The Effect of Density Dependence on Age-Structured Population Growth Modeled with Leslie Matrices

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NSF REU 2000

Abstract

The dynamics that control the growth (and decay) of various plant and animal populations have been of interest historically, and still render study today. Early population models dealt with population as a whole entity and without factors taking into account density dependence based on limited resources. Population models have since evolved to include both age-class structure as well as density dependence. This paper aims to examine the effect of incorporating density dependent factors into a population model structured by age classes. The model used is based on the Leslie matrix model of age-structured population growth, and incorporates a Beverton-Holt style dependency into the survivorship of the juvenile age classes. The dependency is proportional to the size of the adult age class, motivated by a limited amount of available territory. The primary focus of this paper is the stability of such systems, among other characteristics.

Introduction

Population dynamics have been of interest to mathematicians and other scientists for years. Biologists naturally have interest in the mathematics that govern the growth of living populations, from bacteria and wildflowers to squirrels and wildebeests. Thus over the past century, the dynamics that govern the growth of living things have been thoroughly studied. One of the earliest methods of modeling population growth is given by the differential equation

$$(1.1) \qquad \frac{dN}{dt} = rN$$

where N is the number of organisms in the population and r is the intrinsic growth rate of the population. The solution of this differential equation shows population increasing at an exponential rate

$$(1.2) \qquad N(t) = N_0 e^{rt}$$

where N_0 is the initial population size. An equivalent model is one that uses the difference equation

$$(1.3) \qquad N_{t+1} = \lambda N_t$$

where the population growth is now not continuous, but discrete, and λ is related to r by $\lambda = e^r$.

An exponential population dynamic is not practical, however, due to constraints on resources, such as living space and food. In order to provide a better model of population growth, a carrying capacity (the variable K) was added to the basic model (1.1) which allows growth up to the given capacity and then requires the population to remain at that stable equilibrium size. This equation is

$$(1.4) \quad \frac{dN}{dt} = rN(1 - \frac{N}{K}).$$

Other methods of incorporating some type of density dependent carrying capacity include the Beverton-Holt model

$$(1.5) \quad N_{t+1} = \lambda N_t \left(\frac{1}{1 + \frac{\lambda - 1}{K} N_t} \right)$$

and the Ricker model

$$(1.6) \quad N_{t+1} = N_t e^{r(1 - \frac{N_t}{K})}.$$

These are the two most common density dependent equations. They are examples of two contrasting types of density dependence, called scramble and contest. In the scramble model, all members of a population share all available resources. Thus up to a point, all organism thrive. However, after reaching a threshold population, the equal share of resources is not enough to support an individual, and the entire population dies. This type of population is modeled by the Ricker equation (1.6). In contest population dynamics, again life thrives up to a given threshold. However, when this threshold is reached, there is not enough resource left for new individuals, and so there is stabilization at the threshold population. This type of dynamic is modeled by the Beverton-Holt equation (1.5).

Another change to the standard model of population dynamics came when researchers became interested in modeling the different age classes of a population. It became important to see how each age class depends on the others, and to investigate the dynamics of the separate classes. These age-specific models generally take the form of a system of linear difference equations, for example in a simple case

$$(1.7) \quad \begin{cases} N_{t+1} = 2A_{t+1} = 2(0.93)J_t \\ J_{t+1} = 0.7N_t \\ A_{t+1} = 0.93J_t \end{cases}$$

where N_t, J_t, and A_t represent the newborn, juvenile, and adult classes respectively, at time t. The numbers (2, 0.7, 0.93) are the birth and survival statistics related to the associated classes. For example, 93% of juveniles survive to become adults, 70% of newborns survive to become juveniles, and each adult gives birth to approximately 2 offspring per time period (generally only female organisms are counted).

