

NONLINEAR AGE-STRUCTURED MODELS

by Bianca Luedeker

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Approved:

Terence Blows, Ph.D., Chair

John M. Neuberger, Ph.D.

James W. Swift, Ph.D.

ABSTRACT

Nonlinear Age-structured Models

Bianca Luedeker

Linear Usher matrix models predict only three types of dynamics for a population being modeled: unbounded growth, a tendency to stable carrying capacity, or extinction. In real populations, much more complex dynamics can occur. This paper investigates the dynamics of populations modeled by nonlinear density-dependent Usher matrices. A Beverton-Holt type function incorporated into fecundities or survivorship rates brings about the density dependent effect. This paper looks at a variety of Usher type matrices of increasing generality. For each matrix, the conditions for unbounded growth, extinction, and stability of the carrying capacity are found. When the carrying capacity is unstable, more complex dynamics, such as stable oscillations, can occur. These dynamics are also investigated in the paper.

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Chapter 1

Introduction

In current times, it has become increasingly important to understand how a population behaves throughout time. As the human population increases, populations of plants and animals are quickly decreasing due to habitat loss and other negative effects of a large human population. Population biologists and wildlife managers are often concerned with understanding the current dynamics of a population and making short term predictions of the viability of a population. Is a certain endangered species doomed to extinction, or is there a possibility that it will bounce back if appropriate measures are taken? To answer these types of questions, mathematical models are frequently employed.

The simplest mathematical models used to describe populations are one-dimensional and deterministic. This means that every organism is essentially modeled in the same way regardless of the organism's individual characteristics, such as age, gender, fecundity, and other varying vital rates. Variation due to environmental and temporal factors is also excluded. These models require the user to make a number of unrealistic assumptions. The models are classified as two types: discrete and continuous.

In the discrete model, time is broken down into intervals or steps. In reality, time is continuous, but this does not mean that this model should not be used. Many populations breed only at a certain time of the year, thus the discrete model represents these populations well. The simplest discrete model is given by

$$N_{t+1} = \lambda N_t \tag{1.1}$$

where N_t represents the population size (usually in number of individuals) at time t and N_{t+1} represents the population size one time step later. λ is the per time step growth rate. Note that λ does not vary from year to year, which is unlikely to occur in a real population and is one of the assumptions the user of this model is forced to make. The solution to (1.1) is given by

$$N_t = N_0 \lambda^t \tag{1.2}$$

When using a discrete model, difference equations are used; however, when a continuous model is used, a differential equation replaces the difference equation. An equivalent continuous model to (1.1) is given by

$$\frac{dN}{dt} = rN \quad (1.3)$$

where N is the population size and r is the intrinsic growth rate. The solution to (1.3) is

$$N(t) = N_0 e^{rt} \quad (1.4)$$

where N_0 is the initial population size. Note that λ in (1.1) must be e^r for the two models to be equivalent. No matter how the population actually grows, either discretely or continuously, either model can be used.

If (1.1) or (1.3) is used, then there are only three types of dynamics that can occur. If $0 < \lambda < 1$ then the population will decline and eventually go extinct. In the case where $\lambda = 1$ the size of the population will remain constant. If $\lambda > 1$ the population will grow unbounded. This is a major problem of both models since the growth of any population is limited by the amount of resources available. If a population is introduced into a new area where resources are plentiful, then exponential growth may be possible for a short time, but certainly not indefinitely. As the population increases in size, the rate of increase will naturally slow; this is known as density dependence. A density dependent effect can be incorporated into the above models by making small changes. From this point in the paper onward, I will only be concerned with the discrete form, so that is the only model that will be altered. One such change that can be made to (1.1) is the addition of some type of carrying capacity K . After the population reaches size K , all growth will cease. There are many choices of nonlinear models that will give this result.

One such model is the Beverton-Holt

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

which will be simplified throughout the rest of the paper as

$$N_{t+1} = \lambda N_t \left(\frac{1}{1 + a N_t} \right) \quad (1.6)$$

where $a = \frac{\lambda-1}{K}$ is a parameter representing carrying capacity. This model is equivalent to the well known logistic differential equation. Another option is the Ricker model

$$N_{t+1} = N_t e^{r(1 - \frac{N_t}{K})} \quad (1.7)$$

The shape of the two nonlinear functions differ significantly and imply different types of dynamics (see Figure 1.1). The Beverton-Holt model represents a contest density dependent effect where the population grows monotonically until some threshold limit is reached. At this point, the size of the population remains stable. The Ricker model represents a scramble density dependent effect. In this scenario, the population is much less stable and complex dynamics can occur. Varying the values of the parameters r and K can result in exponential growth, stable cycles, and even chaos.

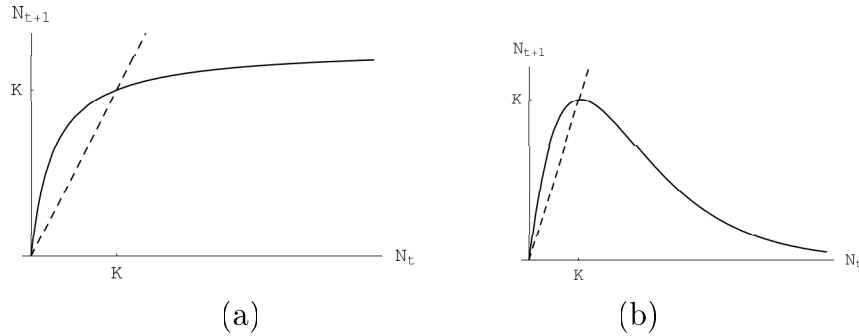


Figure 1.1: Figure (a) is a plot of (1.5) where specific values of K and λ have been chosen. The solid curve is the Beverton-Holt function and the dotted line is $y = x$. Figure (b) is a plot of (1.7) where typical values for r and K have been selected. The solid curve is the Ricker function and the dotted line is $y = x$. In both figures, note the change that occurs when the carrying capacity K is reached.

Even though (1.5) and (1.7) are more realistic than (1.1), they are both too simple to represent the complex dynamics of most population. In many populations, the age of an organism significantly affects its vital rates, in particular, time step to time step survivorship and fecundity. This is especially true of organisms whose life cycle can be broken up into distinct stages (frequently newborns and adults, or newborns, subadults, and adults). In order to model the distinct stages, a system of equations is required. A commonly used model is the Leslie matrix model. A general n -stage post-breeding Leslie matrix model is of the form

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \\ \vdots \\ \vdots \\ N_{n-1,t+1} \end{bmatrix} = \begin{bmatrix} m_1 p_0 & m_2 p_1 & \dots & \dots & m_{n-1} p_{n-2} & 0 \\ p_0 & 0 & & & \vdots & 0 \\ 0 & p_1 & \ddots & & \vdots & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \ddots & 0 & 0 \\ 0 & 0 & \dots & 0 & p_{n-2} & 0 \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \\ \vdots \\ \vdots \\ N_{n-1,t} \end{bmatrix} \quad (1.8)$$

where $N_{i,t}$ is the size of the i^{th} stage at time t , $N_{i,t+1}$ is the size of the i^{th} stage one time step later, p_i is the probability of an individual in the i^{th} stage surviving to the next time step (and thus, moving into the next stage), and m_i is the number of offspring produced per individual in the i^{th} stage per time step (the fecundity). Usually, only the females are represented in such models. Note that in this model, there is only one stage, N_0 , that does not produce offspring. Furthermore, each individual is in one stage for exactly one time step and after an individual reaches a maximum age, it dies. Because of these constraints, this model is frequently altered.

The model analyzed in this paper is not the above Leslie matrix, but a similar Usher matrix. The matrix studied is the Usher matrix

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \\ \vdots \\ \vdots \\ N_{n-1,t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & \dots & 0 & m_{n-1}p_{n-2} & ms \\ p_0 & 0 & & & \vdots & 0 \\ 0 & p_1 & \ddots & & \vdots & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \ddots & 0 & 0 \\ 0 & 0 & \dots & 0 & p_{n-2} & s \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \\ \vdots \\ \vdots \\ N_{n-1,t} \end{bmatrix} \quad (1.9)$$

where only the last two stage classes reproduce. Here m is the number of offspring produced by a member of the last stage class during one time step, and s is the probability that a member of the last stage class lives to the next time step. Note the similarities and differences between this matrix and (1.8). If an individual reaches the last stage, then it may survive to the next time step while remaining in the same stage. As in the Leslie matrix, each individual not in the last stage is each stage for one time step. To represent a population, one might choose a matrix with an infinite number of stages since an organism could live an unpredictable number of time steps into the future, with decreased probability of surviving as the steps progress. The last stage class in (1.9) is a lumping of the “last” infinitely many stages. This may be done as long as the fecundity and survivorship does not vary throughout these stages. Using this matrix, the population must have a single newborn stage, many subadult stages where survivorship may vary throughout different stages and no subadults reproduce, and two adult stages, which is the only source of new individuals.

Information can be gained about the populations represented by (1.8) and (1.9) by looking just at the eigenvalues and eigenvectors. Since the nonzero entries of these matrices are probabilities and the product of probabilities and the number of young produced, the matrices are clearly nonnegative. Furthermore, many of these matrices are irreducible [8].

Definition 1.0.1 *Irreducible:* A matrix A is called reducible if there is a permutation

that puts it into the form

$$\tilde{A} = \begin{pmatrix} B & 0 \\ C & D \end{pmatrix}$$

where B and D are square matrices. Otherwise A is called irreducible.

Cushing [4] states that all Usher matrices where the entries on the subdiagonal and the entry in the upper right corner are greater than zero are irreducible. In this case, the Perron-Frobenius Theorem can be used [8]. In cases where the Usher matrix is not irreducible, Theorem 1.0.2 may be used instead [8].

Theorem 1.0.2 *A nonnegative matrix A always has a nonnegative characteristic value r such that the moduli of all other characteristic values of A do not exceed r . To this maximal characteristic value r there corresponds a nonnegative eigenvector.*

Theorem 1.0.3 *Perron-Frobenius: An irreducible nonnegative matrix always has a positive characteristic value r that is a simple root of the characteristic equation. The moduli of all other characteristic values do not exceed r . This root is called the Perron root. There exists a positive eigenvector corresponding to the Perron root.*

The root r is the growth rate of the population. If $r < 1$ then the population will go extinct. If $r > 1$ then the population will grow exponentially without bound. In the special case where $r = 1$, the population will tend towards an equilibrium state. The normalized right eigenvector corresponding to r gives the stable age distribution of the population and the normalized left eigenvector gives the reproductive value of each class [4]. If there are two or more eigenvalues of the same modulus, then cycles can occur. This can occur if the matrix is reducible.

Just like the first one-dimensional model considered, the model above is linear. What happens when there is a carrying capacity? The goal of this paper is to investigate the effects of density dependence, in the form of a Beverton-Holt function, on the dynamics of a population modeled by (1.9). This can be done by including a single density dependent function in survivorships, fecundities, or both. In particular, in this paper the questions of what are the values of N_0, N_1, \dots at carrying capacity, for what parameter values is the carrying capacity stable, and, if the carrying capacity is not stable, then what kind of dynamics occur will be answered. In chapter 2, we will discuss what research has already been done on this problem and what other matrices and density dependent functions have been investigated.

Chapter 2

History and Previous Work

Interest in mathematical matrix models began in the 1940's. P.H. Leslie was one of the pioneers in this area, and it is from his work that the name Leslie matrix originates. In his first papers on the subject, Leslie established key properties of Leslie matrices. One such property is that the dominant eigenvalue and the corresponding eigenvector give the stable growth rate and stable age distribution respectively. However, when Leslie began he only considered linear systems of difference equations. Hence, the field of nonlinear population models was wide open.

Another pioneer in the research of matrix models was M.B. Usher. In his paper, Usher generalized the work of Leslie by studying the properties of nonlinear matrix models [13]. Besides looking at just Leslie matrices, Usher investigated matrices where individuals can survive more than one time step once they reach the final stage (Usher matrices), and matrices where individuals can stay in a stage class for more than one time step (Lefkovich matrices). One key observation that Usher made was that Leslie and Usher matrices are irreducible and nonnegative, thus, the Perron-Frobenius theorems may be applied.

2.1 Scalar Nonlinearities

In the followup to the 1945 paper, Leslie presents some further results pertaining to constant matrices and begins to investigate the properties of nonlinear matrix models [10]. Leslie's treatment of nonlinear matrices is not as broad as Usher's in this paper. He considers two extreme cases: one where fecundity is decreased due to limited resources and one where survivorship is decreased due to limited resources, but leaves the case where both mortality and fecundity are affected for future studies. In the case where mortality is effected, Leslie multiplies the entire original scalar matrix by a generalized Beverton-Holt function $q(N) = \frac{1}{\alpha + \beta N}$, where N is the total population size. Two large assumptions are involved in this process: the total population size

plays a key role, and the density dependent factor is independent of age. Leslie's main concern was the trajectory of the population, which he found to follow the logistic curve. Leslie covers the case where fecundity is nonlinear in a similar fashion. Instead of multiplying the entire matrix by a nonlinear term, Leslie only multiplies the top row by a nonlinear term.

