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A STUDY OF THE EFFECT OF DENSITY DEPENDENCE IN A MATRIX POPULATION MODEL

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ABSTRACT. We study the behavior of solutions of a three dimensional discrete time nonlinear matrix population model. We prove results concerning the existence of equilibrium points, boundedness, permanence of solutions, and global stability in special cases of interest. Moreover, numerical simulations are used to compare the dynamics of two main forms of the density dependence function (rational and exponential).

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1. INTRODUCTION

The following form of a discrete time age structured population model was introduced by Greenman et al. in [9].

$$
\begin{cases} x_{n+1} = \Phi z_n \exp\{-(c_1 x_n + c_2 y_n + z_n)\} \\ y_{n+1} = \gamma x_n \\ z_{n+1} = \gamma y_n + \sigma z_n \end{cases} \qquad n = 0, 1, \dots \tag{1.1}
$$

The dynamic variables x_n, y_n and z_n denote the number of juveniles, subadults, and adults, respectively, at time n. The parameter Φ represents the per capita reproduction rate of adults; γ and σ represent per capita survival rates. The parameters c_1 and c_2 measure the contributions of x_n and y_n to the density dependence, respectively [9]. Obviously, a biologically meaningful analysis requires the parameter Φ to be positive and $0 \le c_1, c_2, \gamma, \sigma < 1$. In [9], following the empirical evidence, the authors applied the density dependence only to the reproduction rate (in the first equation of the system).

Structured population models have been analyzed over the years in the literature. A basic mathematical framework for these models can be found in both books (Cushing [3] and Caswell [2]) and articles (Levin and Goodyear [12], Bergh and Getz [1], Silva and Hallam [22] and [23], Dennis et al.[6], Cushing [4], Cushing and Li [5], Neubert and Caswell [20], etc.). Just as there are many paths through which density dependence can enter the model and affect the vital rates [20], there are also quite a few density dependence functions that one can consider [3].

Herein we analyze the behavior of solutions when more general density dependence functions are used in the first equation of system (1.1). We discuss the boundedness, persistence, and stability of the following system.

$$
\begin{cases} x_{n+1} = \Phi z_n G(c_1 x_n + c_2 y_n + z_n) \\ y_{n+1} = \gamma x_n \\ z_{n+1} = \gamma y_n + \sigma z_n \end{cases} \qquad n = 0, 1, \dots \tag{1.2}
$$

with parameters $\Phi > 0$ and $0 \le c_1, c_2, \gamma, \sigma < 1$ and non-negative initial conditions. The density dependence function G is assumed to satisfy all of the following assumptions. We call these assumptions $\mathcal{H}$.

(i) G is a decreasing function in $C^1([0, \infty) \to (0, 1])$.
(ii) There is a real number M such that $wG(w) \le M$ for all $w \in [0, \infty)$.
(iii) $G(0) = 1$.

Condition (ii) essentially requires a certain minimum potency in the density function; it is equivalent to saying that G decreases at least as quickly as the function $f(x) = \frac{M}{x}$, for some M. An important consequence of these conditions is that G is bijective, and therefore there is a function $G^{-1} : (0, 1] \to [0, \infty)$.

While it seems more symmetrical and more general to use $G(c_1 x_n + c_2 y_n + c_3 z_n)$ where $0 \le c_1, c_2, c_3 < 1$, in fact the form $G(c_1 x_n + c_2 y_n + z_n)$ represents no loss in generality (if $c_3 \ne 0$). Any model of the first form can be converted to the second form by the substitutions $z_n \to \frac{z}{c_3}$, $\Phi \to \frac{\Phi}{c_3}$, and $c_3 \to c_3\gamma$. (Note that $c_3\gamma < 1$.)

The particular G used in [9] is $G(x) = e^{-x}$, as in the system (1.1), which we call the exponential model. In the biological literature the exponential nonlinearity is referred to as Ricker nonlinearity. In this paper, we propose an alternative, $G(x) = \frac{1}{1+x}$, which gives rise to a system we call rational (models with this type of rational density dependence are also called Beverton-Holt models). We compare the dynamics of solutions of the rational model with those of the exponential model. For the exponential model, boundedness, persistence, and global stability of trajectories in special cases of interest have been discussed in [21].

The paper is organized as follows. Section 2 deals with the existence of equilibrium points. Section 3 is concerned with the boundedness of solutions. Sections 4 and 5 treat the local and global stability of equilibrium points. Finally numerical simulations are reported in Section 6 and conclusions drawn. Our analysis uses tools from nonlinear difference equations theory to address the local and global stability behavior of solutions. Results concerning stability, periodicity and oscillatory properties of various classes of nonlinear difference equations are given for example in Kocic and Ladas [15], Grove and Ladas [10], Kulenovic and Merino [18]; we list in the Appendix those results we use herein.

2. EQUILIBRIUM POINTS

Equilibrium points $(\bar{x}, \bar{y}, \bar{z})$ are solutions of the following system of three equations.

$$\left\{\begin{array}{l} \bar{x} = \Phi \bar{z} G(c_1 \bar{x} + c_2 \bar{y} + \bar{z}) \\ \bar{y} = \gamma \bar{x} \\ \bar{z} = \gamma \bar{y} + \sigma \bar{z} \end{array}\right. \qquad n = 0, 1, \ldots \tag{2.1}$$

Note that $(0,0,0)$ is always an equilibrium point. If $\bar{x} \neq 0$ then solving for $\bar{x}$ yields

$$\bar{x} = \frac{G^{-1}\big((1-\sigma)/(\Phi\gamma^2)\big)}{c_1 + c_2\gamma + \gamma^2/(1-\sigma)}.$$

Corresponding values for $\bar{y}$ and $\bar{z}$ can be obtained from $\bar{y} = \gamma\bar{x}$ and $\bar{z} = \frac{\gamma^2}{1-\sigma}\bar{x}$. This equilibrium exists when $(1-\sigma)/(\Phi\gamma^2)$ is in the domain of G^{-1}, which is $(0,1]$. However, to ensure that this equilibrium point is positive, we need $G^{-1}\big((1-\sigma)/(\Phi\gamma^2)\big) > 0$, and so we must require $(1-\sigma)/(\Phi\gamma^2) \neq 1$, because $G^{-1}(1) = 0$ by (iii) of $\mathcal{H}$. In fact, under the imposed conditions on G, this positive equilibrium point is unique when it exists.

Herein we may write either $(1-\sigma)/(\Phi\gamma^2) < 1$ or the equivalent $\Phi\gamma^2/(1-\sigma) > 1$, whichever is more convenient in context. Denote $R_0 = \Phi\gamma^2/(1-\sigma)$. R_0 is a bifurcation parameter called the (inherent) net reproductive number or *"the expected number of offspring per individual per lifetime"* (see [3], p7). The positive equilibria for the two models analyzed herein are shown below.