Though equations of this type are useful, in the 1940s, Leslie converted these equations into matrix form to produce what is today called the Leslie matrix model for population growth. By writing these linear equations in matrix form, a transition matrix (*Leslie matrix*) is developed, containing important information and properties about the dynamics of the system, as well as allowing for simple long-term simulation. In our earlier example, (1.7) becomes the matrix equation

$$(1.8)\qquad \begin{bmatrix} N_{t+1} \\ J_{t+1} \\ A_{t+1} \end{bmatrix} = \begin{bmatrix} 0 & 2(0.93) & 0 \\ 0.7 & 0 & 0 \\ 0 & 0.93 & 0 \end{bmatrix} \begin{bmatrix} N_t \\ J_t \\ A_t \end{bmatrix}.$$

In general, a Leslie matrix has the form

$$(1.9)\qquad \begin{bmatrix} m_1 p_0 & m_2 p_1 & m_3 p_2 & \cdots & \cdots & m_k p_{k-1} & 0 \\ p_0 & 0 & 0 & \cdots & \cdots & 0 & 0 \\ 0 & p_1 & 0 & \cdots & \cdots & \cdots & 0 \\ 0 & 0 & p_3 & 0 & \cdots & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & \cdots & 0 & p_{k-1} & 0 \end{bmatrix},$$

where m_i is the number of offspring produced by the $(i+1)^{\text{th}}$ age class each time period, and p_i is the survival rate of an organism from class i to class $(i+1)$. In general, a $m_i p_i$ term is called a *fecundity* and a p_i term is called a *survivorship*.

As previously mentioned, a Leslie matrix contains information about characteristics of the population that it represents. Specifically, the eigenvalues and eigenvectors of this transition matrix give important information about the growth dynamics of the associated population. The dominant eigenvector, or *Perron root*, gives the stable growth rate of the population. This is the rate at which the population will grow after stabilizing to one growth rate. The right eigenvector associated with the Perron root gives the stable age distribution of the population. Thus after reaching the stable growth rate, the population distribution between the age classes will be a multiple of the Perron root eigenvalue. The left eigenvector (the eigenvector of the transpose of the Leslie matrix) associated with the Perron root gives the reproductive value of each age class; i.e., the worth of the addition of one member of the age class to the overall population.

In the Leslie matrix case, the existence of a positive, real Perron root and a positive stable age distribution is guaranteed by Perron-Frobenius Theory. The following theorem [1] applies, since a Leslie matrix is both nonnegative and indecomposable.

1.10 Theorem *(Perron-Frobenius) Let A be an n-square nonnegative indecomposable matrix. Then:*

(i) A has a real positive characteristic root r which is a simple root of the characteristic equation of A. If λ_i is any characteristic root of A, then $|\lambda_i| \le r$.

(ii) There exists a positive characteristic vector corresponding to r.

The case of population dynamics with regard to age-class separation, as suggested by Leslie, is well understood. However, this model faces the same problem as general equations (1.1) and (1.3). After reaching a stable growth rate, the modeled population grows unbounded at this rate. Thus this dynamical system does not take into account the limitations on resources that keep a given population at or beneath a carrying capacity. The focus of this paper is to investigate the addition of factors that will make the standard Leslie matrix model tend to a stable carrying capacity, specifically factors that deal with the effect of density-dependence upon population dynamical systems.

Types of Density-Dependent Terms

The addition of density-dependent terms to a Leslie matrix can be done in different ways. The density-dependent factor can be added to the fecundity terms, the survival terms, or both. The density-dependence can be incorporated into all age classes or only certain ones. Additionally, the form of the density-dependence can vary. It can be based on the Beverton-Holt model, the Ricker model, or another specially generated function that simulates the proper dynamics. Many examples of these differing terms can be found in the literature. Cushing cites numerous alternatives in [2].

For the purpose of this paper, a Beverton-Holt style density-dependence was incorporated into the Leslie matrix. Additionally, the density was dependent on the adult population and was placed in the juvenile survivorship positions in the matrix. The physical reasoning was that of limited territory, or land resource. Specifically, if there are a certain number of adult members of the species alive, there is less area for the juveniles to inhabit, and thus juvenile survival rates decrease. The density dependent term was of the form

$$(2.1) \qquad \frac{1}{1+bA_t}$$

where $b \ge 0$ and $b = 0$ implies density independence. It is incorporated in the matrix by multiplication with the juvenile survival rate, p_i. Similar themes can be found in previous literature by Beddington [3] as well as Fisher and Goh [4].

Method of Analysis

The same procedures are performed repeatedly throughout this paper, with respect to different situation and matrices. For simplification purposes, they will be described thoroughly for the simplest case, and then referred back to for later cases. The overall goals are to (1) establish conditions for the occurrence of growth, (2) calculate the equilibrium positions (carrying capacities) for the different age classes, and (3) investigate the stability of those carrying capacities. In some cases, simulations of population growth, as well as numerical analysis, may be incorporated into the procedure.