Cushing too studied the case where a scalar matrix model is multiplied by a nonlinear function and generated some important theorems [3]. The class of functions studied was not restricted to the Beverton-Holt choice. If $\rho(t)$ is the vector of stage class sizes at time t , Cushing used the model

$$\rho(t+1) = h(\rho(t))A\rho(t) \quad (2.1)$$

where A is a Leslie matrix and h is a nonlinear function of the stage class sizes. This allows the nonlinear function to be based on a weighted population total rather than the usual total population. The following theorem holds when h is based on total population size.

Theorem 2.1.1 *Let A be nonnegative, irreducible, and primitive with maximal eigenvector λ and corresponding unit eigenvector η . Let $\rho(t)$ be a solution of (2.1) with $\rho(0) \geq 0$, $\|\rho(0)\| > 0$. Then*

$$\nu(t) = \frac{\rho(t)}{\|\rho(t)\|} \rightarrow \eta \text{ as } t \rightarrow \infty$$

and the total population size $p(t) = \|\rho(t)\|$ satisfies the scalar difference equation

$$p(t+1) = \|A\nu(t)\|h[\nu(t)p(t)]p(t)$$

$$p(0) = \|\rho(0)\| > 0$$

The only constraint imposed on h is that h must be positive. Hence in the above theorem, h may be a Beverton-Holt, Ricker, or some other positive function.

The idea that every element of a matrix model is affected by density dependence in exactly the same way is unrealistic, and much of the research is devoted to examples of models where the elements are affected differently.

2.2 Nonlinearities in Some Terms

In his paper, Usher compiles many numerical examples of nonlinear matrices in order to make generalizations. Included is a Leslie matrix where both fecundities and survivorship rates are density dependent; both functions used are independent of age and depend upon total population size. The fecundity function is a Beverton-Holt

type and the survivorship one is a Ricker. Two more examples are a 3×3 Leslie matrix where only one survivorship rate is density dependent, and another 3×3 Leslie matrix where two very different functions for fecundities are used. From these examples, Usher concludes that three types of dynamics can occur in density dependent matrices, a sigmoidal increase to carrying capacity, a sigmoidal increase with damped oscillations, or stable oscillations. The density dependent functions that are more sensitive to changes in population size tend to produce oscillations.

In a more recent paper by Ugarčović and Weiss, specific examples of a Leslie model where density dependence is included only in fecundities is studied [14]. Here the Ricker function $e^{-\lambda N}$, where λ is a parameter and N is the total population size, is included in the top row. This is similar to what Leslie did originally. Through numerical techniques, the authors find complex dynamics including four types of bifurcations leading to stable cycles, strange attractors, and chaos. Since all of the work is done numerically, the investigation of a general case is not covered.

Cooke and Leon address the problem of a general case, but only in a very limited fashion, the 2×2 case [2]. The matrix used is

$$\begin{bmatrix} f_0(N) & f_1(N) \\ p_0(N) & p_1(N) \end{bmatrix}$$

where each entry represents a different function of N , the total population size. The authors find three conditions necessary to ensure a stable carrying capacity and apply the results to a model of a bird population.

In much of the research, density dependent terms are incorporated into the matrix only in the fecundity terms. The assumption here is that density dependent effects occur mostly in the first year or stage of life. The case where density dependence occurs in the survivorship probabilities is mostly overlooked. In two papers [11] and [15], Wikan investigates the case where the fecundities are fixed and the survivorship parameters are density dependent in Leslie matrices. In the first paper, the only density dependent function considered is of the Ricker type. In the second paper the class of functions is extended to all functions p such that $p' < 0$. In the second paper, the generalized Beverton-Holt equation is one of the examples studied in detail.

In both papers the authors consider matrices of 2, 3, and 4 dimensions and generalize the results to any n dimensional case. The results for both papers are similar. The carrying capacity becomes unstable through a Hopf bifurcation, which is when a pair of complex conjugate eigenvalues of the linearized system crosses the unit circle. These Hopf bifurcations lead to cycles of size four and "pseudo-cycles" of size four where there are four attractors, but the cycle is not exact. As the parameters were increased to move farther into the unstable region, the pseudo-cycles became exact. Furthermore, the authors were also able to find chaotic regions in their examples.

One of the more recent papers by Pykh and Efremova covered a lot of territory in the field of nonlinear matrix models [6]. The type of matrix studied is again a Leslie matrix, but the size of the matrix is arbitrary. Every element in the matrix is effected by density dependence. The fecundities are functions of the form $b_i\varphi(N)$ and the survivorship functions are of the form $a_i\psi_i(N)$. Here the a_i and b_i are constants and N is the total population density. The only constraints placed on φ and the ψ_i are that the functions are positive, their first derivatives are positive, and the limits as N approaches infinity are less than 1. These constraints are met by the Ricker and Beverton-Holt functions, as well as a variety of others. Using this model, the authors generate theorems for the existence and uniqueness of a positive equilibrium and find the conditions needed to ensure stability of such points.

2.3 Nonlinearities Not Based on Total Population Size

In the majority of papers published on the subject of nonlinear age-structured models, the nonlinear function used is a function of total population size. The choice of basing density dependence on total population size is often automatic and stated without any reasoning to support such a choice. It is the accepted convention. In my research, I have found three exceptions.

The first is a paper by Bergh and Getz [1]. The model employed is a popular Leslie age-structured model used in fishery management. In the model, density dependent terms are included only in the first row of the matrix, again this is because density dependence is thought to have the greatest impact on animals during the first year of life. The function used is a function only of $N_{0,t}$, which in this application is defined to be the number of zygotes or the biomass of the zygotes. Essentially, $N_{0,t}$ is a weighted sum of the size or biomass of the other stages. In the model, the same function is applied to every element of the first row.

Another paper that uses a weighted sum of the population size of each stage instead of the total population size is one by Desharnais and Liu [5]. The weighted sum used is much more complicated and varies depending on the element of the matrix. The general model used is another Leslie matrix, except that every entry is a different density dependent function. For example, the survivorship functions are given by $s_i\exp[-\sum_{j=1}^n \gamma_{ij}n_j(t)]$ where γ_{ij} is a weight that measures the sensitivity of the survivorship of an individual in stage i to the density of individuals in stage j and $n_j(t)$ is the size of stage j at time t . The analysis is not carried out on this general system, but on a much more specific example.

A matrix difference equation of the form (1.9) where $m_{n-2} = 0$ is studied in a paper by Fisher and Goh [7]. The nonlinear term was included only in the one fecundity term and the nonlinearity was a function only of the mature and reproductive females.

This model is similar to the model studied in the next chapter. However, instead of retaining the structure of the system, Fisher and Goh collapse the system into a single difference equation. In their model, the number of mature females at time $t+1$, which they denoted $N_k(t+1)$, is a function of $N_k(t-k)$.

2.4 Summary and Overview

This work presented in the next few chapters is unique in the fact that density dependence is based only on the size of the last stage class and the matrix form is retained throughout the analysis. Most of the research that exists focuses on a Leslie matrix model. Here the model chosen is the less popular Usher model. The Ricker model, which is known to produce exotic dynamics even in the one dimensional model, is a function studied frequently in the literature; no doubt because of its tendency towards instability. In this paper, the Beverton-Holt model is used in order to determine what conditions are necessary to cause a relatively stable model to display complex dynamics. Density dependent terms are included in both the fecundity and the survivorship while most papers tend only to look at density dependence in fecundity.

In Chapter 3, I investigate the model studied in the Fisher and Goh paper where the matrix structure is retained. Also in this chapter, the Fisher and Goh model is altered so that the nonlinearity is included in survivorship. Using the Perron-Frobenius Theorem, the dynamics of the system are shown to be fairly simple. In Chapter 4, instead of using just one density dependent term, two density dependent terms are incorporated into the fecundities of an adult and subadult class. The 3×3 system where the fecundities and nonlinear term are the same is explored in depth, as is the 3×3 case where the fecundities vary. Numerical results for higher dimensional cases are presented. Chapter 5 is an investigation of the 3×3 case considered in Chapter 3, but here the two nonlinear functions are allowed to vary.

Chapter 3

One Density Dependent Term

3.1 Density Dependence in m

Throughout the paper, a Beverton-Holt density dependent function that depends only on the number of individuals in the last stage class will be used. In nature, the adult stage will likely have the largest draw on resources than any other stage. For this reason, the Beverton-Holt function used depends only on the number of adults.. Another common choice is to base density dependence on the total number of individuals, but this typically overexaggerates the effect of newborns on the amount of resources. The Beverton-Holt model is much more stable than the Ricker model. Even in the simple one-dimensional Ricker model, chaos can occur. The Beverton-Holt model was chosen to determine at what point a stable model becomes unstable. If there are a total of n stages labeled from 0 to $n - 1$ so that N_{n-1} is the last stage, the function f is defined by

$$f(N_{n-1}) = \frac{1}{1 + aN_{n-1}}. \quad (3.1)$$

In (3.1), the intensity of density dependence depends on the parameter a . The parameter a is always greater than or equal to 0. When $a = 0$ there is no density dependence. As a becomes larger, the density dependent effect becomes greater.

Throughout the paper the following steps will be performed

1. The system will be rescaled to decrease the number of parameters.
2. The stage specific carrying capacities (equilibrium positions) will be found.
3. The stability of the carrying capacity will be determined.

The investigation starts with the simplest case. The Usher matrix (1.9) is altered so that m_{n-1} is set to 0 and m , the only fecundity term, is assumed to be density dependent. This results in the system of equations given by the $n \times n$ matrix

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \\ \vdots \\ \vdots \\ N_{n-1,t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & \dots & \dots & 0 & ms \frac{1}{1+aN_{n-1,t}} \\ p_0 & 0 & & & \vdots & 0 \\ 0 & p_1 & \ddots & & \vdots & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \ddots & 0 & 0 \\ 0 & 0 & \dots & 0 & p_{n-2} & s \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \\ \vdots \\ \vdots \\ N_{n-1,t} \end{bmatrix}. \quad (3.2)$$

First the equations are rescaled to get rid of many parameters. For each stage i , let $M_i = \alpha_i N_i$. Then set

$$\begin{cases} \alpha_{n-1} &= a \\ \alpha_i &= a \prod_{j=i}^{n-2} p_j \quad \text{for all other } i. \end{cases} \quad (3.3)$$

This results in the system

$$\begin{cases} M_{0,t+1} &= cs \frac{1}{1+M_{n-1,t}} M_{n-1,t} \\ M_{1,t+1} &= M_{0,t} \\ M_{2,t+1} &= M_{1,t} \\ &\vdots \\ M_{n-1,t+1} &= M_{n-2,t} + sM_{n-1,t} \end{cases} \quad (3.4)$$

where $c = m \prod_{j=0}^{n-2} p_j$.

Next, the carrying capacity is found. Let M_i^* denote the equilibrium population at each stage i . To find the equilibrium the time subscripts are dropped since the population is at carrying capacity when its size does not change from one time step to the next. The population is at equilibrium when

$$\begin{cases} M_0^* &= cs \frac{1}{1+M_{n-1}^*} M_{n-1}^* \\ M_1^* &= M_0^* \\ M_2^* &= M_1^* \\ &\vdots \\ M_{n-1}^* &= M_{n-2}^* + sM_{n-1}^* \end{cases} \quad (3.5)$$

Solving this system yields two solutions. One is the origin, which will occur in every system and will no longer be mentioned, and one is the true carrying capacity. The

carrying capacity is

$$\begin{cases} M_{n-1}^* &= \frac{cs-1+s}{1-s} \\ M_i^* &= \frac{cs-1+s}{c} \end{cases} \text{ for all other values of } i. \quad (3.6)$$

Note that $1 - s \geq 0$ and $c \geq 0$ since s is a survivorship probability and is between 0 and 1 and c is the product of fecundity and other survivorship probabilities. Thus, the carrying capacity is positive only if $c > \frac{1-s}{s}$. If the carrying capacity is negative or zero, then the population will go extinct or diverge to infinity. These carrying capacities are not valid for $s = 1$ or $c = 0$. If $s = 1$, the only equilibrium point is the origin. Since the population is clearly not headed for extinction, the population must be growing unbounded. If $c = 0$ then again, the only equilibrium point is the origin, and since no individual is reproducing, the population must go extinct.

To analyze the stability of the carrying capacity, the following theorem and definitions, are applied [9].

Definition 3.1.1 *Diffeomorphism*: If $G : \mathbb{R}^n \rightarrow \mathbb{R}^n$ is a smooth map with a smooth inverse, then G is a diffeomorphism.

Definition 3.1.2 *Hyperbolic Fixed Point*: If \bar{x} is a fixed point of G and $DG(\bar{x})$ has no eigenvalues of unit modulus, then \bar{x} is called a hyperbolic fixed point.

Theorem 3.1.3 *Hartman-Grobman*: Let $G : \mathbb{R}^n \rightarrow \mathbb{R}^n$ be a C^1 diffeomorphism with a hyperbolic fixed point \bar{x} . Then there exists a homeomorphism k defined on some neighborhood U on \bar{x} such that $k(G(\xi)) = DG(\bar{x})k(\xi)$ for all $\xi \in U$, where DG is the Jacobian.

