The Effect of Demographic Stochasticity on Density-Dependent Age-Structured Populations

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Abstract

When modeling populations one of the most important aspects one can look at is how the population grows over time and what parameters affect that growth. Similarly, when attempting to explain real world population dynamics it is necessary to look at how a population is altered by differences in survivorship and reproduction rates among individuals from year to year (known as demographic stochasticity). This can be viewed by adding basic stochastic elements into a model. The purpose of this project is to examine the effect that demographic differences have on a density dependent population model with a two stage age structure, and determine if these stochastic additions cause a specific mode to extinction.

Introduction

When dealing with populations it is customary to use difference equations since they have a few key advantages over the more common differential equations. Most importantly, difference equations are more natural for viewing of the population size from generation to generation in order to understand the long term behavior. When using difference equations to model animal populations it is common to use an equation of the form:

$$x_{n+1} = rsx_n$$  \hspace{1cm} (1)

Where \( r \) is the number of progeny per individual per year and \( s \) is the survivorship rate (or fraction of the population that survive to the next time step). With constant survivorship the population grows geometrically towards infinity for \( rs>1 \), remains constant for \( rs=1 \), or declines geometrically to extinction for \( rs<1 \). Although this particular form shows no truly interesting behavior, when the more realistic case of density dependent survivorship is introduced the behavior changes dramatically and becomes much more fascinating to study.
Obviously, unlimited growth of a population, as predicted when survivorship is constant, is unrealistic in the real world. Almost all animal populations have survivorship rates that depend on the size of the population as a result of numerous types of limiting factors. The most important factor that determines how fast a population is able to expand is the resources available. In order to survive, all animals need the basics such as adequate amounts of food and water along with shelter and space. However, as a population grows, it begins to encroach on itself, causing a decline in the resources available. Eventually, the resources become stretched so thin, and competition within the population becomes so fierce, that the ability of individuals to provide for themselves, let alone any progeny, decreases substantially. Thus, the end result is that as the population grows the resources decline, which in turn creates decreasing survivorship values.

In nature, survivorship apparently must depend on the density of the population (figure 1). T.S. Bellows (1981) has shown that there are two common types of survivorship curves in nature. The first is a saturating curve in which the number surviving \( x_s(x) \) initially increases with density, but eventually levels off at a certain value as the density becomes great. The second type is a hump-shaped curve where the number surviving increases with density, but eventually begins to decrease and go towards zero as the density becomes too great and resources are spread too thin (figure 2). Both types of survivorship curves were modeled by Bellows with the function:

\[
x_n S(x_n) = \frac{x_n}{1 + ax_n^b}
\]

where \( a > 0, \ b \geq 1 \). The hump-shape curves (b-d) come about for \( b > 1 \), while the saturating curve (a) is represented by \( b = 1 \).
Figure 1: Survivorship ($s(x)$) vs. Initial Density ($x_0$)

Figure 2: Number Surviving ($x_s(x)$) vs. Initial Density ($x_0$)

Now that there is a realistic survivorship curve available, it is possible to plug it back into the original population model (equation 1) to achieve the more interesting and biologically relevant model:

\[ x_{n+1} = \frac{rx_n}{1 + ax_n^b} \]  
(3)

where all parameters are the same as defined previously. This model was used by Bellows to successfully model several types of insect species, particularly beetles. When \( b=1 \) it is known as the Beverton-Holt model and has been expanded to many fish species including Pacific whiting and Pacific salmon. Unlike our original model this one can exhibit a wide variety of long term behaviors.

In order to understand the behavior of a difference equation it is necessary to know where the stable states or equilibrium occur, which are values of the system that once reached the population will stay at for all time. Mathematically this can be stated as

\[ x_1 = x_2 = x_3 = \ldots = x^* \]

and thus for any equilibrium

\[ f(x^*) = x^* \]  
(4)

When analyzing an equilibrium value it is important to know whether it is stable (neighboring states are attracted to it) or unstable (neighboring states move away from the equilibrium). In order to determine stability it is necessary to see what happens when the system is perturbed slightly from the equilibrium. If values move back towards the equilibrium then it is stable and if they move away it is obviously unstable. This behavior can be determined by performing a Taylor expansion about the equilibrium value. For instance say \( x_n \) is a small perturbation away from the equilibrium:

\[ x_n = x^* + x_n' \]  
(5)
Then in the next time step the size of the perturbation becomes:

\[ x_{n+1}' = x_{n+1} - x^* \]  

(6)

and from the definition of a difference equation we know \( x_{n+1} = f(x_n) \), therefore:

\[ x_{n+1}' = f(x_n) - x^* \]  

(7)

From equation 5 we can substitute in for \( x_n \):

\[ x_{n+1}' = f(x^* + x_n') - x^* \]  

(8)

Now we do a Taylor expansion of the function \( f(x^* + x_n') \) and we get:

\[ f(x^* + x_n') = f(x^*) + \left( \frac{\partial f}{\partial x} \right|_{x^*} x_n' \) + O(x_n'^2) \]  

(9)

But the final term is very small near \( x^* \) so its contribution is negligible and we can make the substitution from equation 4, leaving us with:

\[ f(x^* + x_n') = x^* + \left( \frac{\partial f}{\partial x} \right|_{x^*} x_n' \) \]  

(10)

Plugging this back into equation 8 we are left with:

\[ x_{n+1}' = x^* + \left( \frac{\partial f}{\partial x} \right|_{x^*} x_n' \) x_n' \]  

(11)

or with a simple substitution:

\[ x_{n+1}' = cx_n' \quad c = \left( \frac{\partial f}{\partial x} \right|_{x^*} \]  

(13)

