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A Density-Dependent Leslie Matrix Model

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ABSTRACT

A density-dependent Leslie matrix model introduced in 1948 by Leslie is mathematically analyzed. It is shown that the behavior is similar to that of the constant Leslie matrix. In the primitive case, the density-dependent Leslie matrix model has an asymptotic distribution corresponding to the logistic equation. However, in the imprimitive case, the asymptotic distribution is periodic, with period depending on the imprimitivity index.

INTRODUCTION

The purpose of this paper is to provide a rigorous mathematical analysis of the behavior of a density-dependent Leslie matrix model. The model is an age-dependent analogue of the logistic model. In 1948, Leslie [9] introduced a density-dependent model to illustrate limited population growth.

The matrix model has the form $L(n_t)\mathbf{X}(t)=\mathbf{X}(t+1)$, where $L(n_t)=Lq^{-1}(n_t)$, L is a constant Leslie matrix, $\mathbf{X}(t)$ is a population age distribution, and q is a density-dependent factor. The matrix L, vector $\mathbf{X}(t)$, and factor q are defined below:

$$L=\begin{bmatrix} f_1 & f_2 & \cdots & & f_n \\ s_1 & & & & \\ & s_2 & & & \\ & & \ddots & & \\ & & & s_{n-1} & \end{bmatrix}, \tag{1}$$

$$\mathbf{X}(t)=(x_{1t},x_{2t},\dots,x_{nt})^T,$$

and

$$q(n_t)=\frac{K+(\lambda_0-1)n_t}{K},$$

where f_i is the fertility rate of females of age i ($f_i\geq 0$, $i=1,\dots,n-1$; $f_n>0$), s_i is the survival probability of females of age i ($s_i>0$), x_{it} is the number of females of age i at time t, λ_0 is the dominant eigenvalue of L, and n_t is the population size at time t. The eigenvalue λ_0 is greater than unity, since in the absence of density dependence the population increases exponentially.

Other types of density-dependent Leslie matrices have been studied by Beddington [1], DeAngelis et al. [6], and Horwood and Shepherd [8]. Beddington [1] studied a general density-dependent Leslie matrix where fertility and survival rates were regulated by total population size, that is, $f_i = f_i(n_t)$, $s_i = s_i(n_t)$. He applied the model to two populations with specific functional forms for f_i and s_i and determined local population stability. De Angelis et al. [6] considered a modified Leslie matrix appropriate for fish populations. They assumed that only young-of-the-year suffered density-dependent mortality, that is, $s_1 = s_1(x_{1t},\dots,x_{nt})$. They showed that the eigenvalues of the linearized system can be used to approximate the return time to equilibrium following a perturbation. Horwood and Shepherd [8] also studied a modified Leslie matrix appropriate for fish populations. In their model, only the egg and larval stages experienced density-dependent mortality. They studied the population's sensitivity to noise.

The above analyses were restricted to local analyses, near an equilibrium. In the present analysis, the global behavior of Leslie's density-dependent model (1) will be determined.

Numerical work performed by Leslie [10] demonstrated that the behavior of model (1) in some cases was oscillatory but that the asymptotic limit was the same as for the logistic model. Svirezhev and Logofet [12] performed a local stability analysis of the equilibrium (stable age distribution) and failed to come to a definite conclusion regarding its stability. They hypothesized that if L is primitive, then the equilibrium is stable and the population size is asymptotically close to the logistic model, and if L is imprimitive, the analysis requires an account of higher than first-order terms [12, p. 72]. However, both Leslie [9] and Svirezhev and Logofet [12] showed that in the particular case where the initial distribution $\mathbf{X}_0$ is stable (i.e., $L\mathbf{X}_0 = \lambda_0 \mathbf{X}_0$) and L is primitive, the distribution followed the discrete logistic equation exactly.