In essence, the Hartman-Grobman Theorem states that if the moduli of all the eigenvalues of the Jacobian matrix evaluated at equilibrium are less than 1, then the population is stable at equilibrium. This process of linearizing about a fixed point to determine stability in a system of difference equations is analogous to what is done with differential equations. The Jacobian matrix evaluated at equilibrium in this case is

$$\begin{bmatrix} 0 & 0 & \dots & \dots & 0 & \frac{(1-s)(s+cs-1)}{cs} \\ 1 & 0 & & & \vdots & 0 \\ 0 & 1 & \ddots & & \vdots & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \ddots & 0 & 0 \\ 0 & 0 & \dots & 0 & 1 & s \end{bmatrix}, \quad (3.7)$$

which has characteristic equation

$$h(\lambda) = (-1)^n(\lambda^n - s\lambda^{n-1} - \frac{(1-s)(s+cs-1)}{cs}). \quad (3.8)$$

At this point, assume that $c > \frac{1-s}{s}$; the situation where carrying capacity is not positive will be covered later. With this restriction in hand, every element in (3.7) is nonnegative. Furthermore, this matrix is irreducible. Hence, the Perron-Frobenius Theorem can be invoked. To determine the stability of the carrying capacity, the only information needed is whether the Perron root is larger or smaller than one.

The derivative of (3.8) is

$$h'(\lambda) = (-1)^n \lambda^{n-2}(n\lambda - s(n-1)), \quad (3.9)$$

so the critical points of (3.8) occur when $\lambda = 0$ or $\lambda = \frac{s(n-1)}{n}$. Furthermore, $\frac{s(n-1)}{n} < 1$. The $(-1)^n$ term may be ignored since the roots of $h(\lambda)$ and $-1h(\lambda)$ are the same. This leaves two cases to consider: when n is odd and when n is even. If n is even, then (3.8) is decreasing on $(-\infty, \frac{s(n-1)}{n})$ and increasing on $(\frac{s(n-1)}{n}, \infty)$. If n is odd, then (3.8) is decreasing on $(0, \frac{s(n-1)}{n})$ and increasing on the intervals $(-\infty, 0)$ and $(\frac{s(n-1)}{n}, \infty)$. By the Perron-Frobenius Theorem, (3.8) has a positive real root of maximum modulus. This means that in either the even or odd case, $h(\frac{s(n-1)}{n}) \leq 0$ else no positive real root would exist. Hence, if $h(1) > 0$ the carrying capacity is stable and if $h(1) \leq 0$ the carrying capacity is unstable. Here

$$h(1) = 1 - s - \frac{(1-s)(s+cs-1)}{cs} = \frac{(1-s)^2}{cs} \geq 0. \quad (3.10)$$

Thus, the carrying capacity is stable as long as $s \neq 1$ and $c > \frac{1-s}{s}$. Figure 3.1 shows a typical plot of the characteristic equation for the even and odd n case.

To determine what occurs in the case where the constraint on c is not met, the corresponding linear model is analyzed. If the Perron root of the corresponding linear case is less than one, then no growth can occur in the nonlinear model. This is a consequence of the Hartman-Grobman Theorem [9]. The linear case is represented by the matrix

$$\begin{bmatrix} 0 & 0 & \dots & \dots & 0 & c \\ 1 & 0 & & & \vdots & 0 \\ 0 & 1 & \ddots & & \vdots & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \ddots & 0 & 0 \\ 0 & 0 & \dots & 0 & 1 & s \end{bmatrix} \quad (3.11)$$

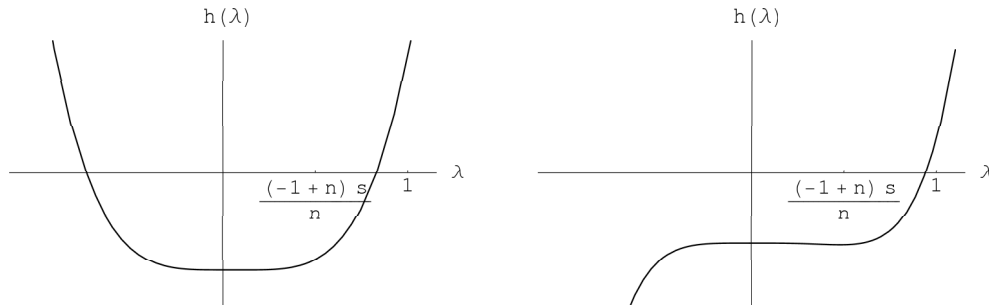


Figure 3.1: The characteristic equation (3.8) for the cases where n is even and where n is odd. In either case, the Perron root is smaller than one.

with corresponding characteristic equation

$$h(\lambda) = (-1)^n(\lambda^n - s\lambda^{n-1} - mc). \quad (3.12)$$

Analyzing (3.12) just as (3.8) yields the fact that no growth occurs unless $c > \frac{1-s}{s}$. Thus, the carrying capacity is stable everywhere the population is not headed for extinction. The following theorem summarizes the results proved in the previous pages.

Theorem 3.1.4 *For a population modeled by a system of difference equations of the form (3.4) where $s \in [0, 1]$ and $c \in (0, \infty)$ three types of dynamics can occur:*

1. *If $c \leq \frac{1-s}{s}$ no positive equilibrium point exists and the population will go extinct.*
2. *If $s < 1$ and $c > \frac{1-s}{s}$ a unique positive equilibrium point exists. This equilibrium is stable.*
3. *If $s = 1$ no positive equilibrium point exists and the population will grow unbounded.*

Figure 3.2 is a graphical display of the above theorem. Figure 3.3 is a plot of the total population size over 50 iterations where c is fixed at 2 and s is allowed to vary for the three by three case.

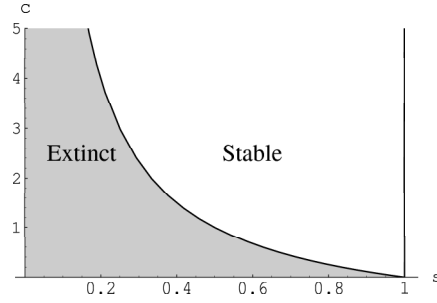


Figure 3.2: The regions in the s - c plane where the carrying capacity is stable and where the population goes extinct for the case where density dependence is in m . On the line $s=1$ the population grows unbounded.

3.2 Density Dependence in s

A more difficult problem is to include the density dependent term in the parameter s . This results in the system with two density dependent entries given by

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \\ \vdots \\ \vdots \\ N_{n-1,t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & \dots & \dots & 0 & ms \frac{1}{1+aN_{n-1,t}} \\ p_0 & 0 & & & \vdots & 0 \\ 0 & p_1 & \ddots & & \vdots & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \ddots & 0 & 0 \\ 0 & 0 & \dots & 0 & p_{n-2} & s \frac{1}{1+aN_{n-1,t}} \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \\ \vdots \\ \vdots \\ N_{n-1,t} \end{bmatrix}. \quad (3.13)$$

The same rescaling process is used as in Section 2.1 and the same values for the α_i are used (3.3). The rescaled system is

$$\begin{cases} M_{0,t+1} &= cs \frac{1}{1+M_{n-1,t}} M_{n-1,t} \\ M_{1,t+1} &= M_{0,t} \\ M_{2,t+1} &= M_{1,t} \\ &\vdots \\ M_{n-1,t+1} &= M_{n-2,t} + s \frac{1}{1+M_{n-1,t}} M_{n-1,t} \end{cases} \quad (3.14)$$

where c is defined as in the above case. Solving (3.14) at equilibrium gives

$$\begin{cases} M_{n-1}^* &= cs + s - 1, \\ M_i^* &= cs - 1 + \frac{s}{s+cs} \text{ for all other values of } i. \end{cases} \quad (3.15)$$

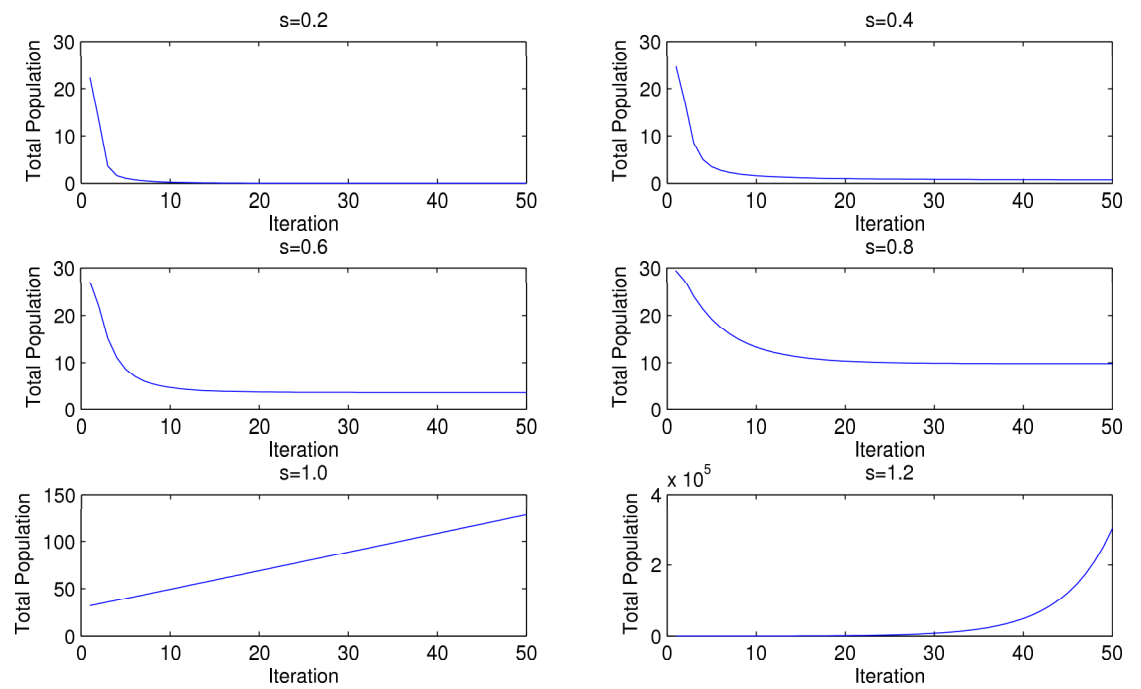


Figure 3.3: Using three stage classes, arbitrary initial population sizes, $c = 2$, and s varying, equation (3.4) was iterated 50 times. The total population size for each of the 50 iterations is plotted for each of the specified values of s .

If $c < \frac{1-s}{s}$ then $M_{n-1}^* < 0$ and $M_i^* < 0$. Hence, the carrying capacity will be positive when $c > \frac{1-s}{s}$. The equilibrium points are not valid for $s = 0$ or $c = 0$; however, it is not hard to see that if one of the two parameters is 0, then the population will go extinct. The same process of analyzing the linear case was applied here to find that if the carrying capacity is not positive, then the population will go extinct.

The Hartman-Grobman Theorem is applied to determine the stability of the carrying capacity. The Jacobian of (3.14) evaluated at equilibrium is

$$\begin{bmatrix} 0 & 0 & \dots & \dots & 0 & \frac{c}{(c+1)^2s} \\ 1 & 0 & & & \vdots & 0 \\ 0 & 1 & \ddots & & \vdots & \vdots \\ 0 & 0 & \ddots & \ddots & \vdots & \vdots \\ \vdots & \vdots & \ddots & \ddots & 0 & 0 \\ 0 & 0 & \dots & 0 & 1 & \frac{1}{(c+1)^2s} \end{bmatrix}. \quad (3.16)$$

Every element in (3.16) is clearly nonnegative. The characteristic equation of this matrix is

$$h(\lambda) = (-1)^n \left(\lambda^n - \frac{1}{(c+1)^2s} \lambda^{n-1} - \frac{c}{(c+1)^2s} \right). \quad (3.17)$$

As in section 3.1, the $(-1)^n$ term can be ignored. The goal is to determine whether the Perron root is larger or smaller than 1. Since the Jacobian is nonnegative, (1.0.3) can be used. The derivative of (3.17) is

$$h'(\lambda) = \lambda^{n-2} \left(n\lambda - \frac{1}{(c+1)^2s} (n-1) \right). \quad (3.18)$$

The critical points occur when $\lambda = 0$ and $\lambda = \frac{n-1}{n(c+1)^2s}$. Note that $\frac{n-1}{n(c+1)^2s} < \frac{n-1}{n(\frac{1-s}{s}+1)^2s} = \frac{s(n-1)}{n} < 1$. If n is even, (3.17) is decreasing on $(-\infty, \frac{n-1}{n(c+1)^2s})$ and increasing on the interval $(\frac{n-1}{n(c+1)^2s}, \infty)$ and if n is odd, (3.17) is increasing on the intervals $(-\infty, 0)$ and $(\frac{n-1}{n(c+1)^2s}, \infty)$, and decreasing on $(0, \frac{n-1}{n(c+1)^2s})$. As in the previous case, $h(\frac{n-1}{n(c+1)^2s}) \leq 0$ otherwise h would not have a positive root. Hence, h looks identical to the characteristic equation produced in the previous case (see Figure 3.1) with the exception that the critical point $\frac{s(n-1)}{n}$ is replaced by $\frac{n-1}{n(c+1)^2s}$. Using these facts and the Hartman-Grobman Theorem, if $h(1) \leq 0$ the system has an unstable critical point. If $h(1) > 0$ the equilibrium is stable. Here

$$h(1) = \frac{cs + s - 1}{(1+c)s}. \quad (3.19)$$

Hence $h(1)$ is positive exactly when the carrying capacity is positive. Thus, when $c > \frac{1-s}{s}$ the population has a stable carrying capacity, otherwise, the population goes extinct. The arguments presented in this section prove the following theorem.