Exponential (Ricker)	Rational (Beverton-Holt)
$G(x) = e^{-x}$	$G(x) = \dfrac{1}{1+x}$
$G^{-1}(x) = -\ln x$	$G^{-1}(x) = \dfrac{1}{x} - 1$
$\bar{x} = \dfrac{\ln\big(\Phi\gamma^2/(1-\sigma)\big)}{c_1 + c_2\gamma + \gamma^2/(1-\sigma)}$	$\bar{x} = \dfrac{\Phi\gamma^2/(1-\sigma) - 1}{c_1 + c_2\gamma + \gamma^2/(1-\sigma)}$

3. BOUNDEDNESS AND PERMANENCE

3.1. **Boundedness.** It is important, as part of determining the utility of a model, to ensure that it never predicts an unbounded explosion in the population. Therefore we prove that every trajectory enters and remains in a closed region. Using similar techniques as in [21], the following lemma demonstrates boundedness for solutions of the system (1.2).

Lemma 3.1. *Assume that hypotheses $\mathcal{H}$ hold. The compact set*

$$[0, \Phi M] \times [0, \gamma\Phi M] \times [0, \gamma^2\Phi M/(1-\sigma)]$$

is invariant and attracting in $\mathbb{R}^3$.

Proof. We show invariance first. Take (x_N, y_N, z_N) in the compact set just described, for some N. Then

$$\begin{aligned} x_{N+1} &= \Phi z_N G(c_1 x_N + c_2 y_N + z_N) && \text{first equation in (1.2)} \\ &\le \Phi z_N G(z_N) && \text{(i) of } \mathcal{H} \\ &\le \Phi M && \text{(ii) of } \mathcal{H} \end{aligned}$$

From the second equation, $y_{N+1} = \gamma x_{N+1} \le \gamma\Phi M$. Finally, using the z-boundaries of the compact set gives

$$z_{N+1} = \gamma y_N + \sigma z_N \le \gamma^2\Phi M + \sigma\frac{\gamma^2\Phi M}{1-\sigma} = \gamma^2\Phi M\left(1 + \frac{\sigma}{1-\sigma}\right) = \frac{\gamma^2\Phi M}{1-\sigma}.$$

Thus the set is invariant.

Next we show that the region is also attracting. Note that since $0 \le \gamma < 1$ from the second equation in (1.2), we have $0 \le y_{n+1} < x_n$ for any $n \ge 0$. If $(x_n)_{n\ge 0}$ is bounded then consequently $(y_n)_{n\ge 0}$ is bounded. And as stated in invariance proof just given, $x_{n+1} \le \Phi M$ for every n, so $\limsup\limits_{n\to\infty} x_n \le \Phi M$. For convenience, say $\limsup\limits_{n\to\infty} x_n = r\Phi M$, with $0 \le r \le 1$, and therefore

$$0 \le \limsup_{n\to\infty} y_n \le r\gamma\Phi M < \infty.$$

From the third equation in (1.2), $z_{n+1} = \sigma z_n + \gamma y_n$, we obtain that for every $\varepsilon > 0$, there is some $N_\varepsilon \ge 0$ such that $z_{n+1} \le \sigma z_n + r\gamma^2\Phi M + \varepsilon$ for all $n \ge N_\varepsilon$. Because $\limsup_{n\to\infty} z_n = \limsup_{n\to\infty} z_{n+1}$, we have $\limsup_{n\to\infty} z_n \le \dfrac{r\gamma^2\Phi M + \varepsilon}{1-\sigma}$. But $\varepsilon > 0$ is arbitrary and $0 \le r \le 1$ and thus

$$\limsup_{n\to\infty} z_n \le \frac{\gamma^2\Phi M}{1-\sigma},$$

as desired. ∎

3.2. **Permanence.** We look at the total population survival, expressed mathematically by the concept of p-permanence (see Definition 8.1 in the Appendix, Section 8). In fact, the p-permanence definition used here incorporates two parts: (1) survival of the total population in the long run and (2) boundedness of the population. Studies of permanence can be found, for example, in [2, 16, 17, 19].

Remark 3.1. The system (1.2) is p-permanent when $(\Phi\gamma^2)/(1-\sigma) > 1$.

To demonstrate this remark, we will apply Theorem 8.1 from the Appendix. That theorem requires that our system be dissipative (Definition 8.2) and forward invariant on $\mathbb{R}^3_+$, and that A_0 be irreducible and have a dominant eigenvalue greater than 1. We establish each of these four criteria in the following paragraphs.

The system is dissipative because from Lemma 3.1,

$$\limsup_{n\to\infty}(x_n + y_n + z_n) \le \frac{\gamma^2 M\Phi}{1-\sigma} + \gamma M\Phi + M\Phi.$$

If we let $D = \gamma^2 M\Phi/(1-\sigma) + \gamma M\Phi + M\Phi$ (here $0 < M < \infty$ and thus $0 < D < \infty$), then system (1.2) is dissipative according to Definition 8.2.

Forward invariance is straightforward from the equations in (1.2) and the fact that G is always positive.

Because $A_{\mathbf{0}}$ is nonnegative and the matrix $(I_3 + A_{\mathbf{0}})^2$ has all entries positive, it follows from Theorem 8.2 that $A_{\mathbf{0}}$ is irreducible. The matrix $A_{\mathbf{0}}$ is nonnegative and irreducible, and therefore the Perron-Frobenius Theorem ([7, 8]) (see also [3]) guarantees that $A_{\mathbf{0}}$ possesses a positive eigenvalue with magnitude greater than or equal to all other existing eigenvalues. Its eigenvalues are the roots of

$$P(\lambda) = \lambda^3 - \sigma\lambda^2 - \Phi\gamma^2.$$

We have $\lim\limits_{\lambda\to\infty} P(\lambda) = \infty$, and thus if $P(1) < 0$ we can guarantee a root grater than 1. Because $P(1) = 1 - \sigma - \Phi\gamma^2$, we have that $P(1) < 0$ just when $\Phi\gamma^2/(1-\sigma) > 1$. Therefore when $\Phi\gamma^2/(1-\sigma) > 1$, by Theorem 8.1 system (1.2) is p-permanent, guaranteeing both survival and boundedness. Moreover when $(\Phi\gamma^2)/(1-\sigma) > 1$, no solutions tend to the $(0,0,0)$ equilibrium.