Thus we come to the conclusion that:

\[ |c| < 1 \quad \text{stable equilibrium} \]  

(14)

\[ |c| > 1 \quad \text{unstable equilibrium} \]  

\[ |c| = 1 \quad \text{test is inconclusive} \]

This makes sense because the perturbation will decrease in the next time step, meaning the system is moving back towards the equilibrium and thus is stable, if the absolute value of \( c \) is less than one.
It is now possible to determine the actual behavior of our population model (equation 3) by applying equilibrium stability analysis. After working out the mathematics it can be seen that for $b<2$ there is a stable equilibrium at $(r-1)^{1/b}$, which all initial populations will move towards as long as $r>1$. If $r$ is too small ($r<1$), though, the only stable equilibrium is zero and thus all populations go extinct. On the other hand, if $b>2$ the nonzero equilibrium loses its stability and creates a period 2 solution. As $r$ increases further the period 2 splits to a period 4, which splits to a period 8, etc… until chaos is reached. This behavior can be seen from the orbital bifurcation diagram (figure 3), which plots values of the long term stable states on the y-axis versus parameter values on the x-axis.

**Figure 3:** Orbital bifurcation diagram for $b = 3.12$ (associated *Triboleum castaneum*) with $r$ varying on the horizontal axis.
Although this single stage model has been successfully used on certain populations, an even more realistic approach is the addition of a stage or age-based structure. The idea behind this approach is that most populations are not just born and then simply reproduce and/or die in one time step. For the purpose of this report, we will look at an age-structured model where only reproduction is dependent on density, while survivorship to adulthood is constant. The model we will examine takes the following form:

\[
yn+1 = s_1 xn
\]

where \(x\) represents the number of juveniles, \(y\) the number of adults, \(v\) is a scaling factor corresponding to the habitat size, \(s_1\) is the adult survivorship, \(r\) is the number of progeny per mature female, and \(a\) and \(b\) are density dependent parameters. By non-dimensionalizing the model with the substitutions \(A = ay\) and \(J = s_1 ax\) the following, easier to analyze model, results:

\[
J' = \frac{r \left( \frac{J}{J} \right)^b}{1 - \left( \frac{J}{J} \right)^b} \\
A' = J
\]

where \(J\) is now the number of juveniles, \(A\) the number of adults, and \(\rho = s_1 ra^{1-b}\).

As stated before the overall purpose of this project will be to analyze the effects of adding stochastic elements to this age structured model. The first step is obviously to understand the basic dynamics of the system. This will involve determining how the number of equilibrium depends on parameter values (explicit determination of the equilibria in terms of parameter values will not be possible as will be shown later). Once the number of equilibria is determined,
it will be possible to then deduce how many period-two states are associated with each equilibrium situation. Finally, the stability of each equilibrium and period-two solution can be found, leading to a determination of the basins of attraction for each stable solution. A basin of attraction is simply a collection of all the points in the Adult verse Juvenile phase plane that correspond to attraction towards a particular stable equilibrium. What this means is that given an initial population of adults and juveniles, the population will move towards a certain stable equilibrium as time progresses, and what equilibrium it moves towards is determined by what basin of attraction the population begins in (unless the population starts at an unstable equilibrium in which case it will stay at that point for all time). Once the basins are known it allows for an understanding of exactly how the population will act under any set of initial population sizes. It is quite important to be able to understand the behavior of the population under any set of parameter values, so that when stochastic elements are introduced, it can easily be seen what influence they have on the dynamics of the system.

When attempting to accurately model a real world population there are thousands of outside influences and individual differences between members of a population, which can affect the population. Attempting to account for each individually would be impossible and this is where stochastic models play an important role. Stochasticity refers to the fact that for most real world populations exact prediction of future population sizes is usually impossible due to randomness in both external and internal growth factors. Even if one has exact knowledge of the current population, only the probability distribution for future population sizes can be determined. Stochastic elements are an important modeling tool because they roughly account for these random aspects, while still keeping the model fairly simple.
In general there are four types of stochasticity that can alter the growth rate of a population: genetic, demographic, environmental, and catastrophes (Boyce 1992). The biological significance of stochasticity is that if population growth varies from one generation to the next, a series of low growth generations can lead to extinction of the population. This is especially true for endangered populations that are already small. Usually environmental and demographic are considered the most important detrimental factors because they occur in almost every population. Environmental stochasticity causes a variation in birth and death rates of a population from season to season in response to changes in predation, weather, competition or disease. Mainly, it refers to any factor external to the population that can alter the growth rates. On the other hand, demographic stochasticity is the effect that random differences among individuals in ability to survive and reproduce from one season to the next, has on population growth rates. The variability occurs even if expected reproduction and survival rates are the same for all individuals and do not change from generation to generation. It is of interest to note that environmental stochasticity plays an important role for both small and large populations, while demographic stochasticity only plays a role for small ones. For the purpose of this project the focus will be on demographic stochasticity and its effect on population size. The overall goal will be to determine if the detrimental effects of stochastic elements lead to an exact pathway to extinction of the population.