Theorem 3.2.1 *For a population modeled by a system of difference equations of the form (3.14) where $s \in [0, 1]$ and $c \in (0, \infty)$ two types of dynamics can occur:*

1. *If $c \leq \frac{1-s}{s}$ no positive equilibrium point exists and the population will go extinct.*
2. *If $c > \frac{1-s}{s}$ a unique positive equilibrium point exists. This equilibrium is stable.*

The summary picture for this case is nearly the same as the summary picture for the previous case; the only difference is that there is no area where the population grows unbounded (see Figure 3.2). Figure 3.4 is a plot of the total population size where c is fixed at 2 and s is allowed to vary for the three by three case.

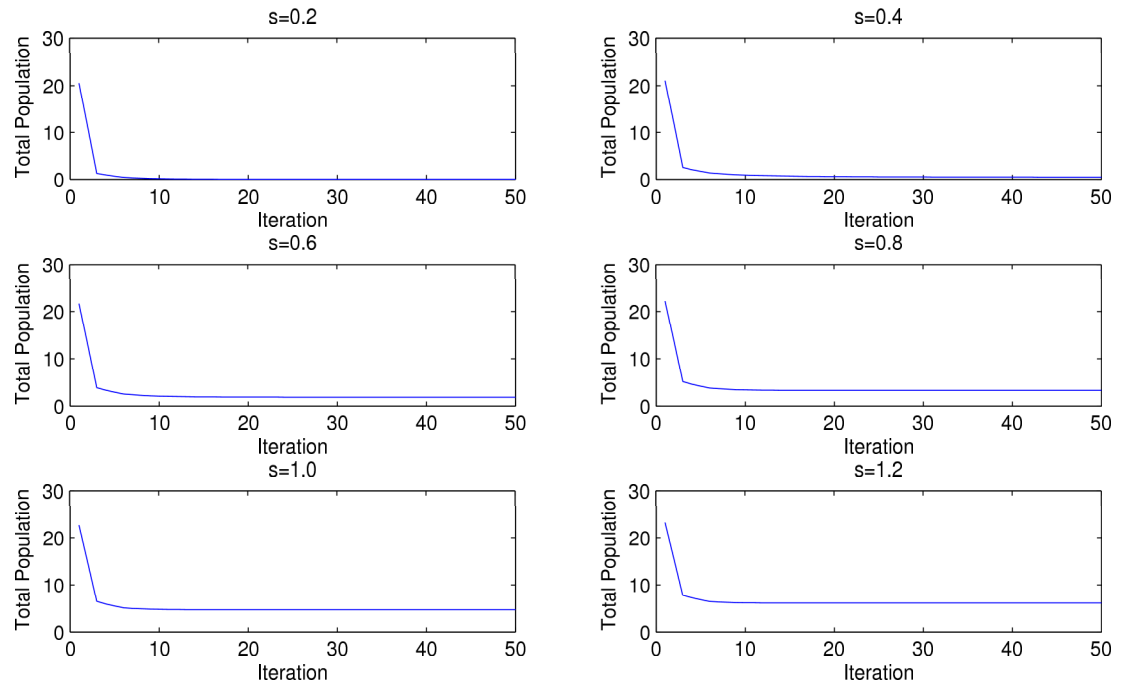


Figure 3.4: Using three stage classes, arbitrary initial population sizes, $c = 2$, and s varying, equation (3.14) was iterated 50 times. The total population size for each of the 50 iterations is plotted for each of the specified values of s .

Chapter 4

Two Identical Density Dependent Terms

4.1 The General 3×3 Case

A natural extension from the last chapter is to ask the question, what happens when there are many adult classes, and density dependence effects the vital rates of all those adult classes. In this chapter, that question is answered, but only in the simplest cases. In Chapter 5, a more general case is considered. The general 3×3 matrix difference equation with two adult classes where density dependence effects only fecundities and not survivorship is

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \end{bmatrix} = \begin{bmatrix} 0 & m_1 p_1 \frac{1}{1+aN_{2,t}} & m_2 s \frac{1}{1+bN_{2,t}} \\ p_0 & 0 & 0 \\ 0 & p_1 & s \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \end{bmatrix}. \quad (4.1)$$

Essentially, the N_1 and N_2 stages are adult stages since they both contribute to the number of young there will be next year, but mortality and fecundity of the two stages differ; if they did not, they could be collapsed into a single stage. The fecundities are m_1 and m_2 , and the survival rates are p_1 and s . Often the N_1 stage represents a sort of subadult class where the organisms are not as mature and produce less offspring than the adult class. Note also that the density dependent effect on fecundities may differ in each class, as represented by the parameters a and b .

4.2 Stability of Carrying Capacity for a Specific Case

In the above general form, the system is hard to analyze, so the much more specific system where $m_1 = m_2 = m$ and $a = b$ will be analyzed first. In matrix form this is

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \end{bmatrix} = \begin{bmatrix} 0 & mp_1 \frac{1}{1+aN_{2,t}} & ms \frac{1}{1+aN_{2,t}} \\ p_0 & 0 & 0 \\ 0 & p_1 & s \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \end{bmatrix}. \quad (4.2)$$

In this system, the last two stages only differ in their survivorship probabilities.

As in the previous chapter, the same process will be followed. The system can be scaled with the same values of α_i and c as usual. This produces the system

$$\begin{cases} M_{0,t+1} = c \frac{1}{1+M_{2,t}} M_{1,t} + cs \frac{1}{1+M_{2,t}} M_{2,t} \\ M_{1,t+1} = M_{0,t} \\ M_{2,t+1} = M_{1,t} + sM_{2,t} \end{cases}. \quad (4.3)$$

The equilibrium occurs when

$$\begin{cases} M_0^* = c + s - 1 \\ M_1^* = c + s - 1 \\ M_2^* = \frac{c+s-1}{1-s} \end{cases}. \quad (4.4)$$

Hence, the population will go extinct whenever $c \leq 1 - s$. When $s = 1$, the only equilibrium is the origin. In the case where $s = 1$ the population will grow unbounded. The Jacobian evaluated at (4.4) is

$$\begin{bmatrix} 0 & 1-s & \frac{(1-c)(s-1)^2}{c} \\ 1 & 0 & 0 \\ 0 & 1 & s \end{bmatrix}. \quad (4.5)$$

In the previous cases, the Jacobian evaluated at equilibrium was always nonnegative as long as the carrying capacity was always positive. This allowed the use of the Perron-Frobenius theorem. Clearly this is not the case with this matrix because for the Jacobian to be positive, $\frac{(1-c)(s-1)^2}{c} \geq 0$, which is when $c < 1$. This implies that there may be two or more eigenvalues of the same modulus. Thus, there is a possibility that cycles can occur. Since the Perron-Frobenius theorem can not be applied the roots of the characteristic equation must be analyzed in a different way. This time around Jury conditions will be used to determine stability. These conditions can be found in Murray [12].

Theorem 4.2.1 Jury Conditions: *The roots of the characteristic equation $p(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$, will have moduli less than 1 if and only if the following conditions are satisfied:*

1. $p(1) > 0$
2. $-p(-1) > 0$
3. $|a_3| < 1$
4. $|b_3| > |b_1|$
5. $|c_3| > |c_2|$

where $b_3 = 1 - a_3^2$, $b_2 = a_1 - a_3a_2$, $b_1 = a_2 - a_3a_1$, $c_3 = b_3^2 - b_1^2$, and $c_2 = b_3b_2 - b_1b_2$.

The characteristic equation of (4.4) is

$$h(\lambda) = -\lambda^3 + s\lambda^2 + (1-s)\lambda - \frac{(1-s)(c+s-1)}{c}. \quad (4.6)$$

Since the Jury conditions are written in terms of an equation with a positive leading coefficient of 1, and the roots of $h(\lambda)$ and $-h(\lambda)$ are the same, finding the roots of (4.6) is equivalent to finding the roots of

$$p(\lambda) = \lambda^3 + (-s)\lambda^2 + (s-1)\lambda + \frac{(1-s)(c+s-1)}{c}. \quad (4.7)$$

In the regions of the s-c plane where p satisfies all 5 Jury conditions, the population will tend to a stable carrying capacity. In the sections where the Jury conditions are not met, more analysis is needed to determine the dynamics of the system. All that can be said is that the carrying capacity is not stable in these regions.

Each condition will be checked individually.

1. In this case, $p(1) = \frac{(1-s)(c+s-1)}{c}$, thus, the first condition is satisfied whenever the population is not tending toward extinction. This first condition will always provide the condition necessary to insure that the population is growing and not growing unbounded. When $\lambda = 1$ a saddle-node bifurcation occurs [11].
2. Here $-1p(-1) = 2s - \frac{(1-s)(c+s-1)}{c}$. In order for $-1p(-1) > 0$, $c < \frac{(s-1)^2}{1-3s}$. This condition provides a little more information than knowing where the system switches from unstable to stable. In addition to this information, this condition provides a bifurcation curve $p(-1) = 0$. This is where a period-doubling bifurcation (also known as a flip bifurcation) occurs [11], [4]. Here a one-cycle will become a two-cycle.
3. Note that $|a_3| = 1$ when $c = \frac{(s-1)^2}{-s}$ and $c = \frac{(1-s)^2}{2-s}$. The population is unstable when the value of the s-c pair lies between the two curves. The first curve lies in the negative half of the plane. Clearly, $\frac{(1-s)^2}{2-s} \leq (1-s)^2 < 1-s$, so condition (1) supersedes this condition.

4. Four curves that break the s - c plane into seven regions determine when condition 4 is met. These 4 curves are:

$$(a) \frac{1}{2}(1-s)^2(s-2-\sqrt{8-4s+s^2})$$

$$(b) \frac{1}{2}(1-s)^2(s-2+\sqrt{8-4s+s^2})$$

$$(c) \frac{(1-s)^2(2-3s-\sqrt{s}\sqrt{4+s})}{2(1-4s+2s^2)}$$

$$(d) \frac{(1-s)^2(2-3s+\sqrt{s}\sqrt{4+s})}{2(1-4s+2s^2)}.$$

Curve (a) is negative on the interval $(0,1)$ so this condition can be ignored. Curve (d) has a vertical asymptote at $1-\frac{\sqrt{2}}{2}$ and is negative whenever $s > 1-\frac{\sqrt{2}}{2}$, so this part of the curve can be ignored. This leaves four regions to consider. Note that curve (b), $\frac{1}{2}((1-s)^2(s-2+\sqrt{8-4s+s^2})) < \frac{1}{2}((1-s)^2(s-2+3)) = \frac{1}{2}(1-s)(1-s)(s+1) = \frac{1}{2}(1-s)(1-s^2) < \frac{1}{2}(1-s)(1-s^2) < 1-s$ and curve (c), $\frac{(1-s)^2(2-3s-\sqrt{s}\sqrt{4+s})}{2(1-4s+2s^2)} < 1-s$. Hence, points below these two curves do not satisfy Jury condition (1). Above curve (c) the condition is met. Note that curve (d) always lies within the curve $\frac{2s-s^2-1}{3s-1}$. Hence, any point inside this region does not satisfy condition (2). Any point that is between curve (c) and curve (d) satisfies condition (4). Figure 4.1 shows the curves produced by condition (4), $c = 1-s$, and $c = \frac{(s-1)^2}{1-3s}$. Note that the first two conditions supercede this one since all the new curves lie within the curves produced by the first two conditions.

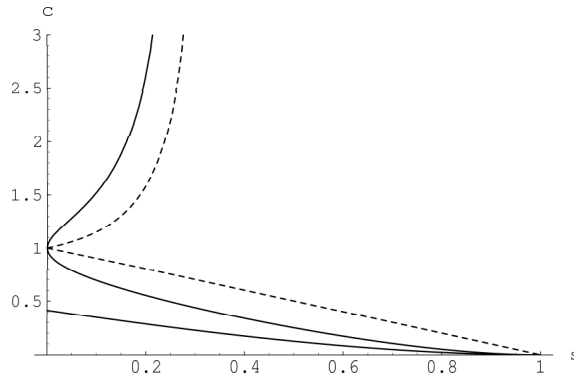


Figure 4.1: The two dashed curves are the curves $c = 1-s$ and $c = \frac{(s-1)^2}{1-3s}$. The other curves are those produced by condition (4) lying in Quadrant I. Since the solid curves fall between the dashed curves and the axes, this shows condition (4) is not needed.

5. There are six curves that determine where condition 5 is satisfied. These are:

- (a) $1 - s$
- (b) $\frac{1}{2}((1 - s)^2(s - 2 - \sqrt{8 - 4s + s^2}))$
- (c) $\frac{1}{2}((1 - s)^2(s - 2 + \sqrt{8 - 4s + s^2}))$
- (d) $\frac{2s - s^2 - 1}{3s - 1}$
- (e) $\frac{2s - s^2 - 1}{s}$
- (f) $\frac{(1 - s)^2}{2 - s}$.

All of these curves are from previous conditions.

The following theorem summarizes the results:

Theorem 4.2.2 *For a population modeled by a system of difference equations of the form (4.3) where $s \in [0, 1]$ and $c \in (0, \infty)$ four types of dynamics can occur:*

1. *If $c \leq 1 - s$ no positive equilibrium point exists and the population will go extinct.*
2. *If $1 - s < c < \frac{2s - s^2 - 1}{3s - 1}$ a unique positive equilibrium point exists. This equilibrium is stable.*
3. *If $c \geq \frac{2s - s^2 - 1}{3s - 1}$ a unique positive equilibrium point exists. This equilibrium is unstable.*
4. *If $s = 1$ the population grows unbounded.*

This theorem is presented visually in Figure 4.2. It is uncertain what kind of dynamics take place in the unstable region.