The Basic Model

The simplest application of this density-dependent term is to the 3x3 matrix with one class each of newborns, juveniles, and adults. For clarification in later matrices, only an adult age class can breed, and that is the distinction between juveniles and adults. After addition of the density dependent term (2.1), the system of equations (no longer linear) becomes

$$(3.1) \qquad \begin{cases} N_{t+1} = m_2 p_1 J_t \\ J_{t+1} = p_0 \dfrac{1}{1+bA_t} N_t \\ A_{t+1} = p_1 J_t \end{cases}$$

with matrix representation

$$(3.2) \qquad \begin{bmatrix} 0 & m_2 p_1 & 0 \\ \frac{p_0}{1+bA_t} & 0 & 0 \\ 0 & p_1 & 0 \end{bmatrix}.$$

Determining conditions for growth: In this case, to examine the conditions needed for any growth to occur at all, we first look at the density independent case; i.e., with $b = 0$. We then find the eigenvalues; more importantly the Perron root, of that associated matrix (3.2 with $b = 0$)

$$(3.3) \qquad \begin{bmatrix} 0 & m_2 p_1 & 0 \\ p_0 & 0 & 0 \\ 0 & p_1 & 0 \end{bmatrix}.$$

Calculation of eigenvalues of (3.3):

Solve $\begin{vmatrix} -\lambda & m_2 p_1 & 0 \\ p_0 & -\lambda & 0 \\ 0 & p_1 & -\lambda \end{vmatrix} = 0$. Expand around the top row. Then

$(-\lambda)(\lambda^2) - m_2 p_1 (p_0 \lambda) = 0$. So the characteristic equation for matrix (3.3) is

$$(3.4) \qquad \lambda(\lambda^2 - m_2 p_2 p_0) = 0$$

giving roots of 0, $\pm\sqrt{m_2 p_2 p_0}$. So the Perron root is $\sqrt{m_2 p_2 p_0}$. For any growth to occur at all, the Perron root must be larger than 1, or $m_2 p_2 p_0 > 1$. Thus the obvious condition for growth of the density-dependent system is that $m_2 p_2 p_0 > 1$.

Calculating equilibrium populations: The next step is to find the equilibrium populations of each ages class, that is the carrying capacity that is reached due to the addition of the density dependent term. This is accomplished by solving (3.1) under the conditions $N_{t+1} = N_t$, $J_{t+1} = J_t$, and $A_{t+1} = A_t$;i.e., the conditions that each year's population is equal to that of the previous year. This can be done simply by basically removing the subscripts and solving for *N*, *J*, and *A*. In this case, our system of equations becomes

$$(3.5) \qquad \begin{cases} N = m_2 p_1 J \\ J = p_0 \dfrac{1}{1+bA} N \\ A = p_1 J \end{cases}.$$

Solving (3.5):

By substitution we get $A = p_1 p_0 \dfrac{1}{1+bA} m_2 p_1 \dfrac{A}{p_1}$. If $A \neq 0$ (that is if we choose the equilibrium not to be at the origin) we get $1 + bA = m_2 p_1 p_0$, or $A = \dfrac{m_2 p_1 p_0 - 1}{b}$.

Resubstitution of this value for *A* into the other equations in (3.5) then yields the following solutions

$$(3.6) \qquad \begin{aligned} N &= \frac{m_2(m_2 p_1 p_0 - 1)}{b} \\ J &= \frac{m_2 p_1 p_0 - 1}{p_1 b} \\ A &= \frac{m_2 p_1 p_0 - 1}{b} \end{aligned} .$$

By designating the adult carrying capacity as *K*, we can write (3.6) in terms of *K* as

$$(3.7) \qquad \begin{aligned} N &= m_2 K \\ J &= \frac{K}{p_1} \\ A &= K \end{aligned} .$$

Checking stability of equilibrium positions: Our next step is to check the stability of these equilibrium positions. To do this we take the *Jacobian matrix*; i.e., the matrix of partial derivatives, of (3.2) evaluated at the equilibrium population, and find the eigenvalues of this new matrix. Then, according to the *Hartman-Grobman Theorem*, if the absolute value (or length in the case of complex eigenvalues) of all of the eigenvalues of this Jacobian matrix are less than 1, then the equilibrium positions are stable.