4. STABILITY OF EQUILIBRIUM POINTS

We view system (1.2) in a matrix form:

$$\mathbf{X}_{n+1} = A_{X_n}\mathbf{X}_n \tag{4.1}$$

where $n = 0, 1, 2, \ldots$ and $\mathbf{X}_n = (x_n, y_n, z_n)^T$. The entries of matrix A_{X_n} are denoted by a_{ij} and they are continous functions of x_n, y_n and z_n. The nonlinear matrix structure is

$$A_{\mathbf{X}} = \begin{pmatrix} 0 & 0 & \Phi G(c_1x + c_2y + z) \\ \gamma & 0 & 0 \\ 0 & \gamma & \sigma \end{pmatrix} \text{and} \quad X = \begin{pmatrix} x \\ y \\ z \end{pmatrix}$$

The matrix $A_{\mathbf{X}}$ has all entries nonnegative and

$$A_{\mathbf{0}} = \mathbf{J}_{(0,0,0)} = \begin{pmatrix} 0 & 0 & \Phi \\ \gamma & 0 & 0 \\ 0 & \gamma & \sigma \end{pmatrix}.$$

The characteristic equation associated with $(0,0,0)$ is

$$\lambda^3 - \sigma\lambda^2 - \Phi\gamma^2 = 0. \tag{4.2}$$

Let g stands for the expression $G'(c_1\bar{x} + c_2\bar{y} + \bar{z})$, which can be evaluated for the specific model in advance, based only on G and the model parameters c_1 and c_2. The characteristic equation about the positive equilibrium is

$$\begin{aligned} \lambda^3 + (-\sigma - \Phi\bar{z}c_1g)\lambda^2 + (\sigma\Phi\bar{z}c_1g - \gamma\Phi\bar{z}c_2g)\lambda \\ + (\gamma\sigma\Phi\bar{z}c_2g - \gamma^2\Phi\bar{z}g - 1 + \sigma) = 0. \end{aligned} \tag{4.3}$$

Using the Schur Cohn criteria (see Appendix), the local asymptotic stability of the positive equilibrium is given by the intersection of the conditions below. Criterion (i) becomes equivalent to

$$\Phi\bar{z}\Big[-(\sigma+1)c_1 + \gamma(\sigma+1)c_2 - \gamma^2\Big]g < 2. \tag{4.4}$$

Criterion (ii) becomes equivalent to the conjunction of

$$\Phi\bar{z}\Big[(3\gamma^2 - 3\sigma\gamma c_2 - c_1) + (\sigma c_1 - \gamma c_2)\Big]g < 4\sigma \tag{4.5}$$

and

$$\Phi\bar{z}\Big[(3\gamma^2 - 3\sigma\gamma c_2 - c_1) - (\sigma c_1 - \gamma c_2)\Big]g > 4\sigma - 6. \tag{4.6}$$

More algebraic manipulations of criterion (iii) yield the following equivalent expression.

$$\begin{aligned}(4.7)\quad \Phi^2\bar{z}^2\Big[\gamma^4 - 2\gamma^3\sigma c_2 + \gamma^2\sigma^2 c_2^2 - \gamma^2 c_1 + \gamma\sigma c_1 c_2\Big]g^2 \\ + \Phi\bar{z}\Big[2\gamma^2 + 3\gamma\sigma^2 c_2 - 3\gamma^2\sigma - 2\gamma\sigma c_2 + 2\sigma c_1 - \gamma c_2 - c_1\Big]g \\ + [2\sigma^2 - 3\sigma + 1] < 1\end{aligned}$$

From a specific function G, such as the rational or exponential examples studied herein, one can obtain amenable conditions for local asymptotic stability of the positive equilibrium $(\bar{x}, \bar{y}, \bar{z})$. This has been done for the exponential model in [21], and one could do a similar analysis for the rational model, but that is not our purpose here. Explicit calculations of the LAS boundaries for a different model (the LPA, flour beetle model) were done in [3].

4.1. Global Asymptotic Stability of the Extinction Equilibrium.

Our analysis of the global asymptotic stability of the extinction equilibrium point is summarized in the following theorem:

Theorem 4.1. *Assume conditions $\mathcal{H}$ hold and the model parameters, in addition to satisfying the criteria from Section 1, also satisfy $\sigma \neq 0$ and $\Phi\gamma^2/(1-\sigma) < 1$. Then the extinction equilibrium $(0,0,0)$ of system (1.2) is globally asymptotically stable.*

Proof. Local stability follows by checking the Schur Cohn criteria (i) through (iii) (see Appendix) with $a_0 = -\Phi\gamma^2$, $a_1 = 0$, and $a_2 = -\sigma$ using algebra; we therefore do not show the verification here. It suffices to show that $(0,0,0)$ is a global attractor. Suppose $(x_n, y_n, z_n)_{n\geq 0}$ is a non-negative solution of system (1.2). We prove that $\lim_{n\to\infty}(x_n, y_n, z_n) = (0,0,0)$. From the first equation of (1.2) and (i) of $\mathcal{H}$,

$$x_{n+1} = \Phi z_n G(c_1 x_n + c_2 y_n + z_n) \leq \Phi z_n. \tag{4.8}$$

The second and third equations of (1.2) give $z_{n+1} = \gamma^2 x_{n-1} + \sigma z_n$, and by (4.8) therefore $z_{n+1} \leq \gamma^2\Phi z_{n-2} + \sigma z_n$ for any $n \geq 2$. Now consider the difference equation

$$r_{n+1} = \gamma^2\Phi r_{n-2} + \sigma r_n \qquad n = 0, 1, 2, \ldots \tag{4.9}$$

with $r_{-2} = z_{-2}$, $r_{-1} = z_{-1}$ and $r_0 = z_0$. By induction $z_{n+1} \leq r_{n+1}$ for all $n \geq 0$. Equation (4.9) is of the appropriate form for Theorem 8.5 in the Appendix and it satisfies all that theorem's hypotheses. Theorem 8.5 tells us that $\lim_{n\to\infty} r_n = 0$ and thus $\lim_{n\to\infty} z_n = 0$. By (4.8) we get $\lim_{n\to\infty} x_n = 0$. Taking the limit in the second equation of system (1.2) therefore gives $\lim_{n\to\infty} y_n = 0$ also. ∎

5. Global Attractivity of the Positive Equilibrium. Special Cases

In addition to the previous section's analysis of the extinction equilibrium, this section addresses the positive equilibrium. We find sufficient conditions in the parameter space where the trajectories of the rational system converge to the equilibrium. While global attractivity results for systems are quite rare, at the moment we can provide analytical proofs for only a few special cases of interest of the rational model. Case 1 assumes $c_1 = c_2 = 0$, meaning that the younger members of the population (newborns and juveniles) do not impact density dependence. Case 2 assumes $c_1 = 0$ and $c_2 > 0$, meaning that newborns do not impact density dependence, but juveniles do, though generally to a lesser degree than adults. It is worth noting that the positive equilibrium is not locally asymptotically stable for all values of the parameters for which

$(\Phi\gamma^2)/(1-\sigma) > 1$. Computer simulations in the following section complement this analysis. Let us consider Case 1 first. The rational system becomes the following.

$$\begin{cases} x_{n+1} = \Phi z_n/(1+z_n) \\ y_{n+1} = \gamma x_n \\ z_{n+1} = \gamma y_n + \sigma z_n \end{cases} \qquad n = 0, 1, \dots \tag{5.1}$$

In the discussion of global stability of solutions in cases (1 and 2), we make use of the remark that when $(\Phi\gamma^2)/(1-\sigma) > 1$, the populations will never approach the zero equilibrium.