4.3 Stability of the Two-Cycle in the Specific Case

Based on many computer runs, it would seem that a stable two-cycle, where the population alternates between two different values, occurs everywhere in the unstable region; a proof of this has been elusive. The coordinates of the two-cycle can be found easily, but in order to show that this two-cycle is stable, Jury conditions must be applied to a twice iterated Jacobian. This process is too algebraically cumbersome to carry out.

In order for a stable two-cycle to occur, the population must contain the same number of individuals after every two time steps. To find the two values that the

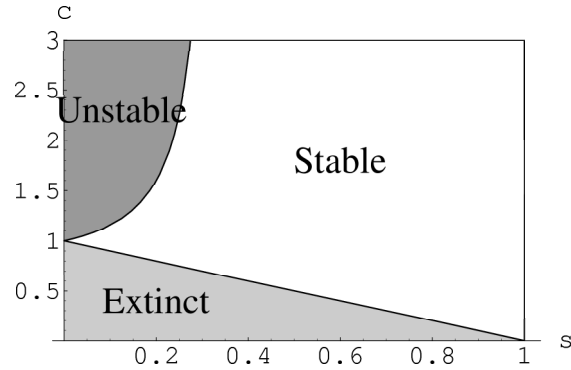


Figure 4.2: The regions in the s - c plane where the carrying capacity is stable, unstable, and where the population goes extinct for the system (4.3). The population grows unbounded when $s = 1$. A vertical asymptote representing the boundary between the stable and unstable regions occurs at $s = \frac{1}{3}$.

population alternates between in the two-cycle, the equations for time $t + 2$ in terms of time t are needed. These are

$$\begin{cases} M_{0,t+2} = cM_{1,t+1} \frac{1}{1+M_{2,t+1}} + csM_{2,t+1} \frac{1}{1+M_{2,t+1}} & = \frac{c(M_{0,t} + s(M_{1,t} + sM_{2,t}))}{1+M_{1,t} + sM_{2,t}} \\ M_{1,t+2} = M_{0,t+1} & = \frac{c(M_{1,t} + sM_{2,t})}{1+M_{2,t}} \\ M_{2,t+2} = M_{1,t+2} + sM_{2,t+2} & = M_{0,t} + s(M_{1,t} + sM_{2,t}) \end{cases} \quad (4.8)$$

To find the coordinates of the two-cycle, the time subscripts are dropped leaving the system

$$\begin{cases} M_0 = \frac{c(M_0 + s(M_1 + sM_2))}{1+M_1 + sM_2} \\ M_1 = \frac{c(M_1 + sM_2)}{1+M_2} \\ M_2 = M_0 + s(M_1 + sM_2) \end{cases} \quad (4.9)$$

The solution to this system of equations results in the coordinates of all two cycles. Since the equations are long, they will not be reproduced here. However, there are some key aspects of this two-cycle to make note of. First of all, there are four separate solutions to this system. One is the trivial solution and another is the carrying capacity; every one-cycle is also two-cycle where the population alternates between two identical values. The other two solutions make up the true two-cycle. The coordinates of the true two-cycle contain the radical $\sqrt{(1+s)(1-c+s)(1-c-2s+3cs+s^2)}$. The two-cycle can only exist where the radicand is nonnegative. This occurs exactly when $c \geq \frac{2s-s^2-1}{3s-1}$, which we already knew from Jury condition (2).

Recall that the first two Jury conditions are usually simple to check, and insight

into the dynamics of the system may be gained by checking them. Of particular interest is condition (2). This will produce a flip bifurcation curve, in this case that is where the two-cycle doubles to become a four-cycle. Here, $p(-1) = 0$ when $c = \frac{2-s^2 \pm \sqrt{1-2s+s^2+4s^3-2s^5-s^6}}{3+2s+s^2} < \frac{2s-s^2-1}{3s-1}$. Thus, no four-cycles occur, which also rules out the possibility of any 2^n -cycles where $n > 1$.

This test does not give any information on any size cycle not of the form 2^n . It is still possible that dynamics such as a three-cycle or chaos can occur. Hence, we must rely on computer simulations. To check whether this two-cycle persisted throughout the region $c \geq \frac{2s-s^2-1}{3s-1}$ various values of c and s were chosen. For each pair of points, equation (4.3) was iterated 10,000 times using initial population sizes $N_{0,0} = N_{1,0} = N_{2,0} = 10$. The total population size at each time step, $N_t = N_{0,t} + N_{1,t} + N_{2,t}$, was calculated and stored after each iteration. The last 50 total population sizes were graphed and visual inspection was used to determine whether a two-cycle was occurring. Although for many pairs the convergence to a two-cycle was slow (the graphs tended to display more complex dynamics than a two-cycle for shorter runs), there was no evidence to suggest that anything more complex than a two-cycle existed. Figure 4.3 is a sample of the graphs produced from the computer runs. In this plot, the first 100 total population sizes are graphed for the values $c = 3$ and $s = 0.01$.

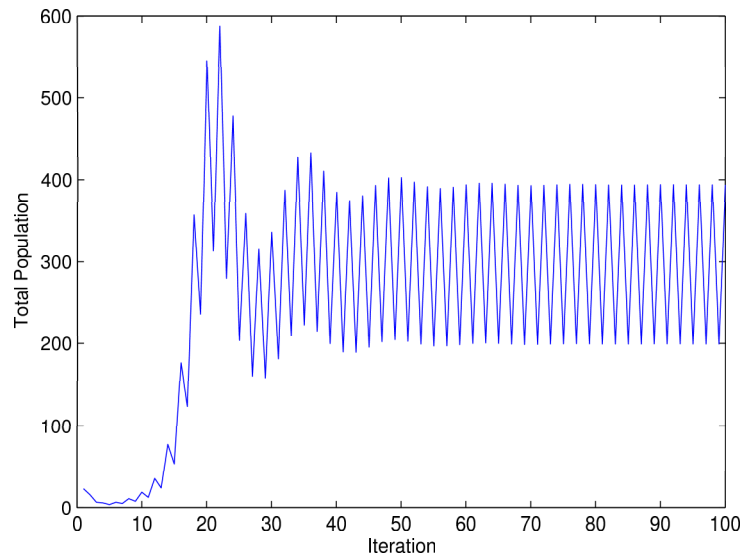


Figure 4.3: A plot of the total population for the first 100 iterations of equation (4.3) where $c = 3$ and $s = 0.01$. The population first experiences a period of growth before settling into a two-cycle. Other choices of c and s also produced total population sizes that converged to a two-cycle.

4.4 The Case with Different Fecundities

In this section, the 3×3 matrix difference equation will be generalized to allow for varying fecundities between the subadult and adult classes which is more likely to be found in nature. Instead of the parameter m , parameters m_1 and m_2 will be used to represent the fecundities of the classes N_1 and N_2 respectively. When rescaling, the parameter c is replaced with c_1 and c_2 in response to this change, yielding the system

$$\begin{cases} M_{0,t+1} &= c_1 \frac{1}{1+M_{2,t}} M_{1,t} + c_2 s \frac{1}{1+M_{2,t}} M_{2,t} \\ M_{1,t+1} &= M_{0,t} \\ M_{2,t+1} &= M_{1,t} + s M_{2,t} \end{cases} . \quad (4.10)$$

In order to simplify the analysis, c_2 will be written in terms of c_1 . As long as $c_1 \neq 0$, then $c_2 = g c_1$ where g is a nonnegative constant. The case where $c_1 = 0$ was covered in Chapter 3. To make things notationally simpler, since subscripts are no longer necessary c will be used instead of c_1 .

The carrying capacity of (4.10) is

$$\begin{cases} M_0^* &= c + s - 1 - cs + cgs \\ M_1^* &= c + s - 1 - cs + cgs \\ M_2^* &= \frac{c+s-1-cs+cgs}{1-s} \end{cases} . \quad (4.11)$$

The carrying capacity is only positive when $c > \frac{1-s}{1-s+gs}$. Figure 4.4 shows the extinction curves for $g = \frac{1}{4}, \frac{1}{2}, 1, 2, 4$. The case where $g = 1$ is the special case analyzed in the last chapter. Note that as g becomes smaller, that is as m_1 becomes larger compared to m_2 , the likelihood of extinction becomes greater. In fact, as $g \rightarrow 0$ the extinction curve approaches $c = 1$. As $g \rightarrow \infty$ the extinction curve approaches $c = 0$. The situation where g is small represents a population where subadults produce more offspring per capita than adults. A discontinuity occurs in the extinction curves in the $c_1 = 0$ case. Recall from Chapter 3, that the carrying capacity will be positive as long as $c > \frac{1-s}{s}$. One might expect this curve to be the same as in the $g = \infty$ case, but the two are different.

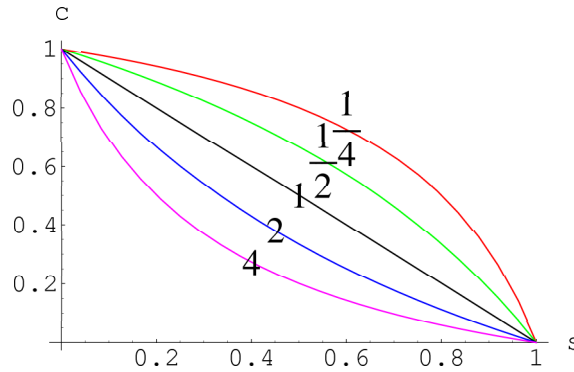


Figure 4.4: The extinction curves for $g = \frac{1}{4}, \frac{1}{2}, 1, 2, 4$. As g increases, the likelihood of extinction decreases.

The next step is to find the Jacobian evaluated at equilibrium. This is

$$\begin{bmatrix} 0 & \frac{1-s}{1+(g-1)s} & \frac{(s-1)^2(1-c)}{c(1+(g-1)s)^2} \\ 1 & 0 & 0 \\ 0 & 1 & s \end{bmatrix}, \quad (4.12)$$

which has characteristic equation

$$h(\lambda) = -\lambda^3 + s\lambda^2 + \frac{1-s}{1+(g-1)s}\lambda - \frac{(1-s)(c+s-1)}{c(1+(-1+g)s)}. \quad (4.13)$$

From the last sections, it is clear that the Jacobian will not always be nonnegative. Thus, the Jury conditions must be applied to (4.13). Written with a positive leading coefficient (4.13) becomes

$$p(\lambda) = \lambda^3 - s\lambda^2 - \frac{1-s}{1+(g-1)s}\lambda + \frac{(1-s)(c+s-1)}{c(1+(-1+g)s)}. \quad (4.14)$$

1. As already stated, the Jury condition $p(1) > 0$ generates the extinction curve. This condition is discussed above.
2. The flip bifurcation occurs where $p(-1) = 0$. This is the curve $c = \frac{(s-1)^2}{1-(2+g)s-(g-1)s^2}$. Figure 4.5 shows this curve for $g = \frac{1}{4}, \frac{1}{2}, 1, 2, 4$. As $g \rightarrow 0$, the curve approaches $c = 1$. As $g \rightarrow \infty$ the vertical asymptote approaches $s = 0$. The population is unstable at carrying capacity when the value of c is to the left of the curve. The phenomenon occurring with the flip bifurcation curves mirror what occurred with the extinction curves; when the subadults produce many more young than the adults, the population tends to destabilize. When the adults produce many more offspring than the subadults both extinction and an unstable carrying capacity become rare.

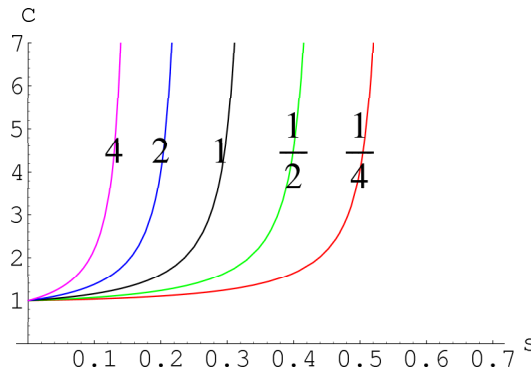


Figure 4.5: The flip bifurcation curves for $g = \frac{1}{4}, \frac{1}{2}, 1, 2, 4$. As g increases the population tends toward increased stability.

3. The condition $|a_3| = 1$ is satisfied on the curves $\frac{(s-1)^2}{-gs}$ and $\frac{(s-1)^2}{2-2s+gs}$. The first curve is always negative, and to satisfy the condition, $c > \frac{(s-1)^2}{-gs}$, so this condition can be ignored. $\frac{1-s}{1-s+gs} \geq \frac{(1-s)^2}{1-s+gs} = \frac{(s-1)^2}{1-s+gs} \geq \frac{(s-1)^2}{2(1-s)+gs}$. Hence the other new curve falls below the extinction curve. Condition (3) is satisfied as long as the population does not go extinct.

4. The condition $|b_3| = |b_2|$ is satisfied on four curves, and like in the previous chapter, lie within curves already dealt with by previous conditions. Figure 4.6 shows these four curves for $g = \frac{1}{4}, \frac{1}{2}, 1, 2, 4$.