So we proceed. The Jacobian matrix of (3.2) is

$$(3.8)\quad \begin{bmatrix} 0 & m_2 p_1 & 0 \\ \frac{p_0}{1+bA_t} & 0 & \frac{-p_0 N_t b}{(1+bA_t)^2} \\ 0 & p_1 & 0 \end{bmatrix},$$

and at equilibrium, by substitution of (3.7), this becomes

$$(3.9)\quad \begin{bmatrix} 0 & m_2 p_1 & 0 \\ \frac{p_0}{1+bK} & 0 & \frac{-p_0 m_2 K b}{(1+bK)^2} \\ 0 & p_1 & 0 \end{bmatrix}.$$

Solving for the eigenvalues of (3.9), we get the characteristic equation

$$(3.10)\quad \lambda\left(\lambda^2 - \frac{1}{m_2 p_1 p_0}\right) = 0.$$

Thus the eigenvalues are $\lambda = 0$ or $\lambda = \pm\sqrt{\frac{1}{m_2 p_1 p_0}}$. But $m_2 p_1 p_0 > 1$. So $|\lambda| < 1$. Thus the equilibrium populations (3.7) are stable.

Extensions of One Density Dependence

Now that the characteristics of the simplest case has been established, we aim to find extensions and generalizations of this case. First we will extend the number of juvenile classes in the population without increasing the number of density dependencies.

The next matrix to tackle is then the 4x4 case represented by

$$(4.1)\quad \begin{bmatrix} 0 & 0 & m_3 p_2 & 0 \\ \frac{p_0}{1+bA_t} & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 \\ 0 & 0 & p_2 & 0 \end{bmatrix}.$$

The condition for growth is similar here to that of the simpler case; i.e., $m_3 p_2 p_1 p_0 > 1$. Solving for the equilibrium populations gives

$$(4.2)\qquad \begin{aligned} N &= m_3 K \\ J^1 &= \frac{K}{p_2 p_1} \\ J^2 &= \frac{K}{p_2} \\ A = K &= \frac{m_3 p_2 p_1 p_0 - 1}{b} \end{aligned}$$

In checking for stability of these carrying capacities, the characteristic equation of the Jacobian matrix associated with this model is $\lambda\left(\lambda^3 - \dfrac{1}{m_3 p_2 p_1 p_0}\right) = 0$. So again, since $m_3 p_2 p_1 p_0 > 1$, we have stability.

We can now generalize to an nxn matrix with $k = n-2$ juvenile classes of the form

$$(4.3)\qquad \begin{bmatrix} 0 & 0 & \cdots & \cdots & 0 & m_{n-1}p_{n-2} & 0 \\ \frac{p_0}{1+bA_t} & 0 & \cdots & \cdots & 0 & 0 & 0 \\ 0 & p_1 & 0 & \cdots & \cdots & 0 & 0 \\ 0 & 0 & p_2 & 0 & \cdots & \cdots & 0 \\ \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot \\ \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot \\ 0 & 0 & \cdots & \cdots & 0 & p_{n-2} & 0 \end{bmatrix}.$$

Again, in the density-independent case; i.e., when $b = 0$, the conditions for growth are similarly $m_{n-1} p_{n-2} p_{n-3} \cdots p_0 > 1$.

Solving for general equilibrium using induction gives the equations

$$(4.4)\qquad \begin{aligned} N &= m_{n-1} K \\ J^i &= \frac{K}{p_k p_{k-1} \cdots p_i} \quad \text{for all } i, 1 \le i \le k, k = n-2. \\ A = K &= \frac{m_{n-1} p_{n-2} p_{n-3} \cdots p_0 - 1}{b} \end{aligned}$$

The characteristic equation of the Jacobian matrix associated with this general case is

$$(4.5)\qquad \lambda\left(\lambda^{n-1} - \frac{1}{m_{n-1} p_{n-2} p_{n-3} \cdots p_0}\right) = 0.$$

So since $m_{n-1}p_{n-2}p_{n-3}\cdots p_0 > 1$, the equilibrium is stable.

Extensions of Two Density Dependencies

Now that the simplest extension of the simplest case is nailed down, the next case to consider is that where there are two classes of density-dependent juveniles, and the density dependence is the same for both juvenile classes. The simplest subcase is the 4x4 matrix

$$(5.1)\qquad \begin{bmatrix} 0 & 0 & m_3p_2 & 0 \\ \frac{p_0}{1+bA_t} & 0 & 0 & 0 \\ 0 & \frac{p_1}{1+bA_t} & 0 & 0 \\ 0 & 0 & p_2 & 0 \end{bmatrix}.$$

When $b = 0$, this matrix reduces identically as matrix (4.1) does under the same conditions, and so the condition for growth is once again $m_3p_2p_1p_0 > 1$.

