

**Proceedings of the
First International Conference
on Difference Equations**

Trinity University, San Antonio, Texas
May 25–28, 1994

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Systems of Difference Equations and Structured Population Dynamics

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July 1, 1994

(Revised)

Abstract

The methodology for modeling the dynamics of discretely structured populations is outlined. General results for the existence and stability of equilibria are given from a bifurcation theory point of view using the inherent net reproductive number as a bifurcation parameter. A general persistence result is also proved. These results are applied to a stage structured model for flour beetles.

1 Introduction

Systems of difference equations, or matrix equations, have a long tradition of use as models in populations dynamics since their utilization by Lewis [12] and Leslie [11]. The desire to relate mathematical models for population level dynamics to the physiological characteristics of individual organisms, and hence more closely to biological data, has greatly increased interest in linear and nonlinear matrix models (e.g. see [1], [10]). Matrix models classify individuals into a finite number of categories whose dynamics are modeled in discrete time. Age-structured models are the most common, although the importance of size-structured and stage-structured models is widely recognized.

In Section 2 the modeling methodology for general matrix models is briefly summarized. In Section 3 a synthesis of a treatment of the existence and stability of

equilibria for general nonlinear matrix models from the bifurcation theory point of view taken in [2], [4], [3], and [5] is given together with some new results, including a general persistence result. In the final Section 4 this theory is applied to a nonlinear matrix model for the dynamics of flour beetles (*Tribolium*).

2 Models for structured populations

Suppose that the individuals in a population are classified according to a finite number $m \geq 1$ of discrete categories or classes. Then a discrete model for the dynamics of the population prescribes how individuals move into and out of these categories at discrete time intervals $t = 0, 1, 2, 3, \dots$. Let $x(t) = \text{col}(x_i(t))$ denote the distribution of individuals at time t based upon these categories, that is, let $x_i(t)$ denote the number (or density) of individuals in class i at time t . ("Number" can mean the number of individual organisms or it mean the number of many other possible units of population size, including biomass, dry weight, etc. For convenience we will speak of "individuals" in each class.)

If we let $\tau_{ij} \in [0, 1]$ denote the fraction of individuals in category j at time t that survive and move into category i at time $t + 1$, then the updated distribution of those individuals present at time t who survive to time $t + 1$ is given by the vector $Tx(t)$ where T is the $m \times m$ "transition matrix" $T = (\tau_{ij})$. (Note that by definition, $\sum_{i=1}^m \tau_{ij} \leq 1$ for all $0 \leq j \leq m$.)

If we assume that the only way to enter the population is by birth and if we let $f_{ij} \geq 0$ denote the number of i class offspring present at time $t + 1$ per j class individual present at time t , then the distribution of newborns at time $t + 1$ is given by the vector $Fx(t)$ where F is the $m \times m$ "fertility" matrix $F = (f_{ij})$.

The distribution $x(t + 1)$ of all individuals (surviving and newborn) at time $t + 1$ is given by

$$x(t + 1) = (F + T)x(t). \quad (1)$$

The coefficient matrix

$$A = F + T \geq 0$$

is called the "projection matrix". If these matrices are constants, i.e. if the fertilities f_{ij} and the survival fractions (or probabilities) τ_{ij} are independent of time, then the system of difference equations (1), sometimes called a "matrix equation", is linear and autonomous. In general, such a model implies exponential dynamics. However, growing populations cannot sustain exponential dynamics indefinitely. Fertilities and survivabilities are ultimately reduced by high population densities and in the model equation (1) the matrices F and/or T become dependent upon $x(t)$. This makes the model

$$x(t + 1) = (F(x(t)) + T(x(t)))x(t) \quad (2)$$

nonlinear and the asymptotic dynamics become considerably more complicated and rich in possibilities.

3 Asymptotic dynamics

Since the projection matrix $A = F + T \geq 0$ is nonnegative, the famous Frobenius Theorem can be applied to the linear matrix equation (1) provided A is also irreducible and primitive, which we now assume. (Necessary and sufficient for this is that $A^p > 0$ for some positive integer p .) From this theorem it follows that A has a strictly dominant, positive, simple eigenvalue $\lambda > 0$ which is associated with a positive eigenvector $v > 0$. It follows that the trivial equilibrium $x = 0$ is (globally asymptotically) stable if $\lambda < 1$ and is unstable if $\lambda > 1$. When $\lambda = 1$ there exists a continuum of infinitely many positive equilibria ($x = cv$ for any positive constant $c > 0$.) Thus, the asymptotic dynamics of a population governed by the linear matrix equation (1) is determined by the dominant eigenvalue λ of the projection matrix A . This eigenvalue also determines the rate of growth or decay (according to the Fundamental Theorem of Demography; see for example [1] or [10]).