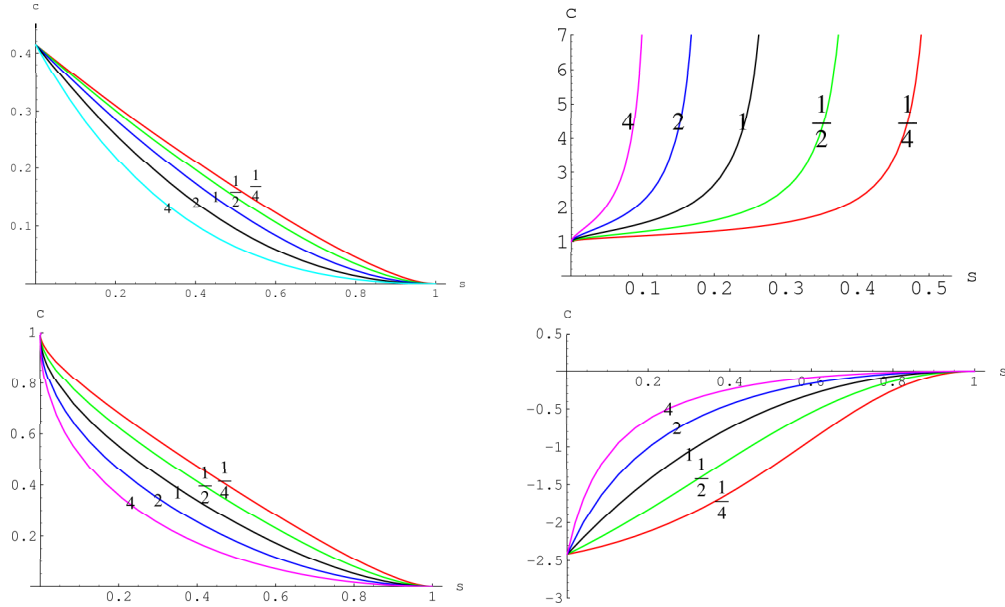


Figure 4.6: Curves produced by condition (4) for $g = \frac{1}{4}, \frac{1}{2}, 1, 2, 4$. This figure shows that condition (4) is not needed since the curves produced by condition (4) lie within the extinction region or the region produced by the flip bifurcation curves.

5. This condition produces six curves, all of which appeared in previous conditions.

The case with two different fecundities varies little from the previous case. The following theorem summarizes this case.

Theorem 4.4.1 *For a population modeled by a system of difference equations of the form (4.10) where $s \in [0, 1]$ and $c \in (0, \infty)$ three types of dynamics can occur:*

1. *If $c \leq \frac{1-s}{1-s+gs}$ no positive equilibrium point exists and the population will go extinct.*
2. *If $s < 1$ and $c > \frac{(1-s)^2}{1-(2+g)s-(g-1)s^2}$ a unique positive equilibrium point exists. This equilibrium is stable.*
3. *Elsewhere the carrying capacity is unstable.*

Again, this analysis does not give any information as to what the dynamics may be in the unstable region, but based on computer runs and on knowledge gained from the last case, there appears to be only two-cycles in the unstable region. The case where $c_1 = 0$ is different than the $g = \infty$ case only in the curve that determines when the carrying capacity is 0. Otherwise, they are identical.

4.5 Extensions to Other Dimensions

So far, only variations on the 3×3 matrix difference equation have been investigated. What happens when the dimensions of the system are increased or decreased but the structure is retained? To answer this question, a computer program was written that detects extinction, stable carrying capacity, and anything from a two-cycle to a four-cycle. The program is included at the end of this chapter. Only the last 50 iterations out of 1000 were used to determine the dynamics. This program was applied to everything from a 2×2 to a 5×5 matrix with density dependence in fecundities only. The results are summarized by the figures below.

The dynamics of every point checked in the 2×2 case has been classified. The 3×3 figure produced here is identical to the summary picture discovered previously. However, the dynamics along the line $s = 0$ were not determined by the program. In the figures for the 4×4 and 5×5 cases, there is still lots of information missing. Note that regions where the dynamics were not determined occur close to the bifurcation curve. Based on the figure for the 5×5 case, it appears as if two period doubling bifurcations take place: one where a one-cycle doubles to become a two-cycle, and one where a two-cycle doubles to a four-cycle. More complex dynamics occur in the regions where the two-cycle is splitting to become a four-cycle.

The bifurcation in the 4×4 case is of an entirely different type. In order to understand what is occurring in this case plots of N_{t+1} versus N_t were created for the last 200 out of 1000 iterations for selected points in region where the dynamics were not determined. If an n -cycle was present, then exactly n -distinct points would be present. If the last 200 iterations were converging to an n -cycle, but hadn't fully converged, n distinct clumps of points would be plotted. The pictures produced do not show any of these patterns. Instead a closed curve is traced by the points. This is indicative that a Hopf bifurcation has occurred, which is when a pair of complex conjugate eigenvalues cross the unit circle. As the carrying capacity becomes unstable, an invariant closed curve is introduced. As c increases and s decreases, the behavior settles down to a three-cycle. This is usually referred to as phase-locking. These results are similar to those of Wikan and Mjølhus [11], [15].

Note that in all the cases investigated, the largest cycle was of size $n - 1$. It is likely that this pattern holds for larger matrix difference equations.

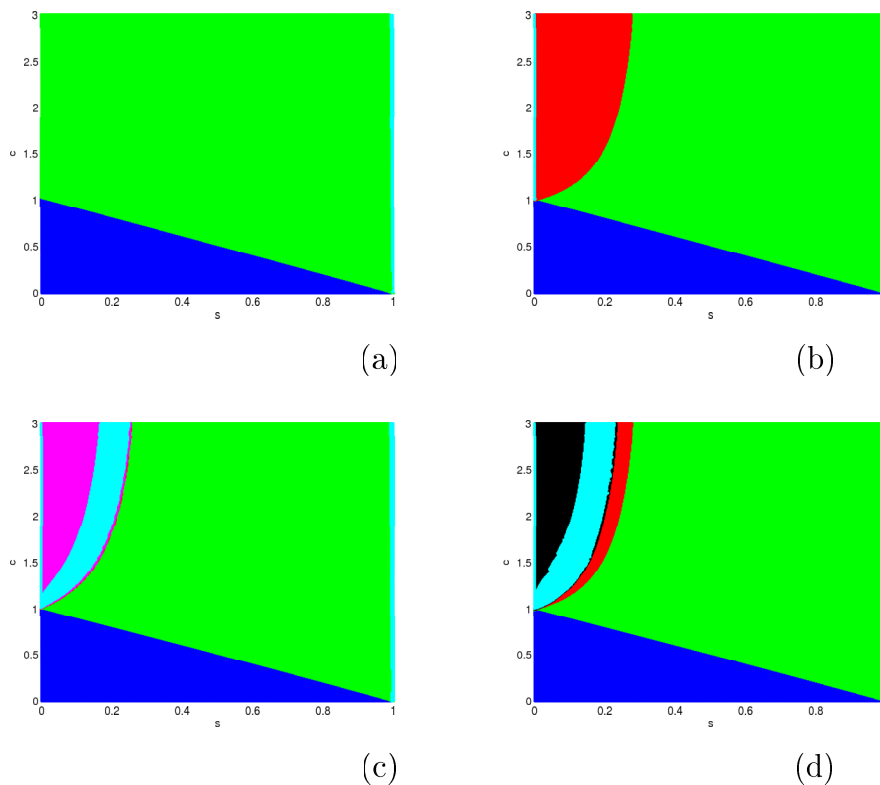


Figure 4.7: Figures generated by the computer program. Plot (a) is the 2×2 case, (b) is the 3×3 , (c) is the 4×4 , and (d) is the 5×5 . Here dark blue represents extinction, green represents a stable carrying capacity, two-cycles occur in red regions, three-cycles in magenta regions, four-cycles in black regions, and the dynamics in cyan regions are undetermined. Notice that the largest cycle seen is of size $n - 1$.

Cycle Finding Program

The program below was written in MATLAB. It was used to determine the type of dynamics occurring in the 5×5 case. The code can be easily altered so that it may be applied to any size matrix difference equation. The type of density dependence incorporated into the model can also be easily changed.

```
%-----
%Cycle Finding Code for the Five by Five Case
%Objective: Calculates and stores the last 50 out of 1000
%population totals for equation 4.3 generalized to the five
%by five case over the s-c plane. From these last 50 totals,
%the program determines the type of dynamics occurring.
```

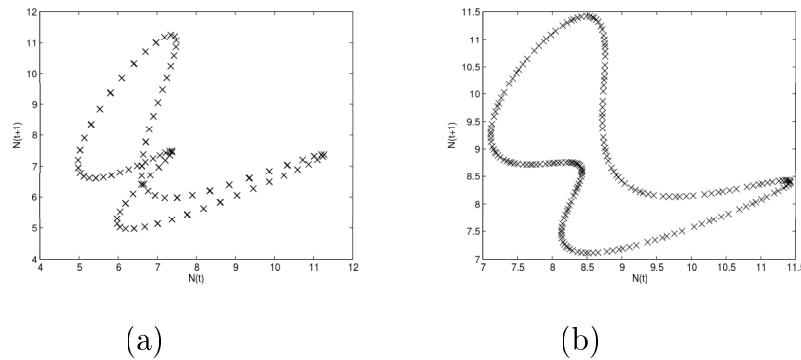


Figure 4.8: Plots of N_{t+1} vs. N_t for the four by four system with (a) $c = 2$, $s = 0.15$ and (b) $c = 2.5$, $s = 0.2$.

```

%-----
function [ext, onecy, twocy, threecy, fourcy, none]=cycle;
tol=.05;
%Initializes matrices that will hold the (s,c) coordinates for
%extinction,one-cycles, two-cycles etc. The coordinate (5,5) was
%chosen since this is outside of the range of possible values for
%s and c, and thus, will not be plotted.
ext=[5;5];
onecy=[5;5];
twocy=[5;5];
threecy=[5;5];
fourcy=[5;5];
none=[5;5];
%Range of possible c values to be checked.
for c=[0:.0075: 3];
    %Range of possible s values to be checked.
    for s=[0:.0025:1];
        %Initial stage sizes l, m, n, o, and p are set at 10.
        l=10;
        m=10;
        n=10;
        o=10;
        p=10;
        %For a given value of (s,c), iterates equation 4.3

```

```

%generalized to the five by five case for 1000 time
%steps.
    for i=[1:1000]
        %Calculating new stage sizes d, e, f, g, and h.
        d=c*(1/(1+p))*o+c*s*(1/(1+p))*p;
        e=l;
        f=m;
        g=n;
        h=o+s*p;
        %Updating stage sizes.
        l=d;
        m=e;
        n=f;
        o=g;
        p=h;
        %Calculating total population size v.
        v(i)=l+m+n+o+p;
    end
%u is a vector containing that last 50 total
%population sizes out of 1000 time steps.
    u=v(951:1000);

%The different distj variables below measure the distance
%the first j-elements of the vector u are from all other
%sets of j-consecutive elements of u. If a j-cycle exists,
%then every element in the vector distj should be small.
%dist0 measures the distance each element of u is from 0.
%If every element in dist0 is small, this indicates that
%the population has gone extinct.
    dist0=abs(u);
    dist1=abs(u-u(1));
    for i=[1:49]
        dist2(i)=abs(norm(u(i:i+1))-norm(u(1:2)));
    end
    for i=[1:48]
        dist3(i)=abs(norm(u(i:i+2))-norm(u(1:3)));
    end
    for i=[1:47]
        dist4(i)=abs(norm(u(i:i+3))-norm(u(1:4)));
    end
end

```



```

    %smlj is the largest element in each distj vector.
    sml0=max(dist0);
    sml1=max(dist1);
    sml2=max(dist2);
    sml3=max(dist3);
    sml4=max(dist4);
%If the largest element in each of the distj is smaller
%than the tolerance than a j-cycle has occurred. The code
%below runs this check, then stores the s-c coordinates
%in the appropriate matrix. The code checks up to a
%four-cycle. If none of these are found, the
%coordinates are stored in the matrix none.
    if (sml0<tol)
        ext=[ext,[c;s]];
    elseif (sml1<tol)
        onecy=[onecy, [c;s]];
    elseif (sml2<tol)
        twocy=[twocy, [c;s]];
    elseif (sml3<tol)
        threecy=[threecy, [c;s]];
    elseif(sml4<tol)
        fourcy=[fourcy, [c;s]];
    else
        none=[none, [c;s]];
    end
end
end
%The coordinates for each type of cycle are plotted using
%different colors using the plot command in a seperate function.

```

Chapter 5

Distinct Density Dependent Terms

5.1 The Case With Different Nonlinear functions

In nature, just as it is likely that the fecundities of the subadult and adult classes vary, it is equally likely that the density dependent effect will be different. In this section, the problem where the fecundities are held the same for both classes and the density dependent effect is varied for the 3×3 case is investigated.