Solution of the system of equations at equilibrium gives

$$(5.2)\qquad \begin{aligned} N &= m_3K \\ J^1 &= \frac{m_3p_0}{\sqrt{m_3p_2p_1p_0}}K \\ J^2 &= \frac{K}{p_2} \\ A = K &= \frac{\sqrt{m_3p_2p_1p_0}-1}{b} \end{aligned}.$$

In terms of stability, the characteristic equation of the associated Jacobian matrix evaluated at the equilibrium populations is

$$(5.3)\qquad \lambda(\lambda^3 + \lambda - M\lambda - M) = 0,\quad M = \frac{1}{\sqrt{m_3p_2p_1p_0}}.$$

Since this equation doesn't factor easily as in the previous cases, we must use different analysis to determine the size of its real and complex roots. Define

$$(5.4)\qquad f(\lambda) = \lambda^3 + \lambda - M\lambda - M.$$

So

$$(5.5)\qquad f'(\lambda) = 3\lambda^2 + 1 - M,$$

which (since $M<1$) is always positive. Since $f(0) = -M$ is negative, there is one real root, and it is positive. But $f(1) = 2 - 2M$ is positive, so the real root lies in (0, 1), and thus is small enough to imply stability. The complex roots take more work.

Now there are two complex roots (conjugates) and one real root to this equation. Call the complex roots z^+ and z^- and the real root x. Then

$$(5.6) \qquad f(\lambda) = (\lambda - z^+)(\lambda - z^-)(\lambda - x)$$

and so

$$(5.7) \qquad -M = (-z^+)(-z^-)(-x)$$

or more precisely,

$$(5.8) \qquad |M| = |z^+||z^-||x| = |z|^2|x|.$$

So then $|z|^2 = \frac{M}{x}$, and thus if it can be shown that $\frac{M}{x} < 1$, stability is shown. Now $f(M) = M^3 + M - M^2 - M = M^2(M-1) < 0$. So x lies in the interval $(M, 1)$ and thus $x > M$. So $\frac{M}{x} < 1$ and the equilibrium position is stable.

The next case to look at is the 5x5 matrix with similar form. Here the matrix is

$$(5.9) \qquad \begin{bmatrix} 0 & 0 & 0 & m_4 p_3 & 0 \\ \frac{p_0}{1+bA_t} & 0 & 0 & 0 & 0 \\ 0 & \frac{p_1}{1+bA_t} & 0 & 0 & 0 \\ 0 & 0 & p_2 & 0 & 0 \\ 0 & 0 & 0 & p_3 & 0 \end{bmatrix}.$$

As expected, in the density independent case, the condition for growth is $m_4 p_3 p_2 p_1 p_0 > 1$.

Equilibrium populations for this case are

$$(5.10) \qquad \begin{aligned} N &= m_4 K \\ J^1 &= \frac{m_4 p_0}{\sqrt{m_4 p_3 p_2 p_1 p_0}} K \\ J^2 &= \frac{K}{p_3 p_2} \\ J^3 &= \frac{K}{p_3} \\ A = K &= \frac{\sqrt{m_4 p_3 p_2 p_1 p_0} - 1}{b} \end{aligned} .$$

Our stability characteristic equation then becomes

$$(5.11) \qquad \lambda(\lambda^4 + \lambda - M\lambda - M) = 0, \quad M = \frac{1}{\sqrt{m_4 p_3 p_2 p_1 p_0}}.$$

Again, the analysis of this equation is more complex than that of previous ones.

So let

$$(5.12)\quad f(\lambda) = \lambda^4 + \lambda - M\lambda - M\,.$$

Since $\lambda = -1$ is a solution to $f(\lambda) = 0$, we can factor to get

$$(5.13)\quad f(\lambda) = (\lambda + 1)(\lambda^3 - \lambda^2 + \lambda - M)\,.$$

Now we let

$$(5.14)\quad g(\lambda) = \lambda^3 - \lambda^2 + \lambda - M\,.$$

Then

$$(5.15)\quad g'(\lambda) = 3\lambda^2 - 2\lambda + 1\,.$$

Since this is quadratic with positive coefficient, g is increasing on the interval $[0,1]$. Now $g(0) = -M$ is always negative, and $g(1) = 1 - M$ which is positive. Therefore the other real root must be in the interval (0, 1), satisfying the conditions for stability. Again, the complex roots take more work, but are analyzed in a the same manner as before. Assuming that $|z|$ is the length of the complex conjugate roots, we again get equation (5.8) from the function *g* (5.14). So again we must show $\frac{M}{x} < 1$.