In the following analysis it will be shown that if L is primitive, the asymptotic limit is the stable age distribution with the population size the same as the logistic. However, if L is imprimitive, the limit is periodic with the period depending on the index of L. The analysis is presented in the following section, and in the concluding section some numerical examples are presented to illustrate the various types of behavior

ANALYSIS

The main portion of the analysis is to find a simple expression for $\mathbf{X}(t)$. The population distribution is

$$\mathbf{X}(t) = q^{-1}(n_{t-1})L\mathbf{X}(t-1) = q^{-1}(n_{t-1})q^{-1}(n_{t-2})L^2\mathbf{X}(t-2)$$
$$= \prod_{i=0}^{t-1} q^{-1}(n_i)L^t\mathbf{X}_0.$$

The product can be simplified inductively,

$$q(n_1) = \frac{K+(\lambda_0-1)n_1}{K} = \frac{K+(\lambda_0-1)(\mathbf{X}_0\cdot\mathbf{1}+L\mathbf{X}_0\cdot\mathbf{1})}{K+(\lambda_0-1)n_0},$$

since

$$n_1 = \mathbf{X}(1)\cdot\mathbf{1} = \frac{KL\mathbf{X}_0\cdot\mathbf{1}}{K+(\lambda_0-1)n_0},$$

where $\mathbf{X}\cdot\mathbf{Y}$ is the dot product of $\mathbf{X}$ and $\mathbf{Y}$ and $\mathbf{1} = [1,1,\dots,1]^T$.

Note that

$$\mathbf{X}(2) = q^{-1}(n_1)q^{-1}(n_0)L^2\mathbf{X}_0 = \frac{KL^2\mathbf{X}_0}{K+(\lambda_0-1)(\mathbf{X}_0\cdot\mathbf{1}+L\mathbf{X}_0\cdot\mathbf{1})}.$$

By induction it follows that

$$\mathbf{X}(t) = \frac{KL^t\mathbf{X}_0}{K+(\lambda_0-1)\left(\sum_{i=0}^{t-1}L^i\mathbf{X}_0\cdot\mathbf{1}\right)}. \tag{2}$$

The theorem will now be stated in regard to the asymptotic behavior of $\mathbf{X}(t)$. Equation (2) will be used to prove the theorem.

THEOREM

(i) *If the matrix L is primitive, then the asymptotic distribution* $\lim_{t\to\infty}\mathbf{X}(t) = \mathbf{N}$, *where* $\mathbf{N}$ *is the stable age distribution corresponding to* $L\mathbf{N} = \lambda_0\mathbf{N}$ *and* $\mathbf{N}\cdot\mathbf{1} = K$.

(ii) *If the matrix L is imprimitive, then the asymptotic distribution* $\lim_{t\to\infty}\mathbf{X}(t) = \mathbf{N}(t)$, *where* $\mathbf{N}(t)$ *is periodic,* $\mathbf{N}(t+h) = \mathbf{N}(t)$, *and h is the index of L.*

The theory developed by Cull and Vogt [3–5] for the constant Leslie matrix L is essential to the proof of the theorem.

Proof. (i) The Jordan canonical form for L is $L = PJP^{-1}$, where $J = \operatorname{diag}\{J_0, J_1,\dots,J_m\}$ and J_i is a Jordan block,

$$J_i = \begin{bmatrix} \lambda_i & 1 & & \\ & \lambda_i & \ddots & \\ & & \ddots & 1 \\ & & & \lambda_i \end{bmatrix}.$$

If L is primitive, by rearrangement we can assume $J_0 = [\lambda_0]$ and the remaining Jordan blocks correspond to the remaining eigenvalues.

By the Perron–Frobenius theorem [7], when L is primitive and irreducible ($f_n > 0$), $\lambda_0 > |\lambda_i|$, $i = 1,\ldots,m$.

It follows that

$$\lim_{t\to\infty}\left(\frac{J}{\lambda_0}\right)^t = \operatorname{diag}\{1,0,\ldots,0\},$$

where 0 is a zero matrix with the same dimension as J_i.

Thus,

$$\lim_{t\to\infty}\left(\frac{L}{\lambda_0}\right)^t \mathbf{X}_0 = \lim_{t\to\infty}\frac{PJ^tP^{-1}}{\lambda_0^t}\mathbf{X}_0 = P\operatorname{diag}\{1,0,\ldots,0\}P^{-1}\mathbf{X}_0$$
$$= \mathbf{CRX}_0 = (\mathbf{X}_0\cdot\mathbf{R}^T)\mathbf{C},$$

where $\mathbf{C}$ is the first column of P and $\mathbf{R}$ is the first row of P^{-1} and $\mathbf{C}$ and $\mathbf{R}$ correspond to right and left eigenvectors of L, that is, $L\mathbf{C} = \lambda_0\mathbf{C}$ and $\mathbf{R}L = \lambda_0\mathbf{R}$. (Note that $\mathbf{R}$ is a row vector. All other vectors are column vectors.)

This argument was used by Cull and Vogt [3, 4] and will be used to simplify the density-dependent matrix equation (2).

