Two Predators and a Common Prey
(Persistence of The Ecosystem)

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ABSTRACT

In this work we discuss the survivability of an ecosystem composed of two competitive predators and their common sole prey, and this is achieved through studying the concept of persistence. Authors such as Freedman and Waltman, and El-Owaidy and Ammar discussed the persistence of such models by assuming non-existence of limit cycles, however; in this paper we actually prove the non-existence of limit cycles by showing global asymptotic stability of equilibria by defining a suitable Lyapunov function and then obtain the system persistence criteria.

Key Words: Ecosystem; Competitive predators; Sole prey.

INTRODUCTION

The question of species survivability is certainly one of the most interesting as far as ecosystem modelling. This question becomes even more interesting when two or more predatory species compete for a single prey. In ecological phraselogy, persistence of the system means that the density of each species remains, asymptotically, above a positive bound independent of the initial conditions, in other words, all species are saved from extinction. Mathematically, however; this means the continued positivity of solutions of the mathematical model representing the ecological phenomenon.

Consider the following ecological differential equation

\[ \dot{x}_i = x_i f_i(x_1, x_2, \ldots, x_n) \quad \text{for} \quad i = 1, 2, \ldots, n \]

the ecosystem represented by the above differential system is said to be uniformly persistent (permanent) if there exists a compact set \( M \) contained in the interior of \( \mathbb{R}_+^n = \{x \in \mathbb{R}^n : x_i \geq 0 \text{ for } 1 \leq i \leq n\} \) such that all orbits end up in \( M \). This assures that each population \( x_i(t) \) is bounded away from zero (extinction) if \( x_i(0) > 0 \) for all \( i \).

The persistence of the system is called “weak” if for all \( i \), \( \lim_{t \to \infty} \sup x_i(t) > 0 \) whenever \( x(0) > 0 \). Under this notion of persistence, however, a population can frequently approach extinction. On the other hand, by the term “strong” persistence we mean that for all \( i \), \( \liminf_{t \to \infty} x_i(t) > 0 \) whenever \( x(0) > 0 \).

In this paper we have used the latter definition of persistence in exactly the same fashion of Freedman and Waltman (Freedman & Waltman, 14984) where it was reformulated as follows:
“A system with initial conditions in the positive cone will persist if there are no $\omega$-limit points of the solution the boundary of the positive cone”.

In other words if $\alpha(X)$ is the orbit through the point $X = (x, y, z)$ with $x > 0, \ y > 0, \ z > 0$ and if $\Omega(X)$ is the $\omega$-limit set of $\alpha(X)$, then $\Omega(X)$ is in the interior of the positive cone.

In this paper consideration is given to studying the interspecific interactions governing the relation between two competing predator populations living exclusively on a common prey. As an original contribution, density-dependent death rates have been considered and in this sense a more realistic extension of the result of El-Owaidy and Ammar (El-Owaidy & Ammar, 1980) have been achieved.

While Freedman and Waltman (Freedman & Waltman, 1984) in theorem 4.1., gave persistence criteria by assuming that there are no limit cycles surrounding an interior equilibrium in a co-ordinate plane. In this paper a proof is given for the non-existence of limit cycles through the construction of a suitable Lyapunov function, furthermore; conditions under which the equilibria are globally asymptotically stable. This is an indication that all the trajectories of the system in the positive octant will spiral toward this equilibrium point, that is, non-existence of limit cycles. Consequently, the criteria of persistence as given in theorem 4.1. under referece, where applied to obtain conditions for persistence of our system. We claim, therefore; that our result seems to be more comprehensive than that in theorem 4.1. of (Freedman & Waltman, 1984).

Section 2, of this work contains the model, Global asymptotic stability of the problem is dealt with in section 3. However; persistence results are studied and illustrated in section 4, finally an illustration of these results by an example is contained in section 5.

The Model:

The following differential system models the interaction of two competing predatory populations $y(t)$ and $z(t)$ lining exclusively on a common prey $x(t)$:

\begin{align*}
\dot{x} &= xf(x) - yp(x) - zq(x) \\
\dot{y} &= y\left[- g(y) + cp(x)\right] \\
\dot{z} &= z\left[- h(z) + dq(x)\right] \\
x(0) &= x_0 > 0, \ y(0) = y_0 \geq 0, \ z(0) = z_0 \geq 0,
\end{align*}

(2.1)

where $\dot{\cdot} = \frac{d}{dt}$ and $c, d$ are positive constants, known as food conversion rates.

We make the following assumptions, which are consistent with models of predator-prey systems.

(A1): $f(x)$; specific growth rate of prey $x$. 
\( f(0) > 0, \ f'(x) \leq 0 \) for all \( x > 0 \), there exists \( k > 0 \) (\( k \) is the carrying capacity of the environment) such that

\[
\begin{align*}
f(x) > 0 \text{ on } 0 \leq x < k, \ f(k) = 0 \text{ and } f(x) < 0 \text{ on } x > k.
\end{align*}
\]

(A2): \( p(x) \); the functional response of the predator \( y \) with respect to the prey \( x \) and \( p(0) = 0 \), \( p'(x) > 0 \), for all \( x \geq 0 \).

(A3): \( q(x) \); the functional response of the predator \( z \) with respect to the prey \( y \) and \( q(0) = 0 \), \( q'(x) > 0 \) for all \( x \geq 0 \).

(A4): it is assumed that \( q(x) = \alpha p(x) \), for \( \alpha \) a positive constant.

(A5): \( g(y) \); density-dependent death rate of the predator \( y \) and \( g(0) > 0 \), \( g'(y) \geq 0 \) for all \( y > 0 \).