Now $g(M) = M^3 - M^2 + M - M = M^2(M-1) < 0$. So *x* lies in the interval (*M*, 1) and thus *x*>*M*. So $\frac{M}{x} < 1$. However, we cannot conclude stability of the equilibrium position due to the Jacobian eigenvalue of -1. Although the effect of this eigenvalue is not completely understood, it does create an oscillatory pattern between two values that neither appears to be convergent or divergent after a large number of iterations. For example, Figure 1 is a simulation of the adult class population in this situation with $m_4 = 1.6$, $p_3 = 0.9$, $p_2 = 0.89$, $p_1 = 0.92$, $p_0 = 0.95$, and $b = 0.01$.

there will be a chart here

Generalization of this case to a larger matrix is much more complex than the previous case of only one density-dependent class. It is relatively simple to determine the conditions for growth and the equilibrium populations. However, establishing the stability of these carrying capacities is not so easy. The stability equation quickly gets complex and difficult to solve or infer stability from. Here we turn to numerical methods to get an idea of the stability of the system. The *nxn* matrix corresponding to these conditions is

$$
(5.16)\quad \begin{bmatrix}
0 & 0 & \cdots & \cdots & 0 & m_{n-1}p_{n-2} & 0 \\
\frac{p_0}{1+bA_t} & 0 & \cdots & \cdots & 0 & 0 & 0 \\
0 & \frac{p_1}{1+bA_t} & 0 & \cdots & \cdots & 0 & 0 \\
0 & 0 & p_2 & 0 & \cdots & \cdots & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
0 & 0 & \cdots & \cdots & 0 & p_{n-2} & 0
\end{bmatrix}.
$$

The condition for growth is as we expect it; i.e., when $b=0$, $m_{n-1}p_{n-2}p_{n-3}\cdots p_0>1$ must be satisfied for the stable growth rate to be greater than 1. The equilibrium carrying capacities are

$$
(5.17)\quad \begin{aligned}
N &= m_{n-1}K \\
J^1 &= \frac{m_{n-1}p_0}{\sqrt{m_{n-1}p_{n-2}p_{n-3}\cdots p_0}}K \\
J^i &= \frac{K}{p_k p_{k-1}\cdots p_i} \text{ for all } i, 1\le i\le k, k=n-2 \\
A = K &= \frac{\sqrt{m_{n-1}p_{n-2}p_{n-3}\cdots p_0}-1}{b}
\end{aligned}.
$$

The stability equation for the general case is

$$
(5.18)\quad \lambda(\lambda^{n-1}+\lambda-M\lambda-M)=0,\quad M=\frac{1}{\sqrt{m_3p_2p_1p_0}}.
$$

In the case where n is odd, $\lambda=-1$ is a root of the stability equation. Because stability is very hard to show in closed form for these equations of higher degree, we turn to numerically analyzing the equation for various size matrices while varying the parameter M over the interval (0, 1), specifically at $M = 0.01, 0.05$, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 0.95, and 0.99. For each such equation, Mathematica was used to take the roots of the equation and then find the absolute value of each root. Except for the odd cases where $\lambda=-1$ is a root, all real and complex roots had size smaller than 1. Thus a possible conclusion is that in the even cases, the equilibrium of this situation is stable, while in the odd case, there is oscillation between two values as seen in Figure 1.

Although this is not proof of these conclusions, it is a good indication of their validity, and further study may be able to prove it.