The sum

$$\sum_{i=0}^{t-1} L^i = P\sum_{i=0}^{t-1} J^iP^{-1}$$

and the limit after division by λ_0^t yields

$$\lim_{t\to\infty} P\sum_{i=0}^{t-1}\frac{J^iP^{-1}}{\lambda_0^t} = \lim_{t\to\infty} P\operatorname{diag}\left\{\frac{\Sigma_{i=0}^{t-1}\lambda_0^i}{\lambda_0^t},0,\ldots,0\right\}P^{-1}$$
$$= P\operatorname{diag}\{(\lambda_0-1)^{-1},0,\ldots,0\}P^{-1}.$$

The above limit follows from $\Sigma J^i = \operatorname{diag}\{\Sigma\lambda_0,\Sigma J_1^i,\ldots,\Sigma J_m^i\}$,

$$\sum J_k^i = (I-J_k)^t(I-J_k)^{-1} \qquad (\text{provided } \lambda_k \neq 1),$$

and

$$\lim_{t\to\infty}\frac{(I-J_k)^t(I-J_k)^{-1}}{\lambda_0^t} = 0,$$

since the spectral radius of J_k, $\rho(J_k) < \lambda_0$, and $\lambda_0 > 1$.

For the particular case $\lambda_k = 1$, $(I-J_k)^{-1}$ does not exist. For sufficiently small ϵ, $\lambda_0 > 1+\epsilon$, let $J_k(\epsilon) = J_k + \epsilon I$. Then

$$\sum J_k^i < \sum J_k^i(\epsilon)$$

and by the above argument $\Sigma J_k^i(\epsilon)/\lambda_0^t$ approaches the zero matrix. Thus for L primitive, from Equation (2) and the analysis above, it follows that

$$\lim_{t\to\infty}\mathbf{X}(t) = \lim_{t\to\infty}\frac{KPJ^tP^{-1}\mathbf{X}_0/\lambda_0^t}{\dfrac{K}{\lambda_0^t}+(\lambda_0-1)\left(\dfrac{P\Sigma_{i=0}^{t-1}J^iP^{-1}\mathbf{X}_0}{\lambda_0^t}\cdot\mathbf{1}\right)}$$
$$= K(\mathbf{X}_0\cdot\mathbf{R}^T)\mathbf{C}/(\mathbf{X}_0\cdot\mathbf{R}^T)\mathbf{C}\cdot\mathbf{1} = \mathbf{N},$$

which is the stable age distribution (constant multiple of $\mathbf{C}$), normalized so that $\mathbf{N}\cdot\mathbf{1} = K$.

(ii) When L is imprimitive and the index is h, there are h eigenvalues whose modulus is λ_0 given by $\lambda_0 w^{j-1}$, $j = 1,\ldots,h$, where $w = e^{i2\pi/h}$ is the hth root of unity.

In this case,

$$\lim_{t\to\infty}\left(\frac{L}{\lambda_0}\right)^t = \lim_{t\to\infty}\frac{PJ^tP^{-1}}{\lambda_0^t} = \lim_{t\to\infty} P\operatorname{diag}\{1,w^t,\ldots,w^{(h-1)t},0,\ldots,0\}P^{-1}$$
$$= P\Phi(t)P^{-1}$$

and by an argument similar to part (i) the limit of the sum is

$$\lim_{t\to\infty}\frac{\Sigma_{i=0}^{t-1}L^i}{\lambda_0^t} = \lim_{t\to\infty}\frac{P\Sigma_{i=0}^{t-1}J^iP^{-1}}{\lambda_0^t}$$
$$= \lim_{t\to\infty} P\operatorname{diag}\left\{\frac{1}{\lambda_0-1},\frac{w^t}{\lambda_0 w-1},\ldots,\frac{w^{(h-1)t}}{\lambda_0 w^{h-1}-1},0,\ldots,0\right\}P^{-1}$$
$$= P\Psi(t)P^{-1}.$$

Note that $\Phi(t+h) = \Phi(t)$ and $\Psi(t+h) = \Psi(t)$ since $w^{j(t+h)} = w^{jt}$.

Thus

$$\lim_{t\to\infty}\mathbf{X}(t) = \frac{KP\Phi(t)P^{-1}\mathbf{X}_0}{P\Psi(t)P^{-1}\mathbf{X}_0\cdot\mathbf{1}} = \mathbf{N}(t) \tag{3}$$

and $\mathbf{N}(t+h) = \mathbf{N}(t)$.

