SEMELPAROUS PERIODICAL INSECTS

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Chapter 1

Introduction

1.1 History

Periodical species are those whose life cycle has a fixed length of n years, and whose adults do not appear every year, but only every nth year. Examples of other semelparous species include annual plants, as well as most salmon populations. Semelparous periodical insects are those periodical insects which reproduce only once in a lifetime (and usually die shortly thereafter). Examples of these include the cicada and the May beetle.

The study of such insects is important because it gives us an insight into other forms of life on Earth. Clearly these insects have evolved into such patterns of reproduction, and the study of them can help to describe the evolution that took place to arrive at this behavior.

For years, the common biological explanation as to why insects evolved into periodical behavior was predation. That is, adults emerge together to reproduce every n years so as to overwhelm the predators, who could only eat a fraction of them. If fewer adults came out every year, it would be more likely that the predators could eat all of them, thus threatening the population with extinction.

In 1977, a mathematician from Oxford named Bulmer put this theory to the test mathematically, testing not only the predation hypothesis but also other hypotheses involving competition between and within what we call *year-classes.* Year-classes are essentially equivalence classes, representing the groups that reproduce together. For insects with life cycles of n years, there are n year-classes. Periodical behavior results from the absence of all but one of these year-classes in any given year. Bulmer found that when competition is more severe between than within year-classes, periodical behavior results. With regard to predation, he found that predators do not lead to periodical behavior per se, but they can have a powerful effect in reinforcing the tendency of competition between year-classes to cause periodical behavior. It is this last fact that motivated our study of predation in semelparous models.

Using the model given in Dr. Jim Cushing's paper "Nonlinear Semelparous Leslie Models", we examined the effect of predation on a semelparous insect model. From this paper we know that there are positive equilibria (with overlapping generations) and synchronous cycles with non-overlapping generations that bifurcate from the trivial (or extinction) equilibrium as the inherent net reproductive number increases through the critical value of 1. Our goal is to determine the effect that an added predation term will have on these bifurcating equilibria and cycles. To do this we need to study how the coefficients in certain approximating expansions depend on a predator coefficient. This analysis will tell us under what circumstances the equilibria and two-cycles are stable and/or unstable. From this, we can either corroborate or refute Bulmer's results.

1.2 General mathematical model

The model from Cushing's paper is

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \end{pmatrix} = \begin{pmatrix} 0 & \frac{n}{1-\mu} f(x_1(t), x_2(t)) \\ (1-\mu) g(x_1(t), x_2(t)) & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix},$$

where $f = \frac{1}{1+\beta_{21}x_1+\beta_{22}x_2}$ and $g = \frac{1}{1+\beta_{11}x_1+\beta_{12}x_2}$. In this model, β_{ij} represents the effect of the jth year-class on the ith year-class. Thus $\beta_{ij} > 0$ (for $i \neq j$) represents competition between year-classes and $\beta_{ii} > 0$ represents competition within year-classes. Also, x_1 and x_2 stand for the juvenile and adult stages of the life cycle, respectively. In this paper we will write J for x_1 and A for x_2, so that it is clearer to which stage we are referring. Following Bulmer, in order to examine the effect of a predator on the system, we multiply the juvenile equation by an exponential decay term dependent on a predation coefficient c:

$$J_{t+1} = \frac{n}{1-\mu} \frac{A_t}{1+\beta_{21}J_t+\beta_{22}A_t}(1-e^{-cA_t}),$$

$$A_{t+1} = (1-\mu)\frac{J_t}{1+\beta_{11}J_t+\beta_{12}A_t}.$$

This term is chosen because the predators attack the adults and thus affect the number of juveniles present at the next year. Note that as we increase the value of c the value of $(1-e^{-cA})$ increases, which corresponds to a greater number of juveniles present. Thus increasing c corresponds to a *decrease* in the predator; this is a non-intuitive point we must keep in mind throughout the discussion.