Extension to Three Density Dependencies

Naturally, the next case to look at involves the 5x5 matrix with three juvenile age classes, all of which are dependent upon the adult population in the same way. Without doing any calculation, by simply looking at a simulation of a population of this type, it is easily seen that this is unstable as in Figure 2. Here the conditions are $m_4=1.9, p_3=0.9, p_2=0.99, p_1=0.92, p_0=0.96$, and $b=0.02$. Notice that the oscillations grow wider as time moves forward without much hope of settling down to a stable carrying capacity. Because of the complex calculations involved in the analysis of this stability point, this case was not studied further.

there will be a chart here, too

Extension to Surviving Adults

Although we can continue to extend the number of density dependent terms we add to the matrix, another case to investigate is one where the number of adult age classes is increased. Similarly to the juvenile classes, we can simply start adding adult classes and then calculating equilibrium positions and stabilities. In this case, we must then consider whether we want the density dependent term to be proportionate to all adult age classes equally ($\frac{1}{1+b(A_t^1+A_t^2+\ldots)}$), all adult age classes differently ($\frac{1}{1+bA_t^1+cA_t^2+\ldots}$), or only on one or two age classes ($\frac{1}{1+bA_t^n}$). Obviously adding all of these non-linearities increases the 'messiness' of the needed calculations, as does the increase of fecundity terms in the top row of the matrix. In order to avoid these problems, first we tackle the case where there is still only one adult age class, but where we allow the adults to survive for more than one time step. To accomplish this, out matrix takes on the form for the simplest case

$$(6.1) \quad \begin{bmatrix} 0 & 0 & ms \\ \frac{p_0}{1+bA_t} & 0 & 0 \\ 0 & p_1 & s \end{bmatrix}.$$

In this matrix, we do not allow the adults to breed until they have been adults for one full time step (a simplification of the top row), and after each time step, a proportion, s, of adults survive to remain adults in the following time step. Thus we take multiple adult age classes and effectively combine them into one. This simplifies calculations to a manageable level.

The case of this type that we chose to look at was the 4x4 matrix

$$(6.2) \quad \begin{bmatrix} 0 & 0 & 0 & ms \\ \frac{p_0}{1+bA_t} & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 \\ 0 & 0 & p_2 & s \end{bmatrix}.$$

In terms of conditions for growth, the necessary condition is that $msp_2p_1p_0+s>1$. Equilibrium carrying capacities are

$$(6.3)\quad \begin{aligned} N &= msK \\ J^1 &= \tfrac{mp_0}{mp_2 p_1 p_0 + 1} K \\ J^2 &= \tfrac{mp_1 p_0}{mp_2 p_1 p_0 + 1} K \\ A = K &= \tfrac{msp_2 p_1 p_0 + s - 1}{b} \end{aligned}$$

Analysis of the Jacobian matrix associated with this one gives the stability equation

$$(6.4)\quad \lambda^4 - s\lambda^3 + \tfrac{(1-s)(ns+s-1)}{ns}\lambda + s - 1 = 0\,,\ n = mp_2 p_1 p_0\,.$$

First we will analyze the real roots of this equation. Letting (6.4) be the function $f(\lambda)$, we see that

$$(6.5)\quad f'(\lambda) = 4\lambda^3 - 3s\lambda^2 + \tfrac{(1-s)(ns+s-1)}{ns}\,.$$

This shows that f is decreasing on $(-\infty, 1)$ and increasing on $(1, \infty)$. Also, $f(0) = s - 1$, which is always negative. So we will examine the values $f(1)$ and $f(-1)$. Now $f(1) = \tfrac{(1-s)(ns+s-1)}{ns} > 0$ always, because of our condition on growth. So any positive real root must have size smaller than 1. Now $f(-1) = 2s - \tfrac{(1-s)(ns+s-1)}{ns}$, which is positive if $2s - \tfrac{(1-s)(ns+s-1)}{ns} > 0$, or equivalently $ns(3s-1) + (s-1)^2 > 0$. This is true when $s \geq \tfrac{1}{3}$. When $s < \tfrac{1}{3}$, this is true if $n < \tfrac{(s-1)^2}{s(1-3s)}$. This function of s reaches its minimum at $s = 0.2$, as can be seen from Figure 3.

there will be a graph here, too

Thus as long as $n < 8$, we have stability in the real roots. If $n > 8$, the equilibrium is unstable. Moving on to the complex roots. We need only examine the case where $n < 8$.

Conclusions

There is still much work to be done in the area of population dynamics of this type. This paper has only touched on a few of the many different ways that even just this one term can be added to a Leslie matrix model. The possibilities are countless. By only covering a small amount of a large topic, the conclusions to make are that this specific density dependent term appears to be promising in the majority of the cases investigated; i.e., there is stability in many of the cases. Further research into the practical applications of these models, as well as further extensions of them, must be done in order to draw an overall conclusion.

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