One can see as follows that the solutions are bounded. From the first equation, $0 < x_{n+1} \leq \Phi$ for $n \geq 0$, and the second equation then gives $0 < y_{n+1} \leq \gamma\Phi$. Using the third equation and $0 < \sigma < 1$ we get $\limsup_{n\to\infty} z_n \leq \gamma^2\Phi/(1-\sigma)$. Then using the equations in (5.1) for substitution, we have

$$z_{n+1} = \gamma y_n + \sigma z_n = \gamma x_{n-1} + \sigma z_n = \frac{\gamma^2 \Phi z_{n-2}}{1+z_{n-2}} + \sigma z_n.$$

Thus in this case we are dealing with the functional equation

$$z_{t+1} = \sigma z_t + \frac{\gamma^2 \Phi z_{t-2}}{1+z_{t-2}}, \tag{5.2}$$

The next theorem gives sufficient conditions for positive equilibrium of equation (5.2) to be globally asymptotically stable.

Theorem 5.1. *Suppose* $\Phi > 0$, $0 < \gamma, \sigma < 1$ *and* $1-\sigma < \gamma^2\Phi \leq (1-\sigma)/(1-\sigma^3)$. *Then the positive solutions of equation* (5.2) *have the property that*

$$\lim_{t\to\infty} z_t = \bar{z} = \frac{\gamma^2\Phi}{1-\sigma} - 1.$$

In fact, the positive equilibrium $\bar{z}$ *is globally asymptotically stable.*

This lemma is illustrated in Figure 1. Four randomly generated rational models are shown, each satisfying the hypotheses of Theorem 5.1, and their convergence shown using a dashed line to indicate the value for total population that corresponds to the $\bar{z}$ to which the lemma states that the model converges.

Proof. We prove that $\bar{z}$ is locally stable and a global attractor. The local stability is done by verifying conditions (4.4) through (4.7) (using the above assumptions together with $c_1 = c_2 = 0$). Note that $g = G'(\bar{z}) = -\left(\frac{1-\sigma}{\gamma^2\Phi}\right)^2$. Since g is negative, condition (4.5) is always satisfied. After replacing g, equation (4.4) is equivalent to $\Phi\left(\frac{\gamma^2\Phi}{1-\sigma} - 1\right)\frac{\gamma^2}{(\frac{\gamma^2\Phi}{1-\sigma})^2} < 2$ which after algebraic manipulations, it changes into

$$(1-\sigma) - \frac{(1-\sigma)^2}{\gamma^2\Phi} < 2.$$

By hypothesis, we have that $-(1-\sigma^3) \geq -\frac{1-\sigma}{\gamma^2\Phi}$. Thus

$$(1-\sigma) - \frac{(1-\sigma)^2}{\gamma^2\Phi} \leq (1-\sigma) - (1-\sigma)(1-\sigma^3) = \sigma^3 - \sigma^4 < 2$$

and inequality (4.4) holds true within the specified hypotheses. Now, let us check condition (4.6). Replacing g and simplifying out, one gets

$$3(1-\sigma) - \frac{3(1-\sigma)^2}{\gamma^2\Phi} < 6 - 4\sigma$$

or equivalently into $-\dfrac{3(1-\sigma)^2}{\gamma^2\Phi} < 3-\sigma$. Since $0<\sigma<1$ then the left side is always negative and the right always positive, so the inequality is always true and condition (4.6) is verified.

The only condition which remains to verify is (4.7), which when $c_1 = c_2 = 0$ simplifies to

$$\Phi^2\bar{z}^2\gamma^4 g^2 + \Phi\bar{z}(2\gamma^2 - 3\gamma^2\sigma)g + 2\sigma^2 - 3\sigma < 0.$$

Substituting in the expressions for g and $\bar{z}$ used earlier in this proof gives a longer inequality, but it can be simplified and factored to yield

$$\left[\frac{1}{\gamma^2\Phi}\left(\frac{\gamma^2\Phi}{1-\sigma} - 1\right)(1-\sigma)^2\right]\left[\frac{(1-\sigma)^2}{\gamma^2\Phi}\left(\frac{\gamma^2\Phi}{1-\sigma} - 1\right) - (2-3\sigma)\right] + \sigma(2\sigma-3) < 0.$$

Notice that the left of the two brackets in this equation is a product of positive quantities, and thus must be positive. However it can also be simplified, as can the second bracket, to yield the following more manageable inequality.

$$\left[1-\sigma-\frac{(1-\sigma)^2}{\gamma^2\Phi}\right]\left[1-\sigma-\frac{(1-\sigma)^2}{\gamma^2\Phi} + (-2+3\sigma)\right] + \sigma(2\sigma-3) < 0. \tag{5.3}$$

Notice that the quantity which appears twice in (5.3), $1-\sigma-\frac{(1-\sigma)^2}{\gamma^2\Phi}$, is clearly less than $1-\sigma$, and thus the inequality (5.3) will be true as long as the following one is.

$$[1-\sigma][1-\sigma+(-2+3\sigma)] + \sigma(2\sigma-3) < 0.$$

However, multiplying out the left hand side of this inequality and combining terms reveals that the entire left hand side simplifies to -1 (which is obviously less than 0).