In order to model demographic stochasticity, an absorbing Markov chain will be used. A Markov chain is a random process in which there are N discrete states with a probability \( p_{ij} \) of transitioning from state i to state j. Also, the probability of moving to a new state of the system depends only on the current state and not on the previous states, and is completely time independent (Beltrami 1993). Absorbing is a term referring to a Markov chain that contains
certain states that once entered are impossible to leave. The non-absorbing states are then said to be communicating states if the probability of reaching one from the other in a finite number of time steps is positive. In an absorbing Markov chain the first s states are absorbing and the remaining N-s states are non-absorbing and communicate. The probabilities of moving between states is then represented in matrix form where each row and each column corresponds to a certain state and the element \( p_{i,j} \) represents the probability of moving from state \( i \) to state \( j \). The sum of all the elements in each row must thus equal one since some sort of move must take place. Finally, the transition matrix takes the form:

\[
P = \begin{bmatrix}
\hat{e} & 0 & \hat{u} \\
\hat{e} & \hat{u} \\
\hat{e}R & Q & \hat{u}
\end{bmatrix}
\]

where the sub matrix \( I \) is an \( s \) by \( s \) identity matrix corresponding to the location of the absorbing states, \( R \) contains the probabilities of moves from non-absorbing to absorbing states, and \( Q \) holds the probabilities corresponding to moves between non-absorbing states. The reason for the choice of a Markov chain is that it is a simple stochastic element to model, and in fact it is even more biologically realistic because it requires both finite and integer-sized populations.

**Calculations**

**Deterministic System Dynamics**

The first step is to take the non-dimensionalized model and determine at what points the equilibria occur. As discussed earlier at an equilibrium \( x_1 = x_2 = x_3 = \ldots = x^* \). This means that for our model where:

\[
J' = \frac{r \begin{bmatrix} 0^b \end{bmatrix}}{1 \begin{bmatrix} 0^b \end{bmatrix}} \begin{bmatrix} 1 \end{bmatrix}
\]

\[
A' = J
\]

(16)
We need $A = A' = A^*$ for an adult equilibrium and $J = J' = J^*$ for a juvenile equilibrium, but $A' = J$ and therefore $A^* = A' = J = J^*$ or simply:

$$A^* = J^*$$  \hspace{1cm} (17)

Which means that in the Adult-Juvenile phase space equilibrium of the system will lie on the line $A = J$.

The next step is to find how the number of equilibria depends on the parameter values. Using the results of equation 17 and substituting $A^*$ in for both $A$ and $J'$ in equation 16 yields the equation:

$$A^* = \frac{A^* b}{1 - c \frac{A^*}{v}}$$  \hspace{1cm} (18)

When solved this equation yields the values of the equilibrium. Obviously one solution is $A^* = 0$, which holds for any set of parameters. Dividing through by $A^*$, which corresponds to removing the zero solution, leaves us with the following function which we’ll call $g(A)$:

$$g(A^*) = \frac{A^* b}{1 - c \frac{A^*}{v}}$$  \hspace{1cm} (19)

This equation cannot be solved explicitly. The only thing that can be done is to see if there is an inequality that will tell how many solutions this equation has under different parameter schemes. This can be done by determining the maximum value of equation 19 and seeing whether it is greater than, less than or equal to zero (corresponding to whether it has 2, 1, or 0 real roots). (For the following section we will focus only on the $A^* > 0$ region since only positive equilibrium
values have a physical meaning and it has already been determined that 0 is always an equilibrium).

The first step is to take the derivative of $g(A^*)$ with respect to $A^*$, which yields:

$$\frac{d(g(A^*)))}{dA^*} = A^* (b^2) \left( v^b b \right) \left( A^* v^b b \right) \left( v^b b \right) (b^b)$$

(20)

From basic calculus we know that a function is increasing when its derivative is positive and decreasing when the derivative is negative, thus $g(A^*)$ must be increasing when $A^{*b} < v^{b}b-v^{b}$ and decreasing when $A^{*b} > v^{b}b-v^{b}$. Next we determine where the extremes of $g(A^*)$ occur by finding the critical points, which is done by setting the derivative equal to zero and solving for $A_c^*$. It can easily be seen that the derivative is zero when $A^{*b} = v^{b}b-v^{b}$, which simplifies to:

$$A_c^* = (b-1)^{1/b}$$

(21)

Now $g(A^*)$ is evaluated at the critical point in order to determine the value of the maxima, yielding:

$$g(A_c^*) = \frac{r^b K 1}{v b}$$

(22)

Hence when the maximum of $g(A^*)$ is greater than zero, $g(A^*)$ has two positive roots for a total of 3 equilibrium (including zero), when it is equal to zero there is one root and two equilibrium, and finally when it is less than zero there are no roots and only one equilibrium. The results are summed up in the following table (and note that since $A^* = J^*$ the results are the same for $J$).
Table 1

<table>
<thead>
<tr>
<th>Inequality</th>
<th>Number of Positive Roots of $g(A^*)$</th>
<th>Total Number of Equilibria (Including Zero)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$vb &gt; r \left( bK \right) \frac{K}{b} 1$</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>$vb = r \left( bK \right) \frac{K}{b} 1$</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>$vb &lt; r \left( bK \right) \frac{K}{b} 1$</td>
<td>2</td>
<td>3</td>
</tr>
</tbody>
</table>

The next step in understanding the basic dynamics of this system is to determine the stability of each of the equilibria. We begin with the origin. In order to check the stability of equilibrium in a two stage system similar steps can be taken as for a one stage system. Suppose we have the following difference equations:

$$x_{n+1} = f(x_n, y_n)$$
$$y_{n+1} = g(x_n, y_n)$$

(23)

Therefore equilibria values must satisfy:

$$x^* = f(x^*, y^*)$$
$$y^* = g(x^*, y^*)$$

Now we take small perturbations $x'$ and $y'$ and perform a Taylor expansion of each of the functions $f$ and $g$ of two variables. This gives:

$$f(x^* + x', y^* + y') = f(x^*, y^*) + (\partial f/\partial x |_{x^*, y^*})x' + (\partial f/\partial y |_{x^*, y^*})y' + \text{negligible terms}$$