There is another quantity that can also be used to determine the asymptotic dynamics of equation (1), namely the "net reproductive number" n . This number is biologically defined as the expected number of offspring per individual over its life span. Mathematically, n is defined as follows. Suppose that the inverse $(I - T)^{-1} = (e_{ij})$ exists. (Sufficient for this is the assumption that there is always some loss from every class at every time step, i.e. that $\sum_{i=1}^m \tau_{ij} < 1$ for all $0 \leq j \leq m$.) The entry e_{ij} of the inverse $(I - T)^{-1}$ is the expected amount of time that an individual will spend in class i given that it starts in class j . Suppose that the matrix $(I - T)^{-1} F$ has a strictly dominant, positive, simple eigenvalue associated with a positive (right) eigenvector $v > 0$ (and a nonnegative left eigenvector $w \geq 0$). This dominant eigenvalue is denoted n and is defined to be the net reproductive number. In [5] this mathematical definition is shown to be consistent with the biological definition given above. Also, the following theorem is proved in [5].

Theorem 1 *Under the assumptions on the constant matrices F , T , and $A = F + T$ described above, the following equivalences hold for the linear equation (1):*

$$n < 1 \Leftrightarrow \lambda < 1 \quad \text{and} \quad n > 1 \Leftrightarrow \lambda > 1 \quad \text{and} \quad n = 1 \Leftrightarrow \lambda = 1$$

Corollary 1 *Under the assumptions of Theorem 1, $x = 0$ is a (globally asymptotically) stable equilibrium of the linear system (1) if and only if $n < 1$ and is unstable if and only if $n > 1$. If $n = 1$ there exists a continuum of infinitely many positive equilibria $x = cv$, $c > 0$ of equation (1).*

As we will now see, in many significant respects the results of this corollary are valid for nonlinear matrix equations (2) as well.

Let $R_+ \doteq [0, +\infty)$ and $R_+^m \doteq R_+ \times \cdots \times R_+$. Let Ω denote an open neighborhood of R_+^m and assume the following smoothness conditions and basic requirements for a

population model:

$$A1 : \begin{cases} A(x) = F(x) + T(x) \text{ where } F(x) = (f_{ij}(x)) \text{ and} \\ T(x) = (\tau_{ij}(x)) \text{ satisfy } f_{ij} \in C^1(\Omega, R_+), \tau_{ij} \in C^1(\Omega, [0, 1]) \\ \text{with } \sum_{i=1}^m \tau_{ij}(x) \leq 1 \text{ for all } x \in \Omega \text{ and } 1 \leq j \leq m \end{cases}$$

In [3] the existence and stability of equilibria for equation (2) were studied as a function of the inherent net reproductive number. In order to defined and explicitly introduce this quantity into the equation we assume

$$A2 : \text{ the inverse } (I - T(x))^{-1} \text{ exists for all } x \in \Omega$$

and

$$A3 : \begin{cases} (I - T(0))^{-1}F(0) \text{ has a strictly dominant,} \\ \text{simple real eigenvalue } n > 0 \text{ with right} \\ \text{eigenvector } v > 0 \text{ and left eigenvector } w \geq 0 \end{cases}$$

The eigenvalue n is called “*inherent net reproductive number*”. It is “inherent” because n would be the net reproductive number if the effects of density were ignored or absent (i.e. $x = 0$ in the projection matrix $A(x) = F(x) + T(x)$). We introduce n into the model equations (2) by normalizing the class specific fertilities with respect to n , i.e. by defining the normalized fertilities $b_{ij}(x) = f_{ij}(x)/n$. Setting $B(x) \doteq (b_{ij}(x))$, we write the model equation as

$$\begin{aligned} x(t+1) &= A(x(t))x(t) \\ A(x) &= nB(x) + T(x) \end{aligned} \tag{3}$$

We saw that when B and T are constant matrices then there is an unbounded continuum of positive equilibrium pairs (n, x) with $n = 1$. We say that the isolated point $n = 1$ is the spectrum of this continuum. In general, for nonlinear equations (3) there exists a continuum of nontrivial equilibrium pairs that bifurcates from the trivial equilibrium at $n = 1$ (Theorem 2 below), but the spectrum (i.e. set of n values) associated with the continuum is an interval with nonzero (and possibly infinite) length.