1.3 Rationale for the choice of coefficients

For our case, we wish to analyze the effect of a predator on Cushing's previous model. Specifically, we want to know if a predator can cause synchronized oscillations (periodical behavior) on its own. We want to make sure that if we see oscillations, that they come from the predator alone. Thus, in this new restricted model we set $\beta_{12} = 0 = \beta_{21}$. That is, we only look at the case where there is no competition between year-classes, for it was competition between year-classes which Bulmer concluded was the cause of the oscillations.

Chapter 2

Results for restricted model

2.1 Existence of equilibria

Throughout all of the calculations in Cushing's paper, it was assumed that the nontrivial equilibrium bifurcated from $n = 1$ (as this is when the trivial equilibrium switched from being stable to unstable). However, after running a number of simulations, we suspected that in our predator model the trivial equilibrium at the origin is always stable. We see from the Jacobian that this is in fact true:

$$\Omega = \begin{pmatrix} 0 & 0 \\ 1-\mu & 0 \end{pmatrix}.$$

Recall that stability results from all the eigenvalues lying inside the unit circle (that is, all the eigenvalues have magnitude less than 1). The eigenvalues of the Jacobian are 0 and 0, and so the equilibrium at the origin is stable always. Thus, we must take a different approach to analyzing the model, as we no longer have the positive equilibria bifurcating from the trivial equilibrium.

We have the following equations for the equilibria J and A (Note that we have converted $\frac{n}{1-\mu}$ back to b since we no longer have the bifurcation at $n = 1$. Also we let $s = 1 - \mu$.):

$$J = b \cdot \frac{A}{1 + \beta_{21}J + \beta_{22}A} \cdot (1 - e^{-cA}),$$

$$A = s \cdot \frac{J}{1 + \beta_{11}J + \beta_{12}A}.$$

Now that we are aware that the equilibria do not bifurcate from $n = 1$, we need to investigate the existence of positive equilibria $J = J(c)$ and $A = A(c)$. (Note that now n does not necessarily need to be near 1 anymore.) Since we want to investigate if predation causes periodicity, we let $\beta_{12} = 0 = \beta_{21}$, and rescale population units so that $\beta_{11} = 1 = \beta_{22}$. Then our equilibrium equations become

$$J = b \cdot \frac{A}{1 + A} \cdot (1 - e^{-cA}),$$

$$A = s \cdot \frac{J}{1+J}.$$

We first solve for J in the second equation:

$$\begin{aligned} A = (1-\mu) \cdot \frac{J}{1+J} \quad &\Rightarrow \quad A(1+J) = s \cdot J \\ &\Rightarrow \quad A + AJ = sJ \\ &\Rightarrow \quad A = sJ - AJ \\ &\Rightarrow \quad A = J(s-A) \\ &\Rightarrow \quad J = \frac{A}{s-A}. \end{aligned}$$

We now substitute this back into the first equation and obtain

$$\frac{A}{s-A} = b \cdot \frac{A}{1+A} \cdot (1 - e^{-cA}).$$

This is equivalent to

$$1 + A = b(s-A)(1 - e^{-cA}). \tag{2.1}$$

Since this equation is impossible to solve analytically, we investigate the existence of a positive equilibrium graphically. If we graph the left hand side of equation (2.1) against the right hand side of equation (2.1), and there is an intersection at $A > 0$, then we know that there exists a positive equilibrium. Otherwise, if the curves never intersect, there is *not* a positive equilibrium. We see that if we let, say, $s = 0.5$, $b = 10$, and $c = 1$, we get the following graph for $A \geq 0$:

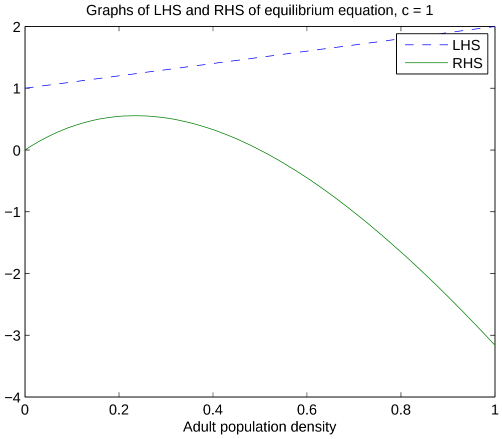

Figure 2.1: $s = 0.5$, $b = 10$, $c = 1$

We see that the curves do not in fact intersect. However, if we let $c = 10$ now, we get this graph instead:

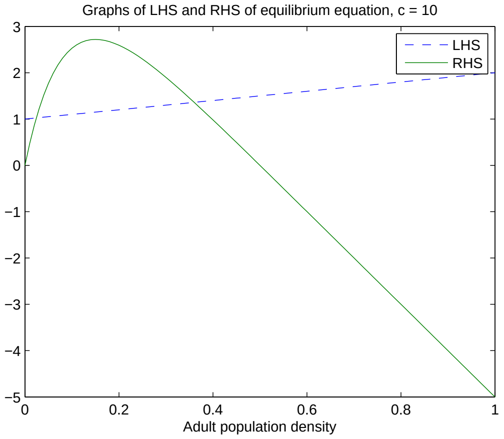

Figure 2.2: $s = 0.5$, $b = 10$, $c = 10$

Now the graphs do intersect! Increasing c, we went from zero positive equilibria to two positive equilibria. The graphs intersect when c is somewhere between 1 and 10, and a saddle-node bifurcation is present. To find the intersection, we look at our equilibrium equation again and solve for c:

$$\begin{aligned} 1 + A = b(s-A)(1-e^{-cA}) \quad &\Rightarrow \quad \frac{1+A}{b(s-A)} = 1 - e^{-cA} \\ &\Rightarrow \quad 1 - \frac{1+A}{b(s-A)} = e^{-cA} \\ &\Rightarrow \quad ln\left(1 - \frac{1+A}{b(s-A)}\right) = -cA \\ &\Rightarrow \quad c = -\frac{ln\left(1 - \frac{1+A}{b(s-A)}\right)}{A}. \end{aligned}$$

In our example, we had $s = 0.5$ and $b = 10$, so we would get

$$c = -\frac{ln\left(1 - \frac{1+A}{10(0.5-A)}\right)}{A}.$$

Here we see the graph when $c = 2.5$,

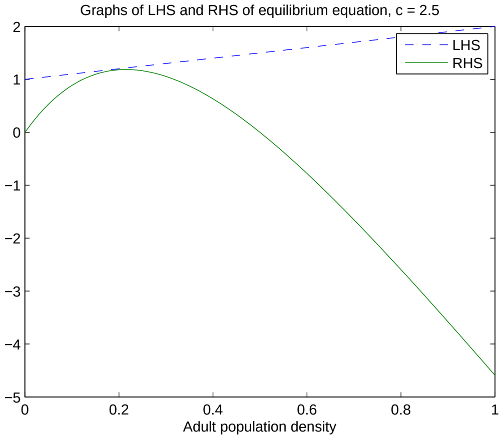

Figure 2.3: $s = 0.5$, $b = 10$, $c = 2.5$

and we do in fact see the tangential intersection very near there.