The same equation results for the expansion of $g$. We now have:
\[ x_{n+1} = a_{11} x_n + a_{12} y_n \]
\[ y_{n+1} = a_{21} x_n + a_{22} y_n \]
\[ a_{11} = (\partial f/\partial x \big|_{x^*, y^*}) \quad a_{12} = (\partial f/\partial y \big|_{x^*, y^*}) \]
\[ a_{21} = (\partial g/\partial x \big|_{x^*, y^*}) \quad a_{22} = (\partial g/\partial y \big|_{x^*, y^*}) \]  

This can be more neatly written in matrix notation as:

\[ x_{n+1} = A x_n \]
\[ A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \quad x_n = \begin{pmatrix} x_n' \\ y_n' \end{pmatrix} \]

The stability can now be determined by finding the characteristic equation and determining when the eigenvalues are of magnitude less than one. The condition for this can be stated by the inequality (Edelstein-Keshet 1988):

\[ 2 > 1 + G > |B| \]  

\[ G = a_{11} a_{22} - a_{12} a_{21} \quad B = a_{11} + a_{22} \]

For our system we have:

\[ f(J, A) = \begin{pmatrix} r \end{pmatrix} \begin{pmatrix} Q^J \end{pmatrix} \begin{pmatrix} v \end{pmatrix} \]
\[ g(J, A) = J \]

The equilibrium located at the origin is therefore stable for all sets of parameters as is shown in the following proof:

\[ a_{11} = (\partial f/\partial J \big|_{0,0}) = 0 \]  
\[ a_{12} = (\partial f/\partial A \big|_{0,0}) = \begin{pmatrix} v^b b \end{pmatrix} \begin{pmatrix} r \end{pmatrix} \frac{A^{(b K 1)}}{(v^b \cdot C \cdot A^b)^2} \big|_{0,0} = 0 \]
\[ a_{21} = (\partial g / \partial J \bigg|_{0,0}) = 1 \quad a_{22} = (\partial g / \partial A \bigg|_{0,0}) = 0 \]

\[ G = a_{11}a_{22} - a_{12}a_{21} = 0 - 0 = 0 \quad B = a_{11} + a_{22} = 0 + 0 = 0 \]

Therefore equation 23 gives us:

\[ 2 > 1 + 0 > 0 \]

which is true and thus the origin is always a stable equilibrium.

The next task is to determine the stability of the nonzero equilibrium. The easiest way to do this is to first look at the two time step dynamics because the system becomes completely uncoupled as is shown below:

\[
J' = \frac{r}{1 \ C} Q^t \ 1^b
\]

\[
A' = J
\]

\[
J'' = J'(A') = J'(J) = \frac{r}{1 \ C} Q^t \ 1^b
\]

\[
A'' = A'(J') = \frac{r}{1 \ C} Q^t \ 1^b
\]

(27)

Now we can plot \( J'' \) versus \( J \) (or \( A'' \) versus \( A \) the results are the same) and the points on the line \( J'' = J \) will give us our equilibrium values. The stability can then be obtained following from the idea of monotone dynamics. This states that for a difference equation of the form \( x_{n+1} = f(x_n) \), if \( f(x) \) is a non-decreasing function, then every solution either decreases or increases towards an equilibrium (Schreiber, In Preparation). Thus for our two time-step scenario we can say that the system either increases or decreases towards an equilibrium as long as we can determine that \( J'' \)
is always increasing in \( J \) (i.e. the first derivative is always positive for positive \( J \)) and \( J'' \) has a finite limit. Taking the derivative yields:

\[
\frac{\partial (J'')}{\partial J} = \frac{\nu b r J^{K} J'}{(\nu C J)^2} \tag{28}
\]

This is always non-negative for positive values of \( J \). Next taking the limit of \( J'' \) as \( J \) goes to infinity gives:

\[
\lim_{J \to \infty} \frac{\alpha b \nu J'}{\nu C J} = \rho \tag{29}
\]

This is a finite number. Therefore both criteria are satisfied, and so we know that in two time steps solutions must move towards an equilibrium.

It is now possible to draw generalized graphs for each of our three equilibrium inequalities and show visually the stability of the equilibria in each situation. For the first situation we know that zero is the only equilibria and the resulting graph takes the form:

![Figure 4](image)

Hence it becomes visually apparent that all solutions move towards zero. For the situation where there are two equilibria we have a slightly different scenario. We know that the origin is stable thus all initial population sizes starting below the upper equilibrium must move towards zero. On
the other hand, all populations greater than the upper equilibrium must move towards it, due to the fact that all solutions must converge to an equilibrium value. The resulting figure becomes:

![Figure 5](image)

Finally, we have the situation where there are three equilibria. Again the origin is stable and all initial populations with sizes less than the middle equilibrium will move towards extinction. Similarly, any initial population size that starts above the high equilibrium will decrease towards it, since all solutions must converge towards an equilibrium. Initial populations that start between the middle and upper equilibrium will also move towards the upper equilibrium. The reason for this is not as apparent as the other scenarios. It is necessary to use a technique referred to as cobwebbing. This is a recursive graphing method which uses the line $J''=J$ to reflect values of $J''$ back to the $J$ axis in order to give the solution for the next time step, and to see what values the population is moving towards. The basic steps are to first choose an initial value $J_0$ and draw a vertical line from that value up to the function $J''$. Next draw a horizontal line from the function $J''$ to the line $J''=J$. The resulting point is $(J_{n+2}, J_{n+2})$. If the values move towards and eventually intersect an equilibrium, then the equilibrium must be stable. Going back to our current situation, we see that for population values starting between the middle and upper equilibrium, the cobwebbing process shows us that the population increases and eventually
intersects the upper equilibrium. Thus in the situation when three equilibrium are present both the origin and the upper equilibrium are stable and the middle equilibrium is unstable.