Theorem 2 Assume A1, A2, A3 hold. Let S denote the set of nontrivial equilibrium pairs of (3).

(a) S contains a continuum $C \subseteq S$ of equilibrium pairs that bifurcates from the trivial equilibrium pair $(n, x) = (1, 0)$, i.e. for which $(1, 0)$ lies in the closure of C . In a sufficiently small neighborhood of $(1, 0)$, C consists of positive equilibria.

(b) If, in addition, the assumptions

$$A4 : A(0) = nF(0) + T(0) \text{ is irreducible and primitive for all } n > 0$$

$$A5 : 0 \leq x = (nB(x) + T(x))x \Rightarrow x = 0 \text{ or } x > 0$$

hold, then C consists entirely of positive equilibria, C is unbounded in $R_+ \times R_+^m$, and the spectrum associated with C is positive.

Proof. (a) The existence of a locally positive continuum C bifurcating from $(1, 0)$ follows from Theorem 1 in [3].

(b) In a sufficiently small neighborhood of the bifurcation point $(1, 0)$ the continuum C consists of positive equilibria by (a). Suppose that C contains an equilibrium pair that is not positive. Then, because it is a continuum, it must contain a nonpositive equilibrium pair (n^*, x^*) with $x^* \geq 0$, $x^* \neq 0$. By A5 follows the contradiction that $x^* = 0$. Thus, C can have only positive equilibrium pairs.

Theorem 1 in [3] offers an alternative: either C is unbounded or it connects to another bifurcation point $(n^*, 0)$ for some real $n^* \neq 1$, i.e. $(n^*, 0) \in cl(C)$ for some $n^* \neq 1$. We now show that A4 rules out the second alternative. Suppose, for purposes of contradiction, that $(n^*, 0) \in cl(C)$ for some $n^* \neq 1$. Choose a sequence $(n_i, x_i) \in C$ that converges to $(n^*, 0)$ such that the sequence of unit vectors $x_i/|x_i| \geq 0$ converges to a unit vector $z \geq 0$ (choose a subsequence if necessary). Dividing the equation $x_i = (n_i B(x_i) + T(x_i)) x_i$ by $|x_i|$ and passing to the limit, we obtain

$$0 \leq z = (n^* B(0) + T(0)) z, \quad |z| = 1 \quad (4)$$

The matrix $n^* B(0) + T(0)$ is irreducible and primitive by assumption A4 and (4) implies that 1 is an eigenvalue associated with a nonnegative eigenvector. It follows that 1 must be the dominant eigenvalue [7]. Theorem 1 in turn implies that $n^* = 1$, a contradiction. Hence, the second alternative is ruled out and the continuum C is unbounded.

All that remains is to show that the spectrum defined by C is positive. If this were not the case, then because C is a continuum it would have to contain an equilibrium pair $(0, x^*)$, $x^* > 0$. The equilibrium equations imply that $x^* > 0$ would have to satisfy the equation $x^* = T(x^*)x^*$. This contradicts assumption A2. •

Let $q(x)$ be the dominant eigenvalue of $Q(x) \doteq (I - T(x))^{-1} B(x)$. By A3, $q(x)$ is defined at least for x close to 0. Since the equilibrium equation $x = (nB(x) + T(x))x$ can be equivalently written as $Q(x)x = x/n$, it follows that

$$nq(x) = 1 \quad (5)$$

for any equilibrium pair (n, x) , including those on C . This invariant is often useful in deducing properties of C (e.g. the spectrum).

Next we consider the stability of both the trivial equilibrium and the positive equilibria on the continuum C in a neighborhood of the bifurcation point $(1, 0)$. A simple linearization of (3) together Theorem 1 yields the following result.