However, this is just one case. For this example to be an accurate representation of the general situation, we must show that we have this saddle-node bifurcation *for every* b and s. So let us go back to our original equation

$$1 + A = b(s - A)(1 - e^{-cA}),$$

which, recall, looked like a fixed straight line and a variable curve that changed shape with c. Note that throughout this process we will assume that $bs > 1$. Let's call the right hand side of the equation $f(A)$, and note that $f(A)$ has roots at 0 and s. Now we look at its second derivative:

$$f''(A) = bce^{-cA}(c(s - A) - 2).$$

On the interval $0 \leq A < s$, $f''(A) < 0$. This implies that $f(A)$ is concave down on this interval. This together with the fact that we have zeros at 0 and s implies that f has a unique maximum between 0 and s. The question we thus have is: Does the maximum always reach the line $1 + A$, for every b, s, and c? If it does, that means we will have a saddle-node bifurcation for every curve f. Clearly we need there to be an intersection, but more importantly, we are looking for a tangential intersection with $1+A$. Thus, the functions must have the same slopes. Since the slope of $1 + A$ is clearly always 1, this is what we need the slope of $f(A)$ to be at the intersection point as well. That is, we want

$$\frac{d}{dA}\, b(s - A)(1 - e^{-cA}) = 1.$$

Thus, our two equations for our two unknowns c and A are

$$\begin{cases} 1 + A = b(s - A)(1 - e^{-cA}) \\ -b(1 - e^{-cA}) + b(s - A)ce^{-cA} = 1. \end{cases}$$

From the first equation, we see that

$$b(1-e^{-cA}) = \frac{1+A}{s-A},$$

$$be^{-cA} = b - \frac{1+A}{s-A},$$

and

$$c = -\frac{1}{A} ln\left(\frac{b-\frac{1+A}{s-A}}{b}\right).$$

If we plug these back into the second equation, we get rid of the c and exponential terms:

$$-\frac{1+A}{s-A} + (s-A)\left(-\frac{1}{A}\right) ln\left(\frac{b-\frac{1+A}{s-A}}{b}\right)\left(b-\frac{1+A}{s-A}\right) = 1.$$

Rearranging terms we rewrite as

$$-\frac{1}{A} ln\left(\frac{b-\frac{1+A}{s-A}}{b}\right) = \frac{1+\frac{1+A}{s-A}}{(s-A)\left(b-\frac{1+A}{s-A}\right)}.$$

Notice that we have this $b-\frac{1+A}{s-A}$ factor both inside and outside the logarithm. We simplify by getting them alone on one side of the equation:

$$\left(\frac{b-\frac{1+A}{s-A}}{b}\right) ln\left(\frac{b-\frac{1+A}{s-A}}{b}\right) = -\frac{A}{b}\cdot\frac{1+\frac{1+A}{s-A}}{s-A}.$$

Define the left hand side of the equation to be $h(A)$, and the right hand side $g(A)$. That is,

$$h(A) = \left(\frac{b-\frac{1+A}{s-A}}{b}\right) ln\left(\frac{b-\frac{1+A}{s-A}}{b}\right), \quad g(A) = -\frac{A}{b}\cdot\frac{1+\frac{1+A}{s-A}}{s-A}.$$

Note that since the logarithm function is undefined for negative numbers, we must have

$$\begin{aligned} b-\frac{1+A}{s-A} > 0 \quad &\Rightarrow \quad b > \frac{1+A}{s-A} \\ &\Rightarrow \quad bs - bA > 1 + A \\ &\Rightarrow \quad bs - 1 > A + bA \\ &\Rightarrow \quad bs - 1 > A(b+1) \\ &\Rightarrow \quad \frac{bs-1}{b+1} > A. \end{aligned}$$

What this means is that our intersection point A must occur between 0 and $\frac{bs-1}{b+1} < s$. Thus we are now only concerned with the interval $0 < A < \frac{bs-1}{b+1}$. So let's determine the features of the function $h(A)$. First, we check the endpoints. We have

$$h(0) = \frac{bs-1}{bs} ln\left(\frac{bs-1}{bs}\right).$$

Since we assumed $bs > 1$, $\frac{bs-1}{bs}$ is a positive number. Also note that since $bs - 1 < bs$, $\frac{bs-1}{bs} < 1$, which implies that $ln\left(\frac{bs-1}{bs}\right) < 0$. Combining these facts, we have that $h(0) < 0$. In fact, this is the case for all $A < \frac{bs-1}{b+1}$ for the same reasoning as for the $A = 0$ case. Finally, we calculated the right endpoint so that $\left(\frac{b-\frac{1+A}{s-A}}{b}\right) = 0$ there. But $ln(0) = -\infty$, so we must take a limit to determine what is happening near the right endpoint. We find that that h goes to 0 there:

$$\lim_{A \to \frac{bs-1}{b+1}} h(A) = \lim_{x \to 0} xln(x) = \lim_{x \to 0} \frac{\frac{1}{x}}{-\frac{1}{x^2}} = \lim_{x \to 0}(-x) = 0.$$

So we have $h(0) < 0$, $h(\frac{bs-1}{b+1}) = 0$, and $h(A) < 0$ for $0 < A < \frac{bs-1}{b+1}$. Now let's carry out a similar analysis of $g(A)$. Clearly, $g(0) = 0$. For all $A > 0$, $-\frac{A}{b} < 0$ and $s - A > 0$. Thus $g(A) < 0$ for $A > 0$. Using the fact that $h(0) < g(0)$ and that $h(\frac{bs-1}{b+1}) > g(\frac{bs-1}{b+1})$, we know that $h(A)$ and $g(A)$ must have at least one intersection on the interval $0 < A < \frac{bs-1}{b+1}$. However, recall that with $h(A)$ and $g(A)$ that we are examining the derivative of $f(A)$, and that intersections between $h(A)$ and $g(A)$ represent local maxima of $f(A)$. But we determined above that $f(0) = 0 = f(s)$, and that $f''(A) < 0$ on this interval, which implies that f has a *unique* local maximum between 0 and s. Thus, the intersection we have guaranteed occurs between h and g is in fact the *only* intersection that we get on our interval. So we have proved that for every choice of b and s, $f(A)$ intersects $1 + A$, and thus there is a saddle-node bifurcation of positive equilibria.

2.2 Existence of synchronous 2-cycles

As for the 2-cycle in this case, we have our usual chain:

$$\begin{pmatrix} J \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ A \end{pmatrix} \to \begin{pmatrix} J \\ 0 \end{pmatrix} \to \cdots$$

In our case we have the following - based on our J and A equations:

$$\begin{pmatrix} J \\ 0 \end{pmatrix} \to \begin{pmatrix} 0 \\ s \cdot \frac{J}{1+J} \end{pmatrix} \to \begin{pmatrix} b \cdot \frac{s \cdot \frac{J}{1+J}}{1+s \cdot \frac{J}{1+J}} \cdot (1 - e^{-c \cdot s \cdot \frac{J}{1+J}}) \\ 0 \end{pmatrix} \to \cdots$$

Thus we must equate the first and third matrices to solve for J. Again this is impossible to do analytically, and so we will take a graphical approach. First we manipulate the equations to make them a little easier to read:

$$
\begin{aligned}
J = b \cdot \frac{s \cdot \frac{J}{1+J}}{1 + s \cdot \frac{J}{1+J}} \cdot (1 - e^{-c \cdot s \cdot \frac{J}{1+J}}) \quad &\Rightarrow \quad J\left(1 + s\frac{J}{1+J}\right) = bs\frac{J}{1+J}(1 - e^{-cs\frac{J}{1+J}}) \\
&\Rightarrow \quad 1 + s\frac{J}{1+J} = bs\frac{1}{1+J}(1 - e^{-cs\frac{J}{1+J}}) \\
&\Rightarrow \quad (1+J) + sJ = bs(1 - e^{-cs\frac{J}{1+J}}).
\end{aligned}
$$

Then we just graph again, with $b = 2$, $s = 0.5$, and $c = 1$:

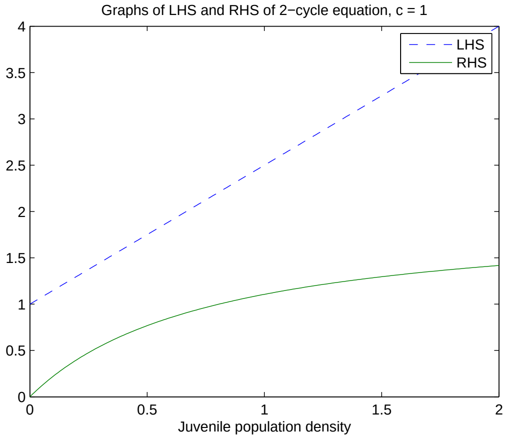

Figure 2.4: $s = 0.5$, $b = 2$, $c = 1$

Again, there is no intersection. However, we try with $c = 4$:

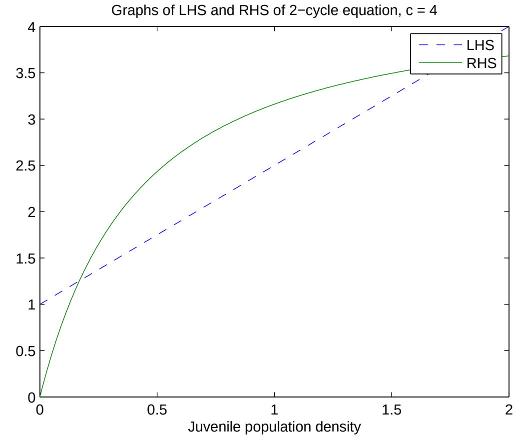

Figure 2.5: $s = 0.5$, $b = 2$, $c = 4$

The graphs once again intersect twice! We have gone from zero 2-cycles to two 2-cycles with increasing c. This time, to find the value of c where we have our saddle-node bifurcation, we solve the 2-cycle equation for c:

$$\begin{aligned} 1 + (1+s)J = bs(1 - e^{-cs\cdot\frac{J}{1+J}}) \quad &\Rightarrow \quad \frac{1+(1+s)J}{bs} = 1 - e^{-cs\cdot\frac{J}{1+J}} \\ &\Rightarrow \quad e^{-cs\cdot\frac{J}{1+J}} = 1 - \frac{1+(1+s)J}{bs} \\ &\Rightarrow \quad -cs\cdot\frac{J}{1+J} = ln(1 - \frac{1+(1+s)J}{bs}) \\ &\Rightarrow \quad -cs = \frac{1+J}{J}\cdot ln\left(1 - \frac{1+(1+s)J}{bs}\right) \\ &\Rightarrow \quad c = -\frac{1+J}{sJ}\cdot ln\left(1 - \frac{1+(1+s)J}{bs}\right). \end{aligned}$$

At first glance, this does not seem like a very illuminating value. But if we recall that $A = s\cdot\frac{J}{1+J}$ and so $J = \frac{A}{s-A}$, we see something interesting:

$$\begin{aligned} c &= -\frac{1+J}{sJ}\cdot ln\left(1 - \frac{1+(1+s)J}{bs}\right) \\ &= -\frac{1}{A}\cdot ln\left(1 - \frac{1+(1+s)\frac{A}{s-A}}{bs}\right) \\ &= -\frac{1}{A}\cdot ln\left(1 - \frac{\frac{s-A+A+sA}{s-A}}{bs}\right) \\ &= -\frac{1}{A}\cdot ln\left(1 - \frac{s(1+A)}{bs(s-A)}\right) \end{aligned}$$

$$= \quad -\frac{ln\left(1 - \frac{1+A}{b(s-A)}\right)}{A}.$$

Our c for the 2-cycle bifurcation is the same as the c for the equilibrium bifurcation! But this is not all. A plausible conjecture as to why the c values are the same is that in fact the equations themselves are the same. Our 2-cycle equation was

$$(1+J) + sJ = bs(1 - e^{-cs\frac{J}{1+J}}). \tag{2.2}$$

Our equilibrium equation was

$$1 + A = b(s-A)(1 - e^{-cA}). \tag{2.3}$$

Recall that $J = \frac{A}{s-A}$. Substituting this in to equation (2.2), we have

$$\left(1 + \frac{A}{s-A}\right) + s\left(\frac{A}{s-A}\right) = bs(1 - e^{-cA}).$$