Cull and Vogt [3] proved an average cyclic property for the constant Leslie matrix, that is, the average of $\mathbf{X}(t)$ over the period h, $(1/h)\Sigma_{i=1}^{h}\mathbf{X}(i)$, equals a stable age distribution. Since $\Phi(t) \neq \Psi(t)$, the limit $\mathbf{N}(t)$ does not have an average cyclic property. However, both the numerator and denominator of Equation (3) have an average cyclic property.

If the initial distribution is a stable age distribution, the limit distribution is the stable age distribution $\mathbf{N}$, regardless of whether L is primitive or imprimitive. Since

$$\mathbf{X}(t) = \frac{KL^t\mathbf{X}_0}{K+(\lambda_0-1)(\Sigma L^i\mathbf{X}_0\cdot\mathbf{1})}$$

$$= \frac{K\lambda_0^t\mathbf{X}_0}{K+(\lambda_0-1)n_0\left[(1-\lambda_0^t)/(1-\lambda_0)\right]},$$

where

$$\sum L^i\mathbf{X}_0\cdot\mathbf{1} = \sum \lambda_0^i n_0 = n_0\frac{1-\lambda_0^t}{1-\lambda_0},$$

it follows that

$$\lim_{t\to\infty}\mathbf{X}(t) = \frac{K\mathbf{X}_0}{n_0} = \mathbf{N}.$$

In addition, for any given distribution $\mathbf{X}_0$ with asymptotic limit $\mathbf{N}(t)$, a constant multiple of $\mathbf{X}_0$ will have the same limit:

$$\lim_{t\to\infty}\mathbf{X}(t) = \lim_{t\to\infty}\frac{KL^t\mathbf{X}_0/\lambda_0^t}{(\lambda_0-1)\left[(\Sigma L^i\mathbf{X}_0/\lambda_0^t)\cdot\mathbf{1}\right]}$$

$$= \lim_{t\to\infty}\frac{KL^tc\mathbf{X}_0/\lambda_0^t}{(\lambda_0-1)\left[(\Sigma L^ic\mathbf{X}_0/\lambda_0^t)\cdot\mathbf{1}\right]},$$

for any $c \neq 0$.

EXAMPLES

Consider the matrices L_1 and L_2:

$$L_1 = \begin{bmatrix} 0 & \frac{3}{2}\lambda_0^2 & \frac{3}{2}\lambda_0^3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{bmatrix},$$

$$L_2 = \begin{bmatrix} 0 & 0 & 6\lambda_0^3 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{bmatrix},$$

where $\lambda_0 > 1$ is the dominant eigenvalue. Matrix L_1 is primitive, and matrix L_2 is imprimitive. Matrix L_2 is an example studied by Bernardelli [2] in the particular case $\lambda_0 = 1$. The stable age distribution corresponding to λ_0 in both cases is $[6\lambda_0^2, 3\lambda_0, 1]^T$.

Several numerical examples illustrate the dependence on initial data and the eigenvalue λ_0. Let $K = 100$, $\lambda_0 = 2$ or 3, and $\mathbf{X}_0 = [25,5,1]^T$ or $[10,10,10]^T$. The population size is graphed in Figure 1a–d. In the primitive