Theorem 3 *Under assumptions A1, A2, A3, and A4 the trivial equilibrium $x = 0$ of the equation (3) is (locally asymptotically) stable if $n < 1$ and is unstable if $n > 1$.*

Thus, $x = 0$ loses stability as n is increased through the critical value $n = 1$. For the positive equilibria from the bifurcating continuum we have the following result, which can be obtained from Liapunov-Schmidt (or regular perturbation) expansion techniques [3].

Theorem 4 Assume that A1, A2, and A3 hold and that the quantity

$$n_1 = -w \cdot (\nabla_x b_{ij}(0) + \nabla_x \tau_{ij}(0)) v$$

is nonzero. Then in a sufficiently small neighborhood of $(1, 0)$ the positive equilibrium from the bifurcating continuum C are (locally asymptotically) stable if $n_1 > 0$ and are unstable if $n_1 < 0$.

It turns out that near the bifurcation point $n = 1 + n_1 \epsilon + O(\epsilon^2)$, $\epsilon > 0$, for those positive equilibria from C [2], [3]. Thus, near the bifurcation point $(1, 0)$, $n > 1$ when $n_1 > 0$ and the stable bifurcation is "to the right" (or "supercritical"). Similarly, the unstable bifurcation is "to the left" (or "subcritical"). Thus, the stability of C near $(1, 0)$ is determined by its direction of bifurcation.

Under rather general conditions we have seen that the trivial equilibrium $x = 0$ is unstable for $n > 1$. This does not mean, however, that there are no solutions starting with nonnegative and nonzero initial conditions that tend to 0 as $t \rightarrow +\infty$, since there might be a stable manifold that intersects the positive cone. Our final result shows that this cannot happen and that in fact the equation (3) is uniformly persistent with respect to the origin.

We make the assumption that the positive cone (minus the origin) is forward invariant, i.e.

$$A5 : \begin{cases} \text{for all solutions of (3), } x(0) \in R_+^m \setminus \{0\} \\ \text{implies } x(t) \in R_+^m \setminus \{0\} \text{ for all } t \geq 1 \end{cases}$$

and that orbits are bounded, i.e.

$$A6 : \begin{cases} \exists m > 0 \ni \text{ for all solutions of (3)} \\ x(0) \in R_+^m \setminus \{0\} \Rightarrow \exists T = T(x(0)) \geq 0 \\ \text{such that } |x(t)| \leq m \text{ for all } t \geq T \end{cases}$$

Definition 1 Equation (3) is "uniformly persistent (with respect to the origin $x = 0$)" if there exists a constant $\eta > 0$ such that $x(0) \in R_+^m \setminus \{0\} \Rightarrow \liminf_{t \rightarrow +\infty} |x(t)| \geq \eta$.

This is a special case of a more general definition of uniform persistence given in [9]. Since all norms are equivalent on finite dimensional Euclidean spaces, in this definition (and in assumption A6) any norm can be used. For example, one norm that can be used is $P(t) = \sum_{i=1}^m |x_i(t)|$, which for nonnegative solutions is equal to the total size of the population. Uniform persistence implies that the population does not go asymptotically extinct in the sense that for any nonnegative and nonzero initial conditions the total population size satisfies $\liminf_{t \rightarrow +\infty} P(t) \geq \eta > 0$.

Lemma 1 In addition to A1 – A4 assume that

$$A7 : nB(0) + T(0) \text{ is nonsingular for all } n > 0$$

Assume $n > 1$. Then there exists a constant $\epsilon > 0$ such that if $x(t)$ is a solution of (3) satisfying $0 < |x(t')| \leq \epsilon$, $x(t') \geq 0$, for some $t' \geq 0$, then $|x(t' + k)| > \epsilon$ for some positive integer $k > 0$.

Proof. Since $nB(0) + T(0)$ is nonsingular, the map defined by $(nB(x) + T(x))x$ is a diffeomorphism in a neighborhood of the origin and hence the Stable Manifold Theorem and the discrete Hartman/Grobman Theorem for maps [8] apply in this neighborhood. By assumption A4 and $n > 1$ it follows from Theorem 1 that $\lambda > 1$. Consequently, the Fundamental Theorem of Demography (see [1] or [10]) implies that the stable manifold of the linearization $x(t+1) = (nB(0) + T(0))x(t)$ of (3) at $x = 0$ cannot intersect $R_m^+ \setminus \{0\}$. The Stable Manifold Theorem for maps implies that the same is true for (3) in a neighborhood of 0. The assertion of the lemma follows from the Hartman/Grobman Theorem for maps. •

Theorem 5 Assume A1 – A7 hold. If $n > 1$, then the equation (3) is uniformly persistent with respect to origin.