The system in question this time is

$$\begin{bmatrix} N_{0,t+1} \\ N_{1,t+1} \\ N_{2,t+1} \end{bmatrix} = \begin{bmatrix} 0 & mp_1 \frac{1}{1+aN_{2,t}} & ms \frac{1}{1+bN_{2,t}} \\ p_0 & 0 & 0 \\ 0 & p_1 & s \end{bmatrix} \begin{bmatrix} N_{0,t} \\ N_{1,t} \\ N_{2,t} \end{bmatrix}. \quad (5.1)$$

This system can be rescaled to

$$\begin{cases} M_{0,t+1} &= c \frac{1}{1+M_{2,t}} M_{1,t} + cs \frac{1}{1+dM_{2,t}} M_{2,t} \\ M_{1,t+1} &= M_{0,t} \\ M_{2,t+1} &= M_{1,t} + sM_{2,t} \end{cases}, \quad (5.2)$$

where $d = \frac{b}{a}$. This rescaling does not work in the case where $a = 0$. Note that in nature, it is expected that $a > b$ so in practical applications, the $a = 0$ case is not likely to arise. Dropping the time subscripts and solving (5.2) yields three equilibrium points. One, is of course, the origin. The other two are

$$\begin{cases} M_0^* &= \frac{r - \sqrt{-4d(-1+s)(-1+c+s)+r^2}}{2d} \\ M_1^* &= \frac{r - \sqrt{-4d(-1+s)(-1+c+s)+r^2}}{2d} \\ M_2^* &= \frac{r - \sqrt{-4d(-1+s)(-1+c+s)+r^2}}{2d(1-s)} \end{cases}, \quad (5.3)$$

$$\begin{cases} M_0^* &= \frac{r + \sqrt{-4d(-1+s)(-1+c+s) + r^2}}{2d} \\ M_1^* &= \frac{r + \sqrt{-4d(-1+s)(-1+c+s) + r^2}}{2d} \\ M_2^* &= \frac{r + \sqrt{-4d(-1+s)(-1+c+s) + r^2}}{2d(1-s)} \end{cases} \quad (5.4)$$

where $r = -1 + s + cs + d(-1 + c + s - cs)$. Note that these equilibrium points are not valid for $d = 0$, so this case must be handled separately. The equilibrium points are also not valid for $s = 1$. It can be checked that the term inside the radical is always positive. Thus, an equilibrium point always exists. Note that $-4d(-1 + s)(-1 + c + s)$ will be positive when $c > 1 - s$. When this occurs (5.3) is negative and (5.4) is positive, so only one positive equilibrium point exists.

What happens when $c < 1 - s$? If this condition is held $-4d(-1 + s)(-1 + c + s) < 0$. When this happens, the sign of r must be known to determine when the equilibrium is positive or negative. When $c > \frac{-1-d+s+ds}{-d-s+ds}$, $r > 0$. The curve $\frac{-1-d+s+ds}{-d-s+ds} = 1 - \frac{1}{d(s-1)-s} > 1 - s$ since $d(s-1) - s < 0$. Thus, if $c < 1 - s$ then $c < \frac{-1-d+s+ds}{-d-s+ds}$, and both equilibrium points are negative. It is impossible for both sets of equilibrium points to be positive. Furthermore, the population goes extinct whenever $c \leq 1 - s$.

Besides this one small fact, using the method of finding the Jacobian and applying Jury conditions in this general case has proven fruitless, as the algebra gets too complicated to handle. Instead, the approach is to consider a number of special cases in order to gain insight into the general case. In the analysis, b is essentially fixed and nonzero while a is allowed to vary, thus allowing d to vary. The specific cases investigated were $a = 0$, $a = \infty$, and $a = b$.

5.1.1 The $a = 0$ Case

When $a = 0$, the resulting matrix is

$$\begin{bmatrix} 0 & c & cs \frac{1}{1+M_{2,t}} \\ 1 & 0 & 0 \\ 0 & 1 & s \end{bmatrix}. \quad (5.5)$$

This case is nearly identical to the case in Section 3.1, so the analysis will be similar. The non-trivial equilibrium point occurs when

$$\begin{cases} M_0^* &= \frac{1-c-s}{c-1} \\ M_1^* &= \frac{1-c-s}{c-1} \\ M_2^* &= \frac{c+s-1}{(c-1)(s-1)} \end{cases}. \quad (5.6)$$

Note that the equilibrium is not valid for $c = 1$ or $s = 1$, but if $s = 1$ then the population tends to infinity and when $c = 1$ the origin is the only equilibrium point.

When $c < 1 - s$, then $c < 1$ and the equilibrium is negative. If $c > 1$, then $c > 1 - s$, and the origin is the only nonnegative equilibrium point. When $1 - s < c < 1$, then the nontrivial equilibrium point exists. However, just because the equilibrium is negative, does not mean the population goes extinct. This is the first time in this paper that there has been two curves to determine when the equilibrium is positive. Recall from the introduction that in order for growth to occur the associated linear matrix must have a Perron root greater than one.

The linear matrix in this case is

$$\begin{bmatrix} 0 & c & cs \\ 1 & 0 & 0 \\ 0 & 1 & s \end{bmatrix}, \quad (5.7)$$

which has characteristic equation

$$h(\lambda) = -\lambda(\lambda^2 - s\lambda - c). \quad (5.8)$$

The Perron root of (5.8) is $\frac{1}{2}(s + \sqrt{4c + s^2})$, which is greater than one when $c > 1 - s$. When $c > 1$ the population is still growing, but without a positive carrying capacity, which means that it is growing unbounded. This has occurred in all previous cases on the line $s = 1$.

The Jacobian matrix evaluated at equilibrium for this case is

$$\begin{bmatrix} 0 & c & \frac{(c-1)^2(s-1)^2}{cs} \\ 1 & 0 & 0 \\ 0 & 1 & s \end{bmatrix}. \quad (5.9)$$

Clearly, every element in (5.9) is positive, so we can avoid using Jury conditions and instead use (1.0.3). The characteristic equation of (5.9) is

$$h(\lambda) = -\lambda^3 + s\lambda^2 + c\lambda + \frac{c^2(1 - 2s) + (s - 1)^2 - 2c(s - 1)^2}{cs}, \quad (5.10)$$

which has derivative

$$h'(\lambda) = -3\lambda^2 + 2s\lambda + c. \quad (5.11)$$

The roots of (5.11) are $\frac{1}{3}(s \pm \sqrt{3c + s^2})$. One is positive, and one is negative. Here (5.10) is decreasing on the intervals $(-\infty, \frac{1}{3}(s - \sqrt{3c + s^2}))$ and $(\frac{1}{3}(s + \sqrt{3c + s^2}), \infty)$ and increasing on $(\frac{1}{3}(s - \sqrt{3c + s^2}), \frac{1}{3}(s + \sqrt{3c + s^2}))$. If c is restricted to $1 - s < c < 1$, then $\frac{1}{3}(s + \sqrt{3c + s^2}) < 1$. This means that if $h(1) < 0$, the population will be stable at carrying capacity. In this case $h(1) = \frac{(c-1)(s-1)(1-c-s)}{cs}$. Note that $h(1)$ is really the same as the $p(1)$ in the Jury conditions, so this gives the conditions for the population to head towards extinction or infinite size again. In conclusion, the population goes extinct when $c < 1 - s$, reaches a stable carrying capacity when $1 - s < c < 1$, and grows unbounded when $c > 1$. Figure 5.1 shows the summary picture for this case.

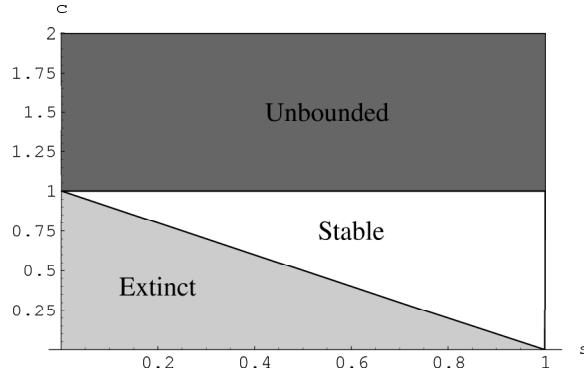


Figure 5.1: The summary picture for the $a = 0$ case. This case is very different than previous examples since the unbounded region occurs whenever $c > 1$ and not just on the line $s = 1$.

5.1.2 The $a = b$ case

The case was covered in section 4.2. If $c \leq 1 - s$ the population goes extinct. If $c \geq \frac{2s-s^2-1}{3s-1}$ there is evidence to suggest a stable two-cycle occurs. Elsewhere the population tends to a stable carrying capacity. See Figure 4.2.

5.1.3 The $a = \infty$ Case

This case was covered in section 3.1. Recall when $a = \infty$, the resulting matrix is

$$\begin{bmatrix} 0 & 0 & cs \frac{1}{1+M_{2,t}} \\ 1 & 0 & 0 \\ 0 & 1 & s \end{bmatrix}. \quad (5.12)$$

This population will go extinct or grow unbounded whenever

$$p(1) = \frac{(1-s)(cs + s - 1)}{cs} \leq 0.$$

Since cs and $1 - s$ are always nonnegative, this can only occur if $c \leq \frac{1-s}{s}$ or $s = 1$. The population grows unbounded when $s = 1$ and goes extinct if $c \leq \frac{1-s}{s}$.

A two-cycle bifurcation will occur whenever

$$p(-1) = 1 + s + \frac{(s-1)^2}{cs} = 0.$$

Clearly $p(-1)$ will always be positive, so a two-cycle will never occur. Recall, that the carrying capacity is always stable. See Figure 3.2.

5.1.4 Summary of the Special Cases

In the above subsections, a scaling with the parameter $d = \frac{b}{a}$ was used. With this rescaling, one would expect the curves that represent extinction, unboundness, and two-cycle bifurcations to change in a continuous manner as d varies.

The extinction curve remains the same when $a = b$ and $a = 0$, but changes instantaneously when $a = \infty$. The unbounded curve remains unchanged when $a = \infty$ and $a = b$, but the unbounded curve for $a = 0$ is very different. The flip bifurcation curve only appears in one of the special cases.

In an effort to determine the dynamics of the population where d is not one of the particular values considered above, the computer program previously employed in Section 4.5 was altered to handle the case with different density dependent terms. The only change that was made was that (5.2) was iterated 1000 times instead of (4.3). The results for six values of $d = \frac{b}{a}$ are displayed in Figure 5.2. Notice the lack of continuity between the $d = 0$ and the $d = .5$ case. The unbounded region changes immediately to the line $s = 1$. As d increases, the two-cycle region becomes larger, as does the region where the population goes extinct. In the $d = \infty$ case, above the line $c = 1$ one would expect to see two-cycles and below this line, one would expect the population to go extinct. This is not consistent with the $a = 0$ case. Another way that $d = \infty$ is if $b = \infty$, which is what is occurring in the figure. A similar argument is true for the $d = 0$ case.

In nature, since a is likely to be larger than b , d will be less than one. When $d < 1$ the population tends towards stability. Hence, in practical applications, exotic dynamics will probably not be found. The numerical analysis indicates that there is very little difference in the population dynamics over the range of possible values of d .

5.2 The $b = 0$ case

An interesting case to look at is when $b = 0$. In this case, there is only one density dependent term and it is in the subadult fecundity rather than the adult fecundity. The results produced are different than the previous cases. When $b = 0$, the resulting matrix is

$$\begin{bmatrix} 0 & c\frac{1}{1+M_{2,t}} & cs \\ 1 & 0 & 0 \\ 0 & 1 & s \end{bmatrix}. \quad (5.13)$$

The non-trivial equilibrium point occurs when

$$\begin{cases} M_0^* &= \frac{(s-1)(c+s-1)}{cs+s-1} \\ M_1^* &= \frac{(s-1)(c+s-1)}{cs+s-1} \\ M_2^* &= \frac{1-c-s}{cs+s-1} \end{cases} . \quad (5.14)$$

If $c < 1-s$, then $c < \frac{1-s}{s}$ and the equilibrium is negative. If $c > \frac{1-s}{s}$, then $c < 1-s$, which also yields a negative equilibrium. However, when $1-s < c < \frac{1-s}{s}$, there is a positive equilibrium. As in the case where $a = 0$, when $c < 1-s$ the population goes extinct, and when $c > \frac{1-s}{s}$ the population grows unbounded. Unfortunately, the Jacobian contains negative terms, so the Jury conditions must be applied to determine stability.

The Jacobian evaluated at equilibrium is

$$\begin{bmatrix} 0 & \frac{s+cs-1}{s-1} & \frac{c-(s-1)^2+c^2(s-2)s-cs^2}{c(s-1)} \\ 1 & 0 & 0 \\ 0 & 1 & s \end{bmatrix}, \quad (5.15)$$

and has characteristic equation

$$h(\lambda) = -\lambda^3 + s\lambda^2 + \frac{cs+s-1}{s-1}\lambda + \frac{-(s-1)^2 - 2c^2s + c(1+2s-2s^2)}{c(s-1)}. \quad (5.16)$$

Looking at the above equation it is obvious that the Jury conditions will be difficult to check. For the most part, a graph of the curves produced by each condition will be given to determine where the conditions hold (as opposed to giving the equation of the curves).

1. The first condition is the same as checking when there is a positive equilibrium point.
2. The flip bifurcation occurs along the two curves $\frac{1-s^2 \pm (s-1)\sqrt{1-10s+s^2}}{6s}$. These two curves together form a closed region of the plane. The two curves are shown in Figure 5.3. This is the first time that this condition has resulted in two separate curves.
3. There are four curves that determine where $|a_3| = 1$. Two of these involve the radical $\sqrt{(s-1)^2(s-2)s}$ which is complex on the interval $(0, 1)$ so it does not play a role here. The remaining two curves are shown in Figure 5.4. Both these curves fall inside of the boundaries created by condition (1), hence this condition does not provide any new information.