Now that we know the stability of each equilibrium (remember that the results of the previous section for $J^*$ hold true also for $A^*$ values since $A^* = J^*$), we can put everything together in order to view the basins of attraction of the system and completely understand its dynamics. We begin by looking at the simplest case, the one in which the origin is the only equilibrium value. From the two time step dynamics, we saw that the juvenile (or adult) population would always go extinct. Thus we know that since both adults and juveniles go extinct no matter where they start out, the entire phase plane must be a basin of attraction for the extinction equilibrium.
The dynamics of the next case, when there are two equilibria (Fig. 5), becomes slightly more interesting because a period-two orbit is formed. From the two time step dynamic work we know that there are 2 equilibria for A and J, the origin which is always stable and an upper equilibrium. We also know that if initial A and J values begin above the upper equilibrium value then they will both decrease to the equilibrium, and if both start below it the entire population goes extinct. Exactly what happens when either A or J starts above its upper equilibrium and the other starts below its upper equilibrium is yet unclear. The answer is that a period-two orbit is formed. For instance, lets say A starts above \( A_{\text{upper}} \) and J starts below \( J_{\text{upper}} \), then we know that at every two time steps A goes to \( A_{\text{upper}} \) and J goes to zero. However, if we look at what happens at every time step things are slightly more interesting. If we go back to equation 16 we see that \( A' = J \), therefore once the system has gone through a few transient time steps and settled down at equilibrium, A values are going to oscillate from \( A_{\text{upper}} \), which we saw it had to be at every two time steps, to 0, which is what J has to be at every two time steps. As for J values, they must also oscillate in the same manner as A except that they begin at 0 and jump to \( J_{\text{upper}} \) in the next time step. The reason for this may not seem quite as clear as it is for A values due to the fact that \( J' = r \frac{1}{1 + C} \cdot \frac{A'}{1 + C} = f(A) \), which would make it seem that J should jump not to \( J_{\text{upper}} \) but to \( f(A_{\text{upper}}) \). A simple proof (which also holds true for period 2 solutions when 3 equilibria are present) shows that \( f(A^*) \) must indeed equal \( A^* \) and \( f(J^*) \) equals \( J^* \).

**Proof:** Start with an initial population at equilibrium \( (J^*, A^*) \).

From two time step dynamics we know that after two time steps we must be back at equilibrium \( (J^*, A^*) \). From equation 16 we know that \( A' = J \) and \( J' = r \frac{1}{1 + C} \cdot \frac{A'}{1 + C} = f(A) \). Therefore in the next time step A goes from \( A^* \) to
J*, while J goes from J* to f(A*), so we are now at the point (f(A*), J*).

If we iterate again A now goes from J* to f(A*) and J goes from f(A*) to
f(J*), thus we’re now at the point (f(J*), f(A*)). This point, though, must
be equal to our original starting point (J*, A*) because, as we stated
earlier, at every two time steps we must end up at the same point we began
at. Thus we have that (J*, A*)=(f(J*), f(A*)). Finally, J*=f(J*) and
A*=f(A*).

Following from the previous proof we now see that at every two time steps we must be at (0,
A*_{upper}) and therefore at every other time step we must be (f(A*_{upper}), 0), but now we know
f(A*_{upper})=A*_{upper}. Also, from equation 17 we have A*_{upper}=J*_{upper}. Finally, we can say that for
points where either J or A starts above its upper equilibrium and the other starts below, a period
two orbit will result, which oscillates between the points (0, A*_{upper}) and (J*_{upper}, 0) or vice versa
depending on which age has the higher starting population. This can all be summed up in the
following graph:

![Figure 8](image-url)
Finally, we are left with the situation where there are three equilibria (Fig. 6) including the origin, the unstable middle equilibrium \((J_{\text{mid}}, A_{\text{mid}})\), and the stable upper equilibrium \((J_{\text{up}}, A_{\text{up}})\). To begin with, we know that if both \(A\) and \(J\) start above the middle equilibrium then they will go to the upper equilibrium, and conversely if they both start below the middle equilibrium they will go extinct. Similar to the last scenario though, there are a number of period-two solutions that come about. In total there are three period-two solutions, two of which are unstable. The first unstable period two results if \(A\) or \(J\) starts below \(A_{\text{mid}}\), while the other starts exactly at it. This means that every two time steps the lower value population will go extinct and the other stays at equilibrium. From the proof we know that this means an oscillation will occur between \((0, A_{\text{mid}})\) to \((J_{\text{mid}}, 0)\) or vice versa. Therefore, any initial populations lying on the line \(A=A_{\text{mid}}\) to the left of the middle equilibrium or the line \(J=J_{\text{mid}}\) below the middle equilibrium will go to this period-two orbit. Next we have the case where \(A\) or \(J\) starts above the middle equilibrium, but the other starts below. For these initial conditions the state with the higher starting value will move to the upper equilibrium value and the other will go to extinction for every two time steps. Again following from the earlier proof, it can be seen that at every other time step the stage with the lower starting value will then go to the upper equilibrium value and the other stage will go to zero. This leaves us with a period-two orbit consisting of oscillations between \((0, A_{\text{up}})\) and \((J_{\text{up}}, 0)\). The final period-two solution forms when one stage starts exactly at its middle equilibrium and the other starts above the middle equilibrium. For these starting conditions the higher valued population goes to its upper equilibrium and the other stays at the middle equilibrium value for every two time steps. At every time step, we once again use the proof shown earlier and see that the stages switch values. Therefore we are left with jumps between \((J_{\text{up}}, A_{\text{mid}})\) and \((J_{\text{mid}}, A_{\text{up}})\). Only initial populations starting on the line \(J=J_{\text{middle}}\)
above the middle equilibrium or the line $A=A_{\text{middle}}$ also above the middle equilibrium, will lead to this period-two orbit. The possible scenarios for the case where three equilibria are present are shown in the following graph:

For the following graphs $b=3, v=5, \rho=30$. Therefore $vb=15<\rho(b-1)^{(b+1)/b}=47.6$, thus there are three equilibria: $A_{\text{up}}^*=29.9=J_{\text{up}}^*, A_{\text{mid}}^*=2.12=J_{\text{mid}}$ and the origin.