Proof. Under the assumptions A5 and A6, Theorem 4.1 of [9] implies that necessary and sufficient conditions for the uniform persistence of (3) with respect to the origin $\{0\}$ are that the origin be both an isolated invariant set and its own stable set. By Lemma 1, it is clear that $\{0\}$ is the largest invariant set in the R_+^m -neighborhood ball of radius ϵ of the origin. Thus $\{0\}$ is an isolated invariant set. Also by Lemma 1, it is clear that the $\limsup_{t \rightarrow +\infty} |x(t)| \geq \epsilon$. This implies that there are no orbits starting in $R_+^m \setminus \{0\}$ that tend to the origin. This means that the stable set for the origin is just the origin. •

4 An application

In this section we will apply the results of the previous section to a nonlinear model designed to describe the dynamics of beetles of the genus *Triolium* (flour beetles). This model has been developed for an ongoing interdisciplinary project whose main goal is to demonstrate rigorously the use and value of nonlinear models in population biology. The project involves the derivation of a biologically based model, the analysis of the dynamics implied by this model, the formulation of a stochastic version of the model on which is based statistical techniques for parameter estimation and model verification with respect to data, and the design and implementation of laboratory experiments to generate the relevant data. Replicate cultures for each set of experimental parameter values permit hypotheses testing and the calculation of confidence intervals. Laboratory experiments will be designed to place the cultures in parameter regions of different dynamics as predicted by the deterministic model. This includes dynamics ranging from equilibration to strange attractors and chaos. The success of this project will provide the most rigorous demonstration to date of the relevance and

usefulness of nonlinear mathematical models in understanding the dynamics of biological populations (including the controversial issue of chaos). An important point is that the entire project, including the experimental design, is fundamentally based upon the mathematical model, which is a set of nonlinear difference equations. For more details on the model and some preliminary results and analysis see [6].

The model is a stage structured model which distinguishes larvae, pupae, and adult beetles whose numbers at time t are $x_1(t)$, $x_2(t)$, and $x_3(t)$ respectively. The beetles are not density dependent (resource limited) and the nonlinear dynamics are driven by cannibalistic interactions between these stages. The model equations are

$$\begin{aligned}x_1(t+1) &= bx_3(t) \exp(-c_{el}x_1(t) - c_{ea}x_3(t)) \\x_2(t+1) &= (1 - \mu_l)x_1(t) \\x_3(t+1) &= x_2(t) \exp(-c_{pa}x_3(t)) + (1 - \mu_a)x_3(t)\end{aligned}\quad (6)$$

where $b > 0$ is the inherent number of larva produced per adult per unit time, $\mu_l \in (0, 1)$ and $\mu_a \in (0, 1)$ are the larval and pupal mortality rates, and the c_{el} , c_{ea} , and $c_{pa} \geq 0$ are "cannibalism coefficients" (egg cannibalism by larva, etc.). Exponential nonlinearities are used because cannibalism occurs only under random contacts. Non-cannibalistic mortality of pupae is relatively small and is ignored in the model. The time unit is the time between larval and pupal stages, which as it turns out is approximately the same as that between pupal and adult stages. Therefore, the system of difference equations (6) has the form of a nonlinear Leslie model with

$$F(x) = \begin{pmatrix} 0 & 0 & bx_3(t) \exp(-c_{el}x_1(t) - c_{ea}x_3(t)) \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

$$T(x) = \begin{pmatrix} 0 & 0 & 0 \\ 1 - \mu_l & 0 & 0 \\ 0 & \exp(-c_{pa}x_3(t)) & 1 - \mu_a \end{pmatrix}$$