If we multiply both sides by $s - A$ we get

$$\begin{aligned} s - A + A + sA &= bs(s-A)(1 - e^{-cA}) \\ s(1+A) &= bs(s-A)(1 - e^{-cA}) \\ 1 + A &= b(s-A)(1 - e^{-cA}). \end{aligned}$$

So as it turns out, equation (2.2) and equation (2.3) are the same. So our results from the equilibrium are the same as for the 2-cycle. That is, at a critical point c_{cr}, we go from having zero positive equilibria and zero 2-cycles to having 2 of each, through a saddle-node bifurcation.

2.3 Stability

As we determined before, the origin is always locally stable. Let's briefly examine stability for the 2-cycle case. Recall that our 1-D map looked like

$$m(J) = b \cdot \frac{s \cdot \frac{J}{1+J}}{1 + s \cdot \frac{J}{1+J}}(1 - e^{-cs\cdot\frac{J}{1+J}}).$$

First we will consider the dynamics on the boundary. Since every term of m is increasing with J, we have that $m(J)$ itself is an increasing function. In addition, $m(0) = 0$, and $\lim_{J\to\infty} m(J) = b \cdot \frac{s}{1+s}(1 - e^{-cs})$. If we note that we can rewrite m as

$$m(J) = bJ \cdot \left[\frac{s \cdot \frac{1}{1+J}}{1 + s \cdot \frac{J}{1+J}}(1 - e^{-cs\cdot\frac{J}{1+J}})\right],$$

we can easily use the product rule to determine that $m'(0) = 0$. So since we have two 2-cycles past c_{cr}, and since the origin is stable, the lesser 2-cycle is unstable and the greater 2-cycle is stable.

As far as dynamics on the plane, we know that instability on the boundary implies instability on the plane, so our lesser 2-cycle is unstable on the plane. As for the greater 2-cycle, recall that

$$J = b \cdot \frac{A}{1+A}(1 - e^{-cA}),$$

$$A = s \cdot \frac{J}{1+J}.$$

Thus the Jacobian looks like

$$\Omega = \begin{pmatrix} 0 & \beta \\ \alpha & 0 \end{pmatrix},$$

where $\alpha = s \cdot \frac{1}{(1+J)^2}$ and $\beta = b \cdot \frac{1}{(1+A)^2} \cdot (1 - e^{-cA}) + b \cdot \frac{A}{1+A} \cdot ce^{-cA}$. Thus, our eigenvalues look like $|\lambda| = \sqrt{\alpha\beta}$. We want to know if $|\alpha\beta| < 1$. Unfortunately, this will not be computationally feasible.

However, we conjecture that on the plane (in 2-D), only the greater equilibrium will be stable, and that the lesser equilibrium and both 2-cycles will be unstable.

Chapter 3

Conclusions

We proved that in the case where interclass competition was absent, there was a saddle-node bifurcation that created two equilibria and two 2-cycles. The existence of such a bifurcation implies that there will be a catastrophic collapse in population due to heavy enough predation. That is, with heavy predation ($c < c_{cr}$), the population dies down to extinction at the stable equilibrium at the origin.

In addition, we notice that the presence of a predator creates an Allee effect with a small enough initial population. This means that even if $c > c_{cr}$, very small populations are always in danger of tending toward the trivial equilibrium and extinction.

Finally, and to answer our initial motivating question, predation cannot cause synchronized oscillations. With the absence of inter-class competition and thus the absence of oscillations, predation did not serve to create its own oscillations. That is, there still exist overlapping generations in the population with the presence of a predator.

Bibliography

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