Figure 10
The above graphs, representing the scenario where three equilibria are present, illustrate the behavior in each basin. The first shows the outcome when both A and J start above the middle equilibrium (both go to the upper equilibrium), the second shows what happens when A starts
above the middle equilibrium and J below (a period-two orbit), and finally the third shows what happens when both A and J start below the middle equilibrium (extinction of the population). Finally, we sum up the deterministic system dynamics in the following table.

Table 2

<table>
<thead>
<tr>
<th>Inequality</th>
<th>Number of Equilibrium</th>
<th>Number of Period-2 Orbits</th>
<th>Number of Basins of Attraction</th>
</tr>
</thead>
<tbody>
<tr>
<td>( v_b &gt; ) ( r \ (b^\frac{K}{b} 1) )</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>( v_b = ) ( r \ (b^\frac{K}{b} 1) )</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>( v_b &lt; ) ( r \ (b^\frac{K}{b} 1) )</td>
<td>3</td>
<td>3</td>
<td>5</td>
</tr>
</tbody>
</table>

(包括吸引线的不稳定周期-2轨)

Stochastic System Dynamics

As stated earlier, the idea behind adding stochastic elements is that in real populations only the probability distribution of possible future states is actually determinable due to numerous random factors. Because of this, deterministic models often fall short. Thus, in order to more accurately view how a two stage population might behave, we want to add demographic stochasticity and see what affects it has on the population. To begin with, we will focus on the effect that stochastic elements have on the adults, then later apply similar (although slightly different techniques) to the juveniles. It is possible to focus on only one stage of the model due to the fact that the two time step dynamics of the adult age stage is completely uncoupled from
the juveniles (i.e. the number of adults in two time steps is completely independent of the number of juveniles, as we will see).

In order to better understand the differences between the stochastic and deterministic approaches lets first look at each schematically:

**Deterministic:** \[ A \rightarrow J' \stackrel{r}{\rightarrow} A'' = J' \]

**Stochastic:** \[ p_1(A) \rightarrow q_1(J) \rightarrow p_2(A) \] (30)

What we have for the deterministic model is that a certain initial population of Adults leads to an exact number of Juveniles in the next time step, which is determined by the density dependent survivorship. In two time steps that initial adult population results in a new adult population equal to the number of juveniles from the previous time step. This process continues on, such that the initial adult population determines the future adult populations independent of initial juvenile population size. In the stochastic model, however, the initial population of adults leads to a probability distribution, \( q_1(J) \), of juveniles in the next time step. In two time steps the initial adult population then leads to a new adult population given by a new population probability distribution, \( p_2(A) \).

The next step is to decide what kind of distribution to use for \( q_1(J) \). There are many different, yet equally acceptable possibilities that can be used for this distribution, but for our case we will use a Poisson Process. This gives the probability distribution of a random variable by the formula \( P_{ij} = e^{-\lambda(i)} \cdot \frac{\lambda(i)^j}{j!} \). In other words, the probability that a system that starts in state \( i \) at time \( t \) is in state \( j \) at time \( t+1 \) is given by \( P_{ij} \), where \( \lambda(i) \) is the mean value of the distribution. For our system, we want the mean value to be equal to the actual value of the deterministic model.
The probability distribution of possible future adult states is then given by a binomial distribution with \( q_1(J) \) trials and a probability of success \( a \). More simply put, though, \( p_2(A) \) is actually just a Poisson distribution with mean \( \lambda(A) = a \).

The only thing left now is to create a Markov chain model using the Poisson distribution as the probability of movement between states. Before calculations regarding dynamics can begin though, we first need to decide on where to truncate the population size and how to define a state. Recall from earlier that a Markov chain requires a finite population size and integer valued states. In order to make our population fit these criteria we will take the nearest integer to the upper equilibrium and define states as integer values above and below this value. Similarly, we define the maximum population size as twice the upper equilibrium. Finally, we are ready to view the effects of demographic stochasticity through the use of a Markov Chain model, where the transition matrix entries are given by the Poisson Probability distribution:

\[
\text{Probability}(A_{t+1} = j \mid A_t = i) = p_{ij} = e^{-\lambda(i)} \cdot \frac{\lambda(i)^j}{j!}
\]

Since demographic stochasticity is a major influence on the growth rate of small populations (i.e. endangered), it is very likely that eventually the population will enter the basin of attraction for extinction. The reason for this is that, if even a short string of generations occur where some individuals randomly have below average birth and survivorship rates, the overall growth rate of the population can be highly affected in a negative way. Therefore, to begin, we want to look at exactly how long it takes for the population to enter the extinction basin, and similarly how many time steps it takes on average to go extinct depending on what state the population starts in. The following graphs display these results for varying values of the
parameter $\rho$, while holding the others constant at $v=5$, $a=.5$ and $b=3$. First we have an orbital bifurcation diagram for the two time step adult dynamics showing equilibria values for varying $\rho$.

![Orbital Bifurcation Diagram for Adults](image)

Figure 13

Now that we know the equilibrium values we can look at how the value of $\rho$, and thus the size and spread of the equilibria, affects the dynamics of the stochastic system.