The last fact to establish is that $\bar{z}$ is a global attractor. Let $(z_t)_{t\geq -2}$ be a positive solution of (5.2). Now, it suffices to show that $\lim_{t\to\infty} z_t = \bar{z}$. This follows from Theorem 8.6 and the analysis that follows it in [14] (p. 1083) with $\lambda = \sigma$, $\beta = \gamma^2\Phi$, $m = 2$, and $r = 1$. ∎

Let us consider Case 2 now. When $c_1 = 0$ and $c_2 > 0$, the rational system becomes the following.

$$\begin{cases} x_{n+1} = \Phi z_n/(1 + c_2 y_n + z_n) \\ y_{n+1} = \gamma x_n \\ z_{n+1} = \gamma y_n + \sigma z_n \end{cases} \qquad n = 0, 1, \ldots \tag{5.4}$$

We could repeat an analysis very similar to that for Case 1 to show that $(z_n)_{n\geq 0}$ is bounded. The positive equilibrium point of (5.4) is

$$\bar{z} = \left(\frac{\gamma^2\Phi}{1-\sigma} - 1\right)/\left(\frac{c_2(1-\sigma)}{\gamma} + 1\right) \tag{5.5}$$

With respect to this equilibrium point we have the following lemma.

Theorem 5.2. *Suppose* $\Phi > 0$, $0 \leq c_2, \gamma, \sigma < 1$, $\gamma^2\Phi/(1-\sigma) > 1$ *and* $c_2(1+\sigma)/\gamma < 1$. *Then the positive trajectories of* (5.4) *converge to the positive equilibrium* $\bar{z}$.

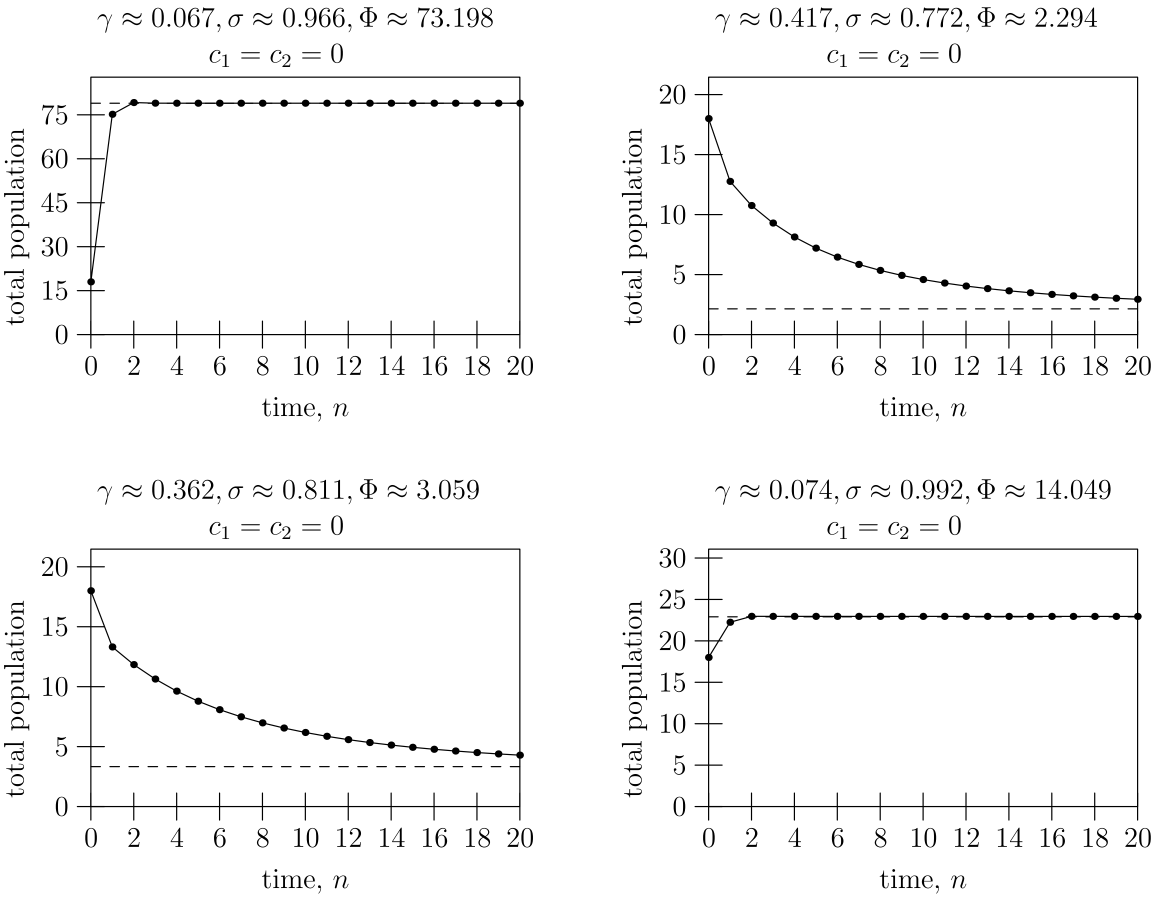

Figure 1: Time series diagrams for four rational models satisfying the hypotheses of Theorem 5.1, and therefore converging to positive equilibria.

This lemma is illustrated in Figure 2. Four randomly generated rational models are shown, each satisfying the hypotheses of Theorem 5.2, and their convergence shown using a dashed line to indicate the value for total population that corresponds to the $\bar{z}$ to which the lemma states that the model converges.

Proof. In the sequel we prove that the positive equilibrium is a global attractor. Algebraic manipulation and substitution applied to (5.4) changes that system into

$$z_{t+1} = \sigma z_t + \frac{\gamma^2 \Phi z_{t-2}}{1 + (c_2/\gamma) z_{t-1} + (1 - c_2\sigma/\gamma) z_{t-2}}. \tag{5.6}$$

We introduce the assumption $1 - c_2\sigma/\gamma > 0$ to ensure that the number of adults will always be positive. (Note that $c_2\sigma/\gamma < c_2(1+\sigma)/\gamma < 1$.) The map associated with the above scalar equation,

$$f(u, v, w) = \sigma w + \frac{\gamma^2 \Phi u}{1 + (c_2/\gamma) v + (1 - c_2\sigma/\gamma) u},$$

is monotonic in each of its arguments (increasing in u, decreasing in v and increasing in w.) It follows by Theorem 8.4 that there exist solutions $\{I_n\}_{n=-\infty}^{\infty}$ and $\{S_n\}_{n=-\infty}^{\infty}$ of the difference equation (5.6) with $I_0 = I$ and $S_0 = S$ such that for all integers n, $I \leq I_n \leq S$ and $I \leq S_n \leq S$.

