pmatrix} f_1(\mathbf{x}) & f_2(\mathbf{x}) & \cdots & f_m(\mathbf{x}) \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \cdots & 0 \end{pmatrix} \qquad T(\mathbf{x}) = \begin{pmatrix} 0 & \cdots & 0 & b\,f(\mathbf{x}) \\ \tau_1(\mathbf{x}) & & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & \tau_{m-1}(\mathbf{x}) & 0 \end{pmatrix}.$$

The entries in the fertility matrix $f_i(\mathbf{x})$ represent the number of newborns produced by an individual of age i, while the entries $\tau_1(\mathbf{x}) \le 1$ represent the transitions from age i to age $i+1$.

The trivial or extinction equilibrium $\mathbf{x} = \hat{0}$ is locally asymptotically stable if all eigenvalues of the Jacobian matrix evaluated at $\mathbf{x} = \hat{0}$, which equals

$$P(\hat{0}) = \begin{pmatrix} f_1(\hat{0}) & \cdots & f_{m-1}(\hat{0}) & f_m(\hat{0}) \\ \tau_1(\hat{0}) & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & \tau_{m-1}(\hat{0}) & 0 \end{pmatrix}$$

are less than one in magnitude. This is true if and only if the inherent net reproduction number

$$n \equiv f_1(\hat{0}) + \sum_{i=2}^{m} f_i(\hat{0}) \prod_{j=1}^{i-1} \tau_j(\hat{0})$$

is less than one. If $n > 1$, then $\mathbf{x} = \hat{0}$ is unstable and under very general conditions, a branch of nontrivial equilibria bifurcates from $\mathbf{x} = \hat{0}$ at $n = 1$. It bifurcates supercritically (positive equilibria correspond to $n > 1$) if the density dependent effects are deleterious and subcritically (positive equilibria correspond to $n < 1$) if Allee effects occur.

A semelparous organism is one that goes through several stages of development, then breeds and dies in the last stage. Examples of this type of organism are numerous insects, such as cicadaes, and fish, like salmon. This changes the fertility matrix to one where $f_i = 0$ for $i = 1, 2, ..., m-1$. The Leslie matrix model can be written:

$$\mathbf{x}(n+1) = P(\mathbf{x})\mathbf{x}(n),$$

$$P(\mathbf{x}) = \begin{pmatrix} 0 & \cdots & 0 & b\,f(\mathbf{x}) \\ (1-\mu_1)g_1(\mathbf{x}) & \cdots & 0 & 0 \\ \vdots & & \vdots & \vdots \\ 0 & \cdots & (1-\mu_{m-1})g_{m-1}(\mathbf{x}) & 0 \end{pmatrix}.$$

Here the functions f and g_i are normalized so that $f(\hat{0}) = g_i(\hat{0}) = 1$ and the inherent net reproductive number is

$$n = b\prod_{i=1}^{m-1}(1-\mu_i).$$

This model falls outside the general bifurcation result of the more general Leslie matrix model with $f_i \neq 0$ for some $i = 1, 2, ..., m-1$. In this case, when n increases through 1, all eigenvalues of the Jacobian matrix simultaneously leave the complex unit circle (m^{th} roots of unity). This is a result from matrix theory because the form of $P(\mathbf{x})$ for a semelparous population is a cyclic matrix. The result is a nongeneric bifurcation and requires special consideration.

Main Results for Semelparous Leslie Models

1. A global branch of positive equilibria bifurcates from the trivial equilibrium, $\mathbf{x} = 0$ at $n = 1$.
2. A branch of periodic cycles of period m (m-cycles) bifurcates from the trivial solution at $n = 1$.
3. The stability of the positive equilibria on the bifurcating branch is not necessarily determined by the direction of the bifurcation.

There are detailed results for the case $m = 2$. In particular, it is shown that either the branch of unique equilibria, C_e, or the branch of the 2-cycles, C_2, is stable, but not both.

[1] Crowder, L. B. Crouse, D. T. Heppell, S. S. and Martin, T. H. (1994). Predicting the impact of turtle excluder devices on loggerhead sea turtle populations, *Ecological Applications*, **4**, 437-445.

[2] Cushing, J. M. (2006), Nonlinear Semelparous Leslie Models, *Math. Biosci. Eng.*, **3**, 17-36.