(Note that for the following graphs, states begin at 1. i.e. the state corresponding to $A=zero$ is actually state 1)
$\rho=60$, starting state $A_{up}^*=29.85=\text{state 30}$, $A_{low}^*=2.12=\text{state 3}$

**Figure 14**

*Probability of Extinction for Adults*

**Figure 15**

*Probability of Extinction for Adults*
$\rho=30$, starting state=$A^{*}_{\text{up}}=14.39$=state 15, $A^{*}_{\text{low}}=3.26$=state 4
\( \rho = 20 \), starting state = \( A_{up}^* = 8.09 = \text{state 9} \), \( A_{low}^* = 5 = \text{state 6} \)
$\rho=18.899$, starting state $A^*_{\text{up}}=6.3$ = state 7 $A^*_{\text{low}}$

**Figure 20**

*Mean Time to Extinction*

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**Figure 21**

*Probability of Extinction for Adults*
Figure 22
Mean Time to Extinction

\[ \rho = 10 \text{ (only equilibria is zero, 29 initial states)} \]

Figure 23
Mean Time to Extinction
These graphs display a few interesting aspects about the dynamics of the stochastic system. First of all, as we expect the addition of demographic stochasticity causes the population to go extinct, but how long the population can persist depends on the parameter values (thus the size and spread of the equilibria) and the starting state. If we assume that a population begins at its upper equilibrium, we see quite a strong dependence of the probability of entering the extinction basin on the value of $\rho$. For instance, when $\rho=60$ the probability of entering the extinction basin by the 1000th time step is only .0015, whereas if we cut $\rho$ in half to $\rho=30$ the probability jumps to about .8. If we again decrease $\rho$ to 20, the population is in the extinction basin by about the 40th time step. Finally, at the value of $\rho$ where only one equilibrium occurs, $\rho=18.899$, the probability of entering the extinction basin is 1 at about 20 time steps. The correlation between extinction times and the value of $\rho$ is also demonstrated on the mean time to extinction graphs. Here we see that the mean time to extinction for the starting state jumps from $11\times10^9$ for $\rho=60$, to 720 for $\rho=30$, to 12 for $\rho=20$ and finally to 9 for $\rho=18.899$. Thus for large values of $\rho$, and thus where the upper and middle equilibria have a large spread, extinction is rather unlikely, especially since so many other factors could affect the population on the time scale it would take demographic stochasticity to force the population to extinction. On the other hand, for lower $\rho$ values, where the spread is fairly small or when only one nonzero equilibrium exists, extinction of the population is almost inevitable.

The other interesting note about these graphs is the apparent threshold dependence of the mean time to extinction of the starting state on the lower equilibrium. This means that the decrease in mean time to extinction when one moves below the lower equilibrium is catastrophic, especially when compared to the fairly minimal increase in mean time as the population’s initial size increases from the lower equilibrium to the upper equilibrium level. For
instance, when $\rho=30$ the mean time to extinction if the population begins at the lower equilibrium level (state 4) is about 550 time steps. If the population were to start just below this level (say state 3) the mean time drops to roughly 210, but increases to only 710 for populations beginning at the upper equilibrium (state 15). Obviously, this is a substantial difference and could play an important role in real world endangered populations because it is crucial to maintain the population size above (well above if possible) the middle equilibrium, otherwise the adult population has a far higher chance of entering the extinction basin and much lower time to actual extinction.

The next step at this point would be to go through a similar process for the dynamics of the juveniles with stochasticity added. With this done we could then put the results of the adults and juvenile dynamics together, much like we did with the deterministic model, in order to determine the overall behavior of the stochastic system. In order to accomplish this, a very similar scheme would be used to that of the adults, although there would be some slight alterations to how the probabilities would be calculated, etc. Unfortunately, there has not been enough time at this point to examine these dynamics and finish the remainder of the project.

One final calculation can be made, which will give a rough idea of what the juvenile dynamics will look like. A crude approximation of the juvenile behavior can be obtained by making the assumption that juveniles and adults are affected in the same way (i.e. the processes are identical for both), but they are completely independent of each other. Again this is a rough assumption because the juveniles are going to be affected differently, but it can give a little insight. We can now take a look at the probability that both juvenile and adults are extinct by a certain time step.
For the following graphs v=5, a=.5 and b=3

\( \rho = 60 \), starting state=\( A_{up}^* = 29.85 = \text{state 30} \), \( A_{low}^* = 2.12 = \text{state 3} \)

**Figure 24**

*Probability of Extinction*

\( \rho = 30 \), starting state=\( A_{up}^* = 14.39 = \text{state 15} \), \( A_{low}^* = 3.26 = \text{state 4} \)

**Figure 25**

*Probability of Extinction*
\( \rho = 20 \), starting state = \( A_{up}^{*} = 8.09 = \text{state 9} \), \( A_{low}^{*} = 5 = \text{state 6} \)

**Figure 26**

*Probability of Extinction*

\( \rho = 18.899 \), starting state = \( A_{up}^{*} = 6.3 = \text{state 7} = A_{low}^{*} \)

**Figure 27**

*Probability of Extinction*
The most important aspect that these graphs show is that the peak probability that both adults and juveniles have entered the extinction basin lags behind the peak probability that the adults have entered the extinction basin. What this means is that it is possible that after the adults have entered the extinction basin (or gone extinct completely) the juveniles could still be at a normal persistence level (i.e. above the middle equilibrium). Overall, this could be important because after the adults go extinct the juveniles could remain at a rather high level for quite a few time steps (assuming the juvenile probability of extinction does indeed lag behind the adults). If this is true then it leaves open the possibility that in every time step there is an oscillatory period two orbit where adults and juveniles exchange values.