4. Condition 4 produces eight new curves where $|b_1| = |b_3|$. As shown in Figure 5.5, all of these curves lie in regions already declared unstable. Two of the curves lie completely in quadrants III and IV and are not shown in Figure 5.5.
5. Condition 5 yields four new curves, which again lie within curves already established. Figure 5.6 shows the curves that do not lie entirely in quadrants III and IV.

The only places where the system does not have a stable carrying capacity is where it diverges to infinity, ($c > \frac{1-s}{s}$), where it goes extinct, ($c < 1 - s$), and where it does not satisfy the second Jury condition. As seen in previous cases, in the region of the s - c plane where the second Jury condition is not satisfied, two-cycles occur (based on many computer runs). Though the problem was more complex, the results are not. Figure 5.7 shows the summary picture for this case.

5.3 Conclusion

When using the Beverton-Holt function to model density dependence, one expects to see simple dynamics. The results of this paper are consistent with this fact. In the 3×3 cases, two-cycles were the most exotic dynamics discovered. In higher dimensions, the dynamics still seemed to retain their simplicity. The most complex dynamics seen were stable cycles of size $n-1$ where n was the dimension of the matrix. There were also transition regions around the bifurcation curves where the dynamics were unpredictable. Unlike the results of papers where a similar model using a Ricker function instead of a Beverton-Holt was studied, chaos was never found.

The matrix difference equations studied in this paper can be easily altered to create a plethora of new problems. One such problem is including density dependence in both the survivorship term and the fecundity terms. This problem is difficult no matter how small the system is due to the fact that a quadratic equation must be solved just to find the carrying capacity. Furthermore, nonnegative terms will be present in the Jacobian evaluated at carrying capacity, so the Jury conditions must be applied. Another option is to base density dependence on total population size rather than just the size of the last stage class. Again this will seriously complexify the algebraic calculations.

Before any new problems can be explored, there are still loose ends in the cases studied in this paper that need to be considered. One problem that still exists is what occurs along the line $s = 0$ in each of the cases. When s , the last column of the matrix representing the system consists entirely of zeros. Will the dynamics of this type of system be the same as dynamics of the same system with the last row and column of the transition matrix removed? Exploring this case will also probably provide insight

as to why the largest cycle is of size $n - 1$. Looking at the dynamics when $s = 0$ may also be helpful in the case with two different density dependent functions.

The piecemeal approach followed in this paper to determine stability of the carrying capacity of a system is very inefficient. Instead, it is preferable to look for another approach in which results may be applied to a large class of matrix difference equations instead of individual cases. These types of techniques do exist in some of the current literature and perhaps can be applied to the types of matrix difference equations studied here.

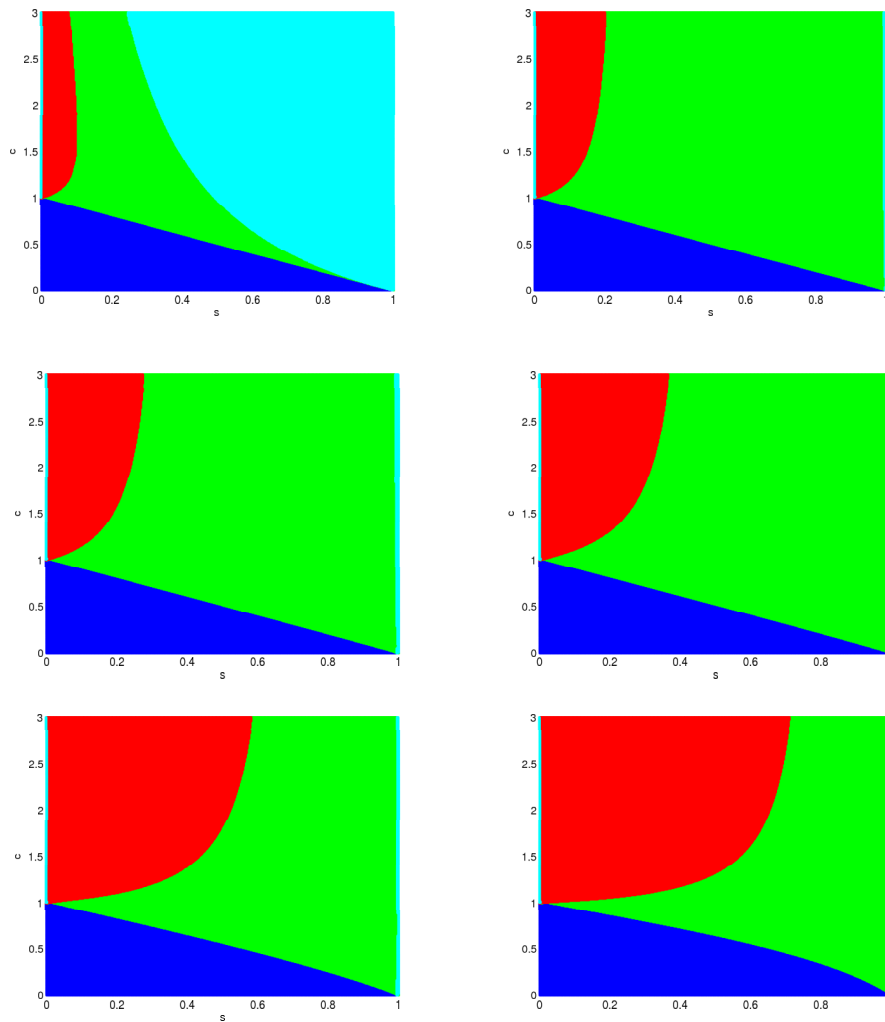


Figure 5.2: The summary pictures for various choices of d . Going from left to right then top to bottom the values are $d = 0, 0.5, 1, 2, 10, 30$. The blue region represents extinction, the cyan unstable, the green stable carrying capacity, and the red two-cycles.

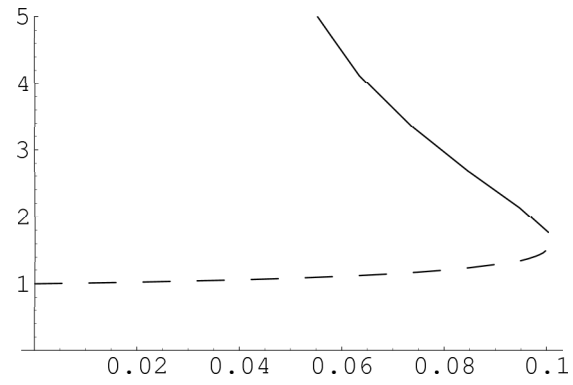


Figure 5.3: The two flip bifurcation curves

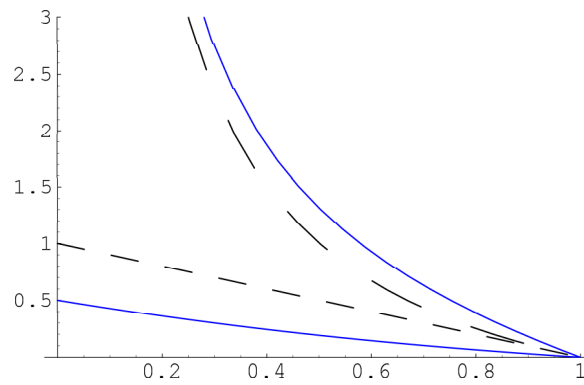


Figure 5.4: The dashed curves are the curves $1 - s$ and $\frac{1-s}{s}$. On the solid curves $|a_3| = 1$. Since the solid curves lie within the dashed curves this shows that condition (3) is not met only when condition (1) is not met. Hence, condition (3) is superfluous.

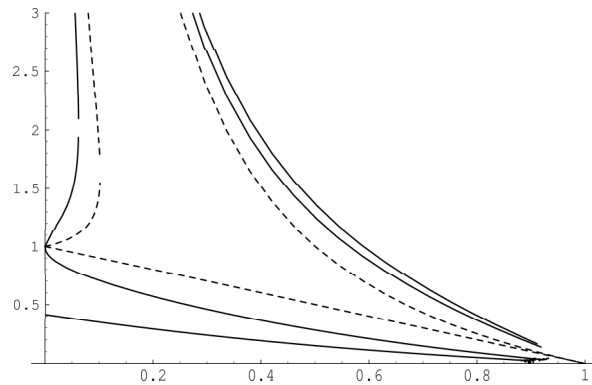


Figure 5.5: The dashed curves are the curves $1 - s$, $\frac{1-s}{s}$, and the two flip bifurcation curves. The other curves are $|b_3| = |b_1|$. Since the solid curves lie within the dashed curves this shows that condition (4) is not met only when condition (1) or condition (2) is not met. This means condition (4) is not needed.

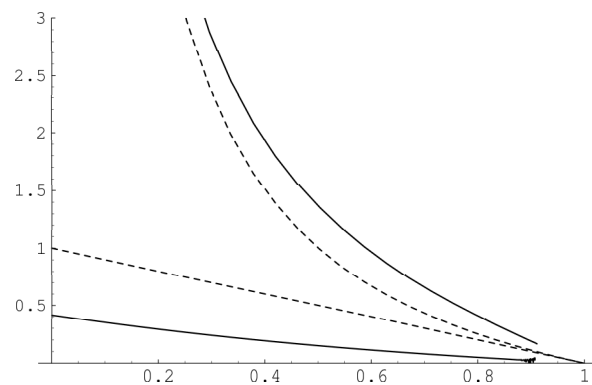


Figure 5.6: The dashed curves are the curves $1 - s$ and $\frac{1-s}{s}$. The other curves are $|c_3| = |c_2|$. Since the solid curves fall within the dashed curves, this shows that condition (5) is not met only when condition (1) is not met. Just like conditions (3) and (4), condition (5) is also unnecessary.

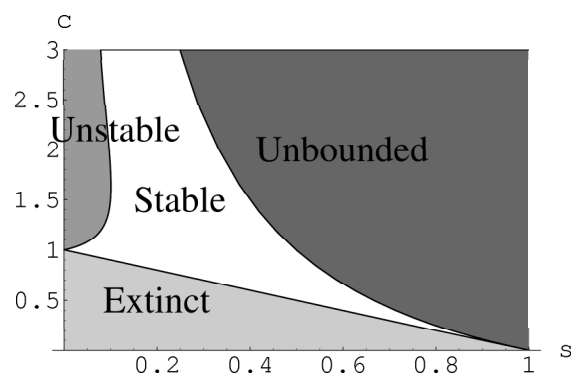


Figure 5.7: The summary picture for the $b = 0$ case.

Bibliography

- [1] M.O. Bergh and W.M. Getz, *Stability of Discrete Age-Structured and Aggregated Delay-Difference Population Models*, Journal of Mathematical Biology **26** (1988), pp. 551-581.
- [2] D. Cooke and J. A. Leon, *Stability of Population Growth Determined by 2×2 Leslie Matrix with Density-Dependent Elements*, Biometrics **32** (1976), pp. 435-442.
- [3] J. M. Cushing, *A Strong Ergodic Theorem for Some Nonlinear Matrix Models for the Dynamics of Structured Populations*, Natural Resource Modeling **3**, (1989), pp. 331-357.
- [4] J. M. Cushing, *An Introduction to Structured Population Dynamics*, Society for Industrial and Applied Mathematics, Philadelphia, 1998.
- [5] R. A. Desharnais and L. Liu, *Stable Demographic Limit Cycles in Laboratory Populations of Tribolium Castaneum*, Journal of Animal Ecology **56** (1987), pp.885-906.
- [6] S. S. Efremova and Y. A. Pykh, *Equilibrium, Stability, and Chaotic Behavior in Leslie Matrix Models With Different Density Dependent Birth and Survival Rates*, Mathematics and Computers in Simulation **52** (2000), pp. 87-112.
- [7] M.E. Fisher and B.S. Goh, *Stability Results for Delayed-Recruitment Models in Population Dynamics*, Journal of Mathematical Biology **19** (1978), pp. 147-156.
- [8] F. R. Gantmacher, *The Theory of Matrices. Volume Two.*, Chelsea Publishing Company, New York, 1960.
- [9] J. Gukenheimer and P. Holmes, *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields*, Springer-Verlag New York Inc., New York, 1983.
- [10] P. H. Leslie, *Some Further Notes on the Use of Matrices in Population Mathematics*, Biometrika **35** (1948), pp. 213-245.

- [11] E. Mjølhus and A. Wikan, *Periodicity of 4 in Age-structured Population Models with Density Dependence*, *Journal of Theoretical Biology* **173** (1995), pp. 109-119.
- [12] J. D. Murray, *Mathematical Biology. Second Edition*, Springer-Verlag New York Inc., New York, 1993.
- [13] M. B. Usher, *Developments in the Leslie Matrix Model*, *Mathematical Models in Ecology*. (J. N. Jeffers ed.) Blackwell, Oxford, 1972.
- [14] I. Ugarcovici and H. Weiss, *Chaotic Dynamics of a Nonlinear Density Dependent Population Model*, *Nonlinearity* **17** (2004), pp. 1689-1711.
- [15] A. Wikan, *Four-periodicity in Leslie Matrix Models with Density Dependent Survival Probabilities*, *Theoretical Population Biology* **53** (1998), pp. 85-97.