Thus

$$I = I_0 = \sigma I_{-1} + \frac{\gamma^2 \Phi I_{-3}}{1 + (c_2/\gamma) I_{-2} + (1 - c_2\sigma/\gamma) I_{-3}}$$
$$\geq \sigma I + \frac{\gamma^2 \Phi I}{1 + (c_2/\gamma) S + (1 - c_2\sigma/\gamma) I}.$$

The above inequality is equivalent to

$$(5.7) \qquad (1-\sigma) I \geq \frac{\gamma^2 \Phi I}{1 + (c_2/\gamma) S + (1 - c_2\sigma/\gamma) I}.$$

On the other hand,

$$S = S_0 = \sigma S_{-1} + \frac{\gamma^2 \Phi S_{-3}}{1 + (c_2/\gamma) S_{-2} + (1 - c_2\sigma/\gamma) S_{-3}}$$
$$\leq \sigma S + \frac{\gamma^2 \Phi S}{1 + (c_2/\gamma) I + (1 - c_2\sigma/\gamma) S},$$

which is equivalent to

$$(5.8) \qquad (1-\sigma) S \leq \frac{\gamma^2 \Phi S}{1 + (c_2/\gamma) I + (1 - c_2\sigma/\gamma) S}.$$

According to our discussion in the permanence section, under the conditions in the hypothesis we have that $S > I > 0$. Then using inequalities (5.7) and (5.8) we get

$$(5.9) \quad (1-\sigma)(1 + (c_2/\gamma)S + (1 - c_2\sigma/\gamma)I) \geq \gamma^2\Phi$$
$$\geq (1-\sigma)(1 + (c_2/\gamma)I + (1 - c_2\sigma/\gamma)S).$$

Since $0 < \sigma < 1$, the above equation gives $(c_2\sigma/\gamma + c_2/\gamma - 1)(S - I) \geq 0$. But $c_2(1+\sigma)/\gamma < 1$ and therefore $I \geq S$ and the conclusion follows. ∎

6. COMPUTER SIMULATIONS

We complement the preceding analytical work with a set of numerical experiments designed with one goal in mind. We show that the rational model is in general more stable than the exponential one. This may be of interest for biologists, suggesting the rational model as a better alternative for designing various policies interventions or obtaining a less oscillatory behavior of the solutions.

Greenman et al. [9] studied the system (1.1) and found it to be too often periodic, stating "*a much broader range of oscillatory behavior than seen in nature is theoretically possible*." We show here that the rational model has a much more stable character, particularly when it comes to periodicity and oscillatory behavior. For this reason, we propose the rational model as an alternative that is more faithful to data observed in nature. In the previous sections, we also detected analytically regions in the parameter space where the solutions are stable.

In order to verify that the rational model is more often stable, we consider the convergence of the orbits by looking into two sub-cases: one for small values of Φ (representing organisms that have small numbers of offspring at a time, such as mammals) and another for larger values of Φ (representing organisms that have large numbers of offspring at a time, such as fish). This yields four cases in all, and in each, we sampled one million random models from parameter space and evaluated the stability of the model. Random models were generated by selecting γ, σ, c_1, and c_2 from a uniform distribution on $[0, 1]$ and selecting Φ from a normal distribution. For small Φ we used $\mu = 8, \sigma = 3$, and for large Φ we used $\mu = 40, \sigma = 10$. (In the rare case

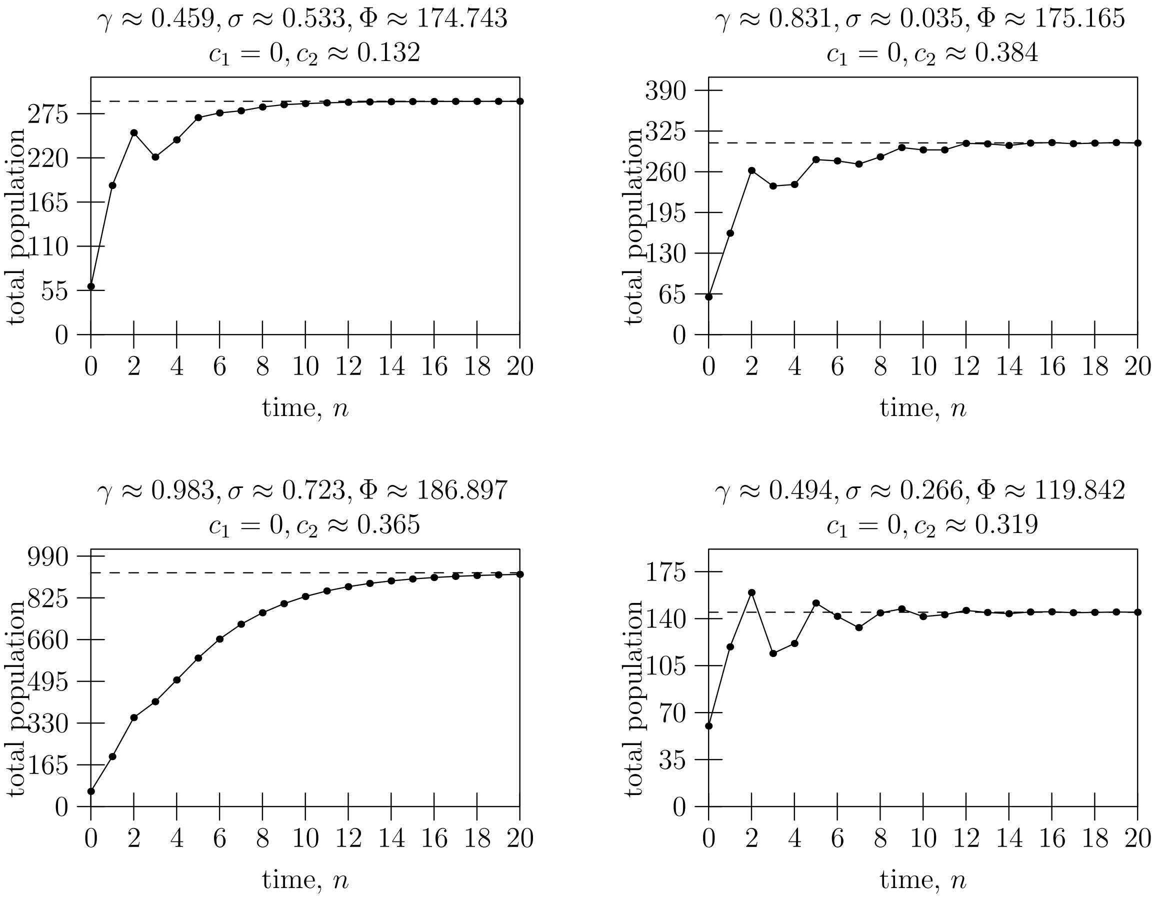

Figure 2: Time series diagrams for four rational models satisfying the hypotheses of Theorem 5.2, and therefore converging to positive equilibria.

when a $\Phi < 0$ was generated, it was discarded and a new Φ chosen from the same distribution to replace it.)