This leads to two possibly significant biological implications. First, even though demographic stochasticity has forced the original adult population (i.e. those original adults and all of its successive generations) to extinction, in every other time step there are still adults in the population due to the persistence of the original juveniles. Secondly, it is possible that this oscillatory behavior could always be a precursor to complete extinction of the population. Thus it is possible that a population affected by demographic stochasticity, which is close to extinction, will follow a specific mode to extinction (i.e. both subpopulations persisting at a relatively high value, then one subpopulation (either the adults or the juveniles) going extinct leading to oscillatory behavior, and finally eventual complete extinction). Determining if a distinct mode to extinction does exist is one of the main goals of this research, due to the fact that in real world populations it could help to determine if an endangered species is dangerously close to collapse by seeing if the population demonstrates this kind of oscillatory behavior.
Conclusion

Our research has shown that for our deterministic density-dependent two-age-stage population model there is the possibility of one, two or three equilibria depending on initial parameter values. Similarly, we saw that in the cases where either two or three equilibria are present there are also a number of associated period-two orbits that can exist. The main point about the deterministic model is that as long as initial parameters allow for nonzero equilibria to exist, then if either the adults or the juveniles have an initial population above the lower nonzero equilibrium, the population will persist for all time.

The problem that arises is that in the real world a deterministic model can not be completely accurate. There are too many random factors that can affect the growth of a population, thus to make a model more realistic it is necessary to use stochastic elements. These stochastic elements can model certain random aspects and thereby give the probability distribution of the future states of the system. For our case we wanted to see what effects demographic differences among individuals had on the overall growth rates of the population. Even though the expected values of birth rates and survival capabilities are known, it is possible that there are random differences between individuals in these rates, and it is important to figure out how these aspects can affect the overall growth rate of the population.

In order to model the effects of demographic stochasticity on the adult population, we turned the deterministic population model into a discretized Markov chain model. The probabilities of moving from one state to another were then determined by a Poisson Process with a mean equal to the exact value of the Adults in two time steps (as given by the deterministic model). The result was that in the long run the population would eventually reach extinction. Interesting to note from our results was the very strong dependence of the probability
of entering the extinction basin on the spread in the equilibrium caused by the size of $\rho$. For large values of this parameter, the values of the nonzero equilibria had a much greater spread, and the probability of entering the extinction basin, assuming the population began at the upper equilibrium value, was miniscule and almost nonexistent. As $\rho$ decreased though, and the nonzero equilibria came closer and closer together, the probability of entering the extinction basin jumped rapidly until at the point of bifurcation (i.e. the point where the two nonzero equilibria coalesce into a single nonzero equilibrium) the adults were in the extinction basin after only 20 time steps.

Another interesting result came about by looking at the mean time to extinction for the possible starting states of the population. This showed a strong dependence on the threshold value of the middle equilibrium. Basically, a population starting below the middle equilibrium (or the only nonzero equilibrium for the case where only one exists) had a much lower mean time to extinction than those starting at or above the equilibrium. Also, the increase in time to extinction for populations starting at values much higher than the middle equilibrium was relatively small.

These results have a few biologically significant implications. First of all, when dealing with an endangered species it is known that demographic stochasticity is a major factor influencing the growth rate. This is mainly because the population is so small that these small differences in individuals can have a much larger impact than in populations with many individuals. Therefore, when dealing with small populations that face the threat of extinction it is possibly important to try management schemes that could increase the value of $\rho$. Going back to the original model we know that $\rho = s_1 r a^{1-h}$, thus the main influences are the survivorship to adulthood and the number of progeny per mature female. Management techniques should
therefore focus on either trying to increase the number of births, which in many populations may be a difficult thing to do, or increasing the survivorship to adulthood. The latter most likely would be an easier objective as survivorship rates often depend on influences of human interaction, either directly or indirectly, with the population. Human interaction could then be limited in numerous ways whether it is through establishment of an animal sanctuary, pollution control, building codes, etc.

Also of note here is that it is not necessary to maintain the population at huge abundances. The fact that the time to extinction does not vary all that much for initial states between the middle equilibrium and the upper equilibrium could play an important role in management. A population starting at a medium abundance, say a couple states above the middle equilibrium, has almost the same time to extinction as a population starting well above the upper equilibrium. In management terms it is going to be much easier to try to maintain the smaller population, and the long term benefits are almost the same as for a larger population.

Obviously, when trying to manage a population, demographic stochasticity is not the only random influence. Populations face many other pressures such as environmental stochasticity and genetic drift that can also hurt growth rates. However, assuming demographic stochasticity is the major influence, it can be determined roughly how long the population has until extinction. Thus managers can determine the time scale on which management techniques that are being used to try to increase population growth need to work. Also, since mean times to extinction are similar for medium and large population abundances, it indicates that while management techniques are being implemented to counter demographic stochasticity, population size need not be very large. A population only needs to be big enough so that it does not get perturbed below
the middle equilibrium by another random influence, otherwise the mean time to extinction will be more or less the same as for a large population.

The next step for this research is to take a similar technique to what was used on the adult population and apply it to the juvenile population. Although the process is very similar, there are some slight alterations that need to be made from the work that was done with adults. Mainly, the transition probabilities will differ due to slightly different dynamics. When this research is completed the hope is that a possible mode to extinction can be identified for the entire population under the influence of demographic stochasticity. As we saw in the results section, if we use the crude approximation that both the adults and juveniles are affected in the same way, but completely independently, then it appears that both subpopulations do not enter the extinction basin at the same time. If this turns out to be true, then it is possible that after either the adults or juveniles go extinct an oscillatory pattern may result where the population jumps between all juveniles in one time step and all adults in the next. The overall goal for future research is to determine if this period-two orbit does actually result when the population is moving towards extinction, so that it can be used biologically to determine if a small population is on the verge of complete extinction.
Works Cited