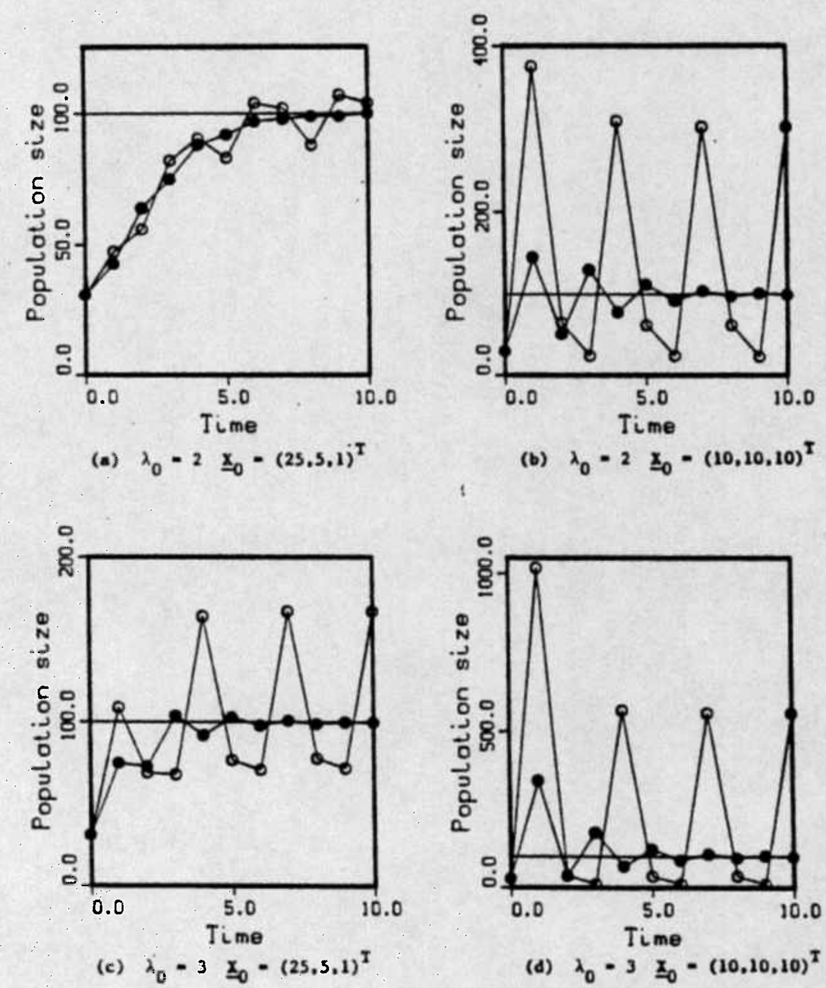

FIG. 1. Population size n_t for the primitive and imprimitive cases, (●) primitive; (○) imprimitive.

TABLE 1

Asymptotic Distribution for the Nonprimitive Case

λ_0	N(t)	$X_0 = [25, 5, 1]^T$	n_t	N(t)	$X_0 = [10, 10, 10]^T$	n_t
2	N(1)	$\begin{bmatrix} 86.9 \\ 17.4 \\ 3.5 \end{bmatrix}$	107.8	N(1)	$\begin{bmatrix} 7.6 \\ 7.6 \\ 7.6 \end{bmatrix}$	22.8
	N(2)	$\begin{bmatrix} 80.3 \\ 20.9 \\ 2.8 \end{bmatrix}$	104.0	N(2)	$\begin{bmatrix} 297.3 \\ 3.1 \\ 2.1 \end{bmatrix}$	302.5
	N(3)	$\begin{bmatrix} 65.6 \\ 19.7 \\ 3.4 \end{bmatrix}$	88.7	N(3)	$\begin{bmatrix} 24.6 \\ 36.9 \\ 0.3 \end{bmatrix}$	61.8
3	N(1)	$\begin{bmatrix} 57.8 \\ 11.6 \\ 2.3 \end{bmatrix}$	71.7	N(1)	$\begin{bmatrix} 4.3 \\ 4.3 \\ 4.3 \end{bmatrix}$	12.9
	N(2)	$\begin{bmatrix} 153.9 \\ 11.9 \\ 1.6 \end{bmatrix}$	167.4	N(2)	$\begin{bmatrix} 555.7 \\ 1.7 \\ 1.1 \end{bmatrix}$	558.5
	N(3)	$\begin{bmatrix} 59. \\ 17.7 \\ 0.9 \end{bmatrix}$	77.6	N(3)	$\begin{bmatrix} 15.2 \\ 22.8 \\ 0.05 \end{bmatrix}$	38.1

case, the population distribution converges to $(100/31)[24,6,1]^T$ for $\lambda_0 = 2$ and to $(100/64)[54,9,1]^T$ for $\lambda_0 = 3$. These are the stable age distributions N, where $N \cdot 1 = 100$. For the initial condition $X_0 = [25,5,1]^T$, which is close to the stable age distribution for $\lambda_0 = 2$, the convergence is monotone (Figure 1*a*). However, as λ_0 increases or as the initial conditions differ greatly from a stable age distribution, oscillations occur (Figure 1*b*–*d*). For the imprimitive case, it is also true that the oscillations become greater for large λ_0 or for initial conditions that are not close to the stable age distribution. The asymptotic distributions for the imprimitive case are listed in Table 1.

The eigenvalue λ_0 is analogous to the intrinsic growth rate r (or e^r) in the logistic equation. The wide variations in population size from year to year are typical of the "boom and bust" character of an r-strategist [11].

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