The results are summarized in Table 6.1. It becomes clear that for small values of Φ, the difference between the rational and exponential models is small, but for large values of Φ it is more significant. When Φ values are chosen from a normal distribution with $\mu = 8, \sigma = 3$ (95% of values therefore between 2 and 14), global asymptotic stability happens an additional 4.06% for rational models. When the distribution parameters are larger, $\mu = 40, \sigma = 10$ (95% of values therefore between 20 and 60), we notice a drastic difference. The rational model is globally stable more than 95% of the time, whereas both these values for the exponential model are only about 57%. Thus the greater stability of the rational models is more pronounced for larger Φ.

To see this difference illustrated, compare the chaotic portions of the bifurcation diagram of the exponential model in Figure 3 with the ordered bifurcation diagrams of rational models shown in Figure 4.

7. CONCLUSIONS

We have generalized an age-structured population model and analyzed the boundedness, permanence, and stability properties of the general form. Some of our results hold for any specific model created from the general form (1.2). Global stability results were established for some

	Exponential models		Rational models	
	small Φ	large Φ	small Φ	large Φ
Global asymptotic stability				
Converge to extinction	18.78%	8.84%	18.78%	8.84%
Converge to positive	75.46%	48.01%	79.52%	86.33%
Total	94.24%	56.85%	98.30%	95.17%

Table 6.1: Comparison of local and global asymptotic stability for exponential and rational models, separated into small Φ *(those chosen from a normal distribution with* $\mu = 8, \sigma = 3$*) and large* Φ *(*$\mu = 40, \sigma = 10$*).*

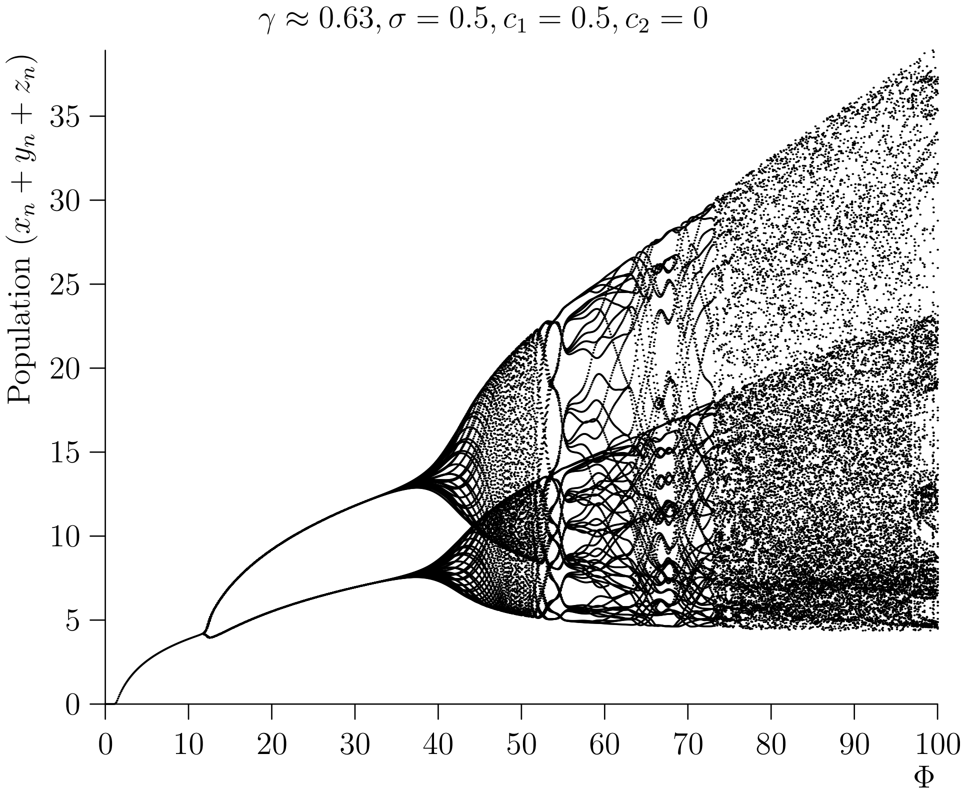

Figure 3: A bifurcation diagram of an exponential model, showing signs of chaotic behavior. The first 100 iterations from the initial point $(10, 20, 30)$ *were discarded, and the next 70 plotted.*

special cases. We have also suggested a rational form of the model and given evidence for why it is more often stable, and therefore more biologically reasonable than the exponential model in existence. The results herein build a good foundation for further study of other forms of the general model.

8. Appendix

In this appendix we include some background material for convenient reference, including notation, definitions, and theorems used earlier in this paper.

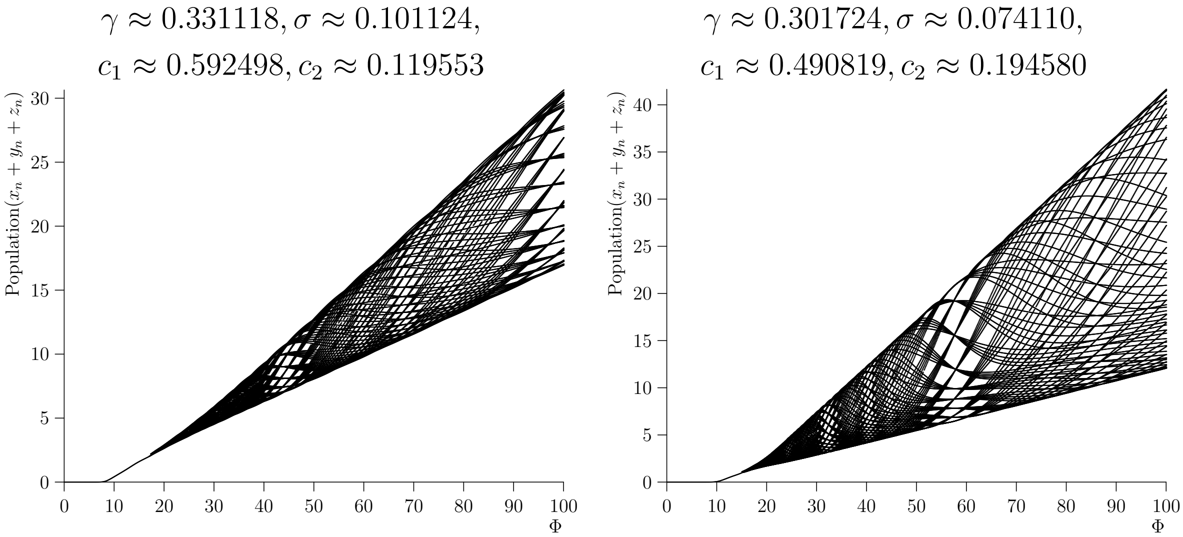

Figure 4: Two bifurcation diagrams of periodic rational models. In each, the first 100 iterations from the initial point $(10, 20, 30)$ *were discarded, and the next 70 plotted.*

We begin with a definition of *permanence*. This is the mathematical term for population survival [16]. The following two definitions are extracted from [16] (p. 618). The nonnegative cone (the set of points in $\mathbb{R}^3$ with $x_n \geq 0, y_n \geq 0, z_n \geq 0$) is denoted by $\mathbb{R}^n_+$.