Clearly, A1 holds with $\Omega = R^3$. It is easy to compute that $\det(I - T(x)) = \mu_a \neq 0$ on R^3 so that A2 holds. A straightforward calculations show that

$$(I - T(x))^{-1} F(x) = b \exp(-c_{el}x_1 - c_{ea}x_3) \begin{pmatrix} 0 & 0 & 1 \\ 0 & 0 & 1 - \mu_l \\ 0 & 0 & \left(\frac{1 - \mu_l}{\mu_a}\right) \exp(-c_{pa}x_3) \end{pmatrix}$$

which has a double eigenvalue 0 and a dominant positive eigenvalue $nq(x)$ where

$$n = b \left(\frac{1 - \mu_l}{\mu_a}\right) \quad \text{and} \quad q(x) = \exp(-c_{el}x_1 - (c_{ea} + c_{pa})x_3)$$

The dominant eigenvalue of $(I - T(0))^{-1} F(0)$ is n and its right and left eigenvectors are

$$v = \begin{pmatrix} 1 \\ 1 - \mu_l \\ \frac{1 - \mu_l}{\mu_a} \end{pmatrix} > 0 \quad w = (0 \ 0 \ 1) \geq 0$$

This shows that $A3$ holds. Simple calculations show that the matrix

$$A(0) = nB(0) + T(0) = \begin{pmatrix} 0 & 0 & b \\ 1 - \mu_l & 0 & 0 \\ & 1 & 1 - \mu_a \end{pmatrix}$$

satisfies $A^4(0) > 0$ and hence $A4$ holds. Also $\det A(0) = b(1 - \mu_l) > 0$ and $A7$ holds. It is easy to verify $A5$. A more tedious, but straightforward calculation shows that the quantity n_1 is positive.

All of the results in the previous section will apply to our model equations (6) if we can verify that the remaining assumption $A6$ holds, i.e. that all solutions satisfying $x(0) \geq 0$ are bounded for $t \geq 0$. The first equation in (6) implies $0 \leq x_1(t+1) \leq b/ec_{ea}$ for all $t \geq 0$, which together with the second equation implies $0 \leq x_2(t+1) \leq (1 - \mu_l)b/ec_{ea}$ for all $t \geq 1$. This proves that the first two components for any solution are bounded for all $t \geq 0$. We have only to show that the third component is bounded. From the third equation in (6) follows $0 \leq x_3(t+1) \leq (1 - \mu_l)b/ec_{ea} + (1 - \mu_a)x_3(t)$ for $t \geq 0$. An induction implies that $0 \leq x_3(t) \leq \alpha(1 + \sigma + \sigma^2 + \dots + \sigma^{t-1}) + \sigma^t x_3(2)$ for $t \geq 2$ where $\alpha = (1 - \mu_l)b/ec_{ea}$ and $\sigma = 1 - \mu_a$. Since $0 < \sigma < 1$, we obtain $0 \leq x_3(t) \leq \alpha/(1 - \sigma) + \sigma^t x_3(2)$ from which we see that $0 \leq x_3(t) \leq \alpha/(1 - \sigma) + 1$ for all sufficiently large t . This verifies $A6$.

At this point we have all of the conclusions from all of the theorems in the previous section. Before summarizing these results we notice some results that follow from equation (5), which for the model equations (6) are

$$n \exp(-c_{el}x_1 - (c_{ea} + c_{pa})x_3) = 1.$$

It is clear from this equation that $n > 1$ for any positive equilibrium and, since the continuum C is unbounded, that both the spectrum and the set of magnitudes $|x|$ of positive equilibria from C are unbounded. Moreover, this equation, which for $n > 1$ is equivalent to

$$c_{el}x_1 + (c_{ea} + c_{pa})x_3 = \ln(n), \quad (7)$$

can be used to show the uniqueness of the positive equilibrium. From the equilibrium equations from last two equations in (3) follows $x_1 = (1 - \mu_l)\mu_a^{-1}x_3 \exp(c_{pa}x_3)$, a monotonically increasing relationship between x_1 and x_3 whose graph can have at most one intersection point with the decreasing straight line defined by equation (7).

We summarize our results about the model equations (6) in the following theorem.

Theorem 6 *If $n \doteq b(1 - \mu_l)/\mu_a < 1$ then (6) has no positive equilibria and $x = 0$ is (locally asymptotically) stable. If $n > 1$ then $x = 0$ is unstable and there exists a unique positive equilibrium. The positive equilibrium is stable at least for n close to 1. In any case, for all $n > 1$ the system (6) is uniformly persistent with respect to $x = 0$.*

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