Definition 8.1. System (4.1) is said to be p*-permanent* if there exist positive constants $\delta > 0$ and $D > 0$ such that

$$\delta \leq \liminf_{n\to\infty}(x_n + y_n + z_n) \leq \limsup_{n\to\infty}(x_n + y_n + z_n) \leq D$$

for all solutions with initial conditions in $\mathbb{R}^3_+ - \{(0, 0, 0)\}$

Definition 8.2. System (4.1) is said to be *dissipative* if there exists a positive constant $D > 0$ such that $\limsup_{n\to\infty}(x_n + y_n + z_n) \leq D$ for all solutions with nonegative initial conditions.

The next theorem (which is Theorem 3 in [17] or Theorem 3.2 in [16]) is used to prove permanence in structured population models; we use it in Section 3.

Theorem 8.1 ([16, 17])**.** *Suppose system* (4.1) *is continous and dissipative. Assume the matrix* $A_{\mathbf{0}}$ *is irreducible and* $A_{\mathbf{X}}\mathbf{X} \in \mathbb{R}^3_+ - \{(0, 0, 0)\}$ *for all* $\mathbf{X} \in \mathbb{R}^3_+ - \{(0, 0, 0)\}$*. System* (4.1) *is permanent if* $A_{\mathbf{0}}$ *has an eigenvalue* λ *with* $|\lambda| > 1$ *(i.e the magnitude of the dominant eigenvalue of* $A_{\mathbf{0}}$ *is greater than one).*

An easily verifiable condition for a matrix to be irreducible is given in [24], p.6.

Theorem 8.2 ([24])**.** A *is a nonnegative irreducible* $n \times n$ *matrix if and only if* $(I_n + A)^{n-1} > 0$.

Schur Cohn criterium (extracted from [18], p.212), is very useful in proving local asymptotic stability.

Lemma 8.3 ([18], p.214)**.** *Necessary and sufficient conditions for all the roots of* $\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0$ *to lie in the open unit disc are*

(i) $|a_2 + a_0| < 1 + a_1$,
(ii) $|a_2 - 3a_0| < 3 - a_1$, *and*
(iii) $a_0^2 + a_1 - a_0 a_2 < 1$.

The following result, due to Karakostas, is instrumental in proving global attractivity results. We use it in Theorem 5.2.

Theorem 8.4 ([13]). *Let $\{x_n\}_{n=-k}^{\infty}$ be a solution to the difference equation*

$$x_{n+1} = f(x_n, \ldots, x_{n-k}).$$

Set $I = \liminf_{n\to\infty} x_n$ and $S = \limsup_{n\to\infty} x_n$, and suppose that $I, S \in J$. Let $\mathcal{L}_0$ be a limit point of the sequence $\{x_n\}_{n=-k}^{\infty}$. Then the following statements are true.

1. *There exists a solution $\{L_n\}_{n=-\infty}^{\infty}$ for the difference equation, called a full limiting sequence of $\{x_n\}_{n=-k}^{\infty}$, such that $L_0 = \mathcal{L}_0$, and such that for every $N \in \{\ldots, -1, 0, 1, \ldots\}$, L_N is a limit point of $\{x_n\}_{n=-k}^{\infty}$. In particular,*
$$I \le L_N \le S \quad \text{for all} \quad N \in \{\ldots, -1, 0, 1, \ldots\}.$$
2. *For every $i_0 \in \{\ldots, -1, 0, 1, \ldots\}$, there exists a subsequence $\{x_{r_i}\}_{i=0}^{\infty}$ of $\{x_n\}_{n=-k}^{\infty}$ such that*
$$L_N = \lim_{i\to\infty} x_{r_i+N} \quad \text{for every} \quad N \ge i_0.$$

The following theorem is helpful in proving global asymptotic stability of the extinction equilibrium.

Theorem 8.5 ([11]). *Consider the difference equation*

$$r_{n+1} = \sum_{i=0}^{k} r_{n-i} F_i(r_n, r_{n-1}, \ldots r_{n-k}),$$

$n = 0, 1, \ldots$ with non-negative initial conditions, and assume further that

1. *$k \in \{0, 1, \ldots\}$,*
2. *$F_0, F_1, \ldots F_k \in C([0,\infty)^{k+1} \to [0,1))$,*
3. *$F_0, F_1, \ldots F_k$ are non-increasing in each argument;*
4. *$\sum_{i=0}^{k} F_i(r_0, r_1, \ldots, r_k) < 1$, for all $(r_0, r_1, \ldots r_k) \in (0,\infty)^{k+1}$, and*
5. *$F_0(r, r, \ldots, r) > 0$ for all $r \ge 0$.*

Then $\bar{r} = 0$ is globally asymptotically stable.

The next theorem is given as Theorem 2 in [14] and it turns out to be useful in proving global attractivity results, especially for all positive solutions of the difference equation of the form

$$z_{n+1} = \lambda z_n + F(z_{n-m}), \tag{8.1}$$

where $0 < \lambda < 1$, m is a positive integer, and F is a nonnegative real valued function defined on $\mathbb{R}_+$.

Theorem 8.6 ([14], p. 1076). *Assume that $F = fg$ where f is continous, positive and decreasing function on $\mathbb{R}_+$ and g is a continuous and increasing function on $\mathbb{R}_+$ with $g(0) \ge 0$ and $g(y) > 0$ for $y > 0$. Assume also that the functions f and g satisfy (i) and (ii), where $\delta = (1-\lambda)/f(0)$ and G is the generalized inverse of G, namely $G(z) = min w \ge 0 : g(w) \ge z$ for $z \ge 0$. Moreover, suppose that the algebraic equation $K = \lambda K + F(K)$ has a unique positive root K. Finally, suppose that f and g are differentiable on $(0,\infty)$, f' is increasing on $(0,\infty)$, g' is decreasing in $(0,\infty)$, and*

$$f(y)g'(y) - f'(y)g(y) < \frac{1-\lambda}{1-\lambda^{m+1}}$$

for all $y \in (0, K]$. Then any positive solution $(z_n)_{n\ge -m}$ of the difference equation (8.1) satisfies $\lim_{n\to\infty} z_n = K$.

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