(A6): \( h(z) \); density-dependent death rate of the predator \( z \) and \( h(z) > 0 \), \( h'(z) \geq 0 \) for all \( z > 0 \).

It is obvious that the system (2.1) has equilibrium \((0,0,0)\). By assumption (A1), \((k,0,0)\) is also an equilibrium point. We assume that each of the predators \( y \) and \( z \) can survive on and coexist with the prey \( x \), in other words there exist equilibrium point \( (x^*, y^*, 0) \) and \( (\hat{x}, 0, \hat{z}) \) such that

\[
\begin{align*}
x^* f(x^*) - y^* p(x^*) &= 0 \\
- g(y^*) + c p(x^*) &= 0
\end{align*}
\]

and

\[
\begin{align*}
\hat{x} f(\hat{x}) - \hat{z} p(\hat{x}) &= 0 \\
- h(\hat{z}) + d q(\hat{x}) &= 0
\end{align*}
\]

where

\[
x^*, y^*, \hat{x}, \hat{z} > 0 \text{ and } x^* < k, \hat{x} < k
\]

Global asymptotic stability of equilibria \((x^*, y^*, 0)\) and \((\hat{x}, 0, \hat{z})\)

**Lemma 3.1.:** Assume (A1)-(A6) hold for the system (2.1.) and in a neighbourhood of \((x^*, y^*, 0)\) in the positive cone, the function \( \frac{xf(x)}{p(x)} \) is strictly decreasing. Then the equilibrium \((x^*, y^*, 0)\) is globally asymptotically stable.

**Proof:**

Consider the following Lyapunov function \( L(x,y,z) \) (Elmabruk, 1996) as:
\[
L(x, y, z) = \int_{x}^{y} \left[ c \left( 1 - \frac{p(x)}{p(s)} \right) + d \left( 1 - \frac{q(x)}{q(s)} \right) \right] ds + \int_{y}^{z} \left[ \frac{s - y^*}{s} \right] ds + z \quad (3.1)
\]

Now \( L(x^*, y^*, 0) = 0 \) and \( L(x, y, z) > 0 \) due to (A2) and (A3) in the region \( \{ (x, y, z) : 0 < x < x^* < k, \ 0 < y^* < y < \beta_1, \ 0 < z < \beta_2, \ \beta_1, \beta_2 \) are positive constants \}.

\[
\frac{d}{dt} L(x, y, z) = c \left[ \frac{x f(x)}{p(x)} - \frac{z g(x)}{p(x)} - y \right] + d \left[ q(x) - q(x^*) \right] \left[ \frac{x f(x)}{q(x)} - \frac{y p(x)}{q(x)} - z \right] + (y - y^*) \left[ (g(y^*) - g(y)) + \frac{d}{\alpha} (q(x^*) - q(x)) \right]
\]

using (2.2), (A4) and with some algebraic manipulations we get

\[
\dot{L}(x, y, z) = \left[ c \left( p(x) - p(x^*) \right) + \frac{1}{\alpha} d \left( q(x) - q(x^*) \right) \right] \left[ \frac{x f(x)}{p(x)} - \frac{x^* f(x^*)}{p(x^*)} \right] + (y - y^*) \left[ (g(y^*) - g(y)) + \frac{d}{\alpha} (q(x^*) - q(x)) \right] + z \left[ c \left( p(x^*) - p \right) \right].
\]

Thus \((x^*, y^*, 0)\) is globally asymptotically stable.

**Lemma 3.2.** Assume (A1)-(A6) hold for the system (2.1.) and in a neighbourhood of \((\hat{x},0,\hat{z})\) in the positive cone, the function \(\frac{x f(x)}{p(x)}\) is strictly decreasing. Then the equilibrium point \((\hat{x},0,\hat{z})\) is globally asymptotically stable.

**Proof:**

Define Lyapunov function \( L(x, y, z) \) as:

\[
L(x, y, z) = \int_{x}^{y} \left[ c \left( 1 - \frac{\hat{p}(x)}{\hat{p}(s)} \right) + d \left( 1 - \frac{\hat{q}(x)}{\hat{q}(s)} \right) \right] ds + y + \int_{y}^{z} \left( \frac{s - \hat{z}}{s} \right) ds \quad (3.2)
\]

Rest of the proof follows as in Lemma 3.1.

**Remark 3.1:**

We consider equilibrium points \((0,0,0)\) and \((k,0,0)\). The eigenvalues of the variational matrix \(V(0,0,0)\) of the system (2.1.) about \((0,0,0)\) are:

\[
\lambda_1 = f(0) > 0, \quad \lambda_2 = -g(0) < 0, \quad \lambda_3 = -h(0) < 0 \quad (3.3)
\]

Clearly \((0,0,0)\) is a hyperbolic point and is unstable along the \(x\)-axis. This implies that the prey population \(x\) grows near \((0,0,0)\) i.e. avoiding extinction.

The eigenvalues of the variational matrix \(V(k,0,0)\) of the system (2.1.) about \((k,0,0)\) are:
\[ \lambda_1 = k f'(k) < 0, \quad \lambda_2 = -g(0) + cp(k), \quad \lambda_3 = -h(0) + dq(k) \]  

(3.4.)

Thus \((k,0,0)\) is asymptotically stable along the \(x\)-axis. This implies that the prey population \(x\) remains in a neighbourhood of \(k\).

**Remark 3.2.**:

For existence of \((x^*, y^*, 0)\) and \((x^*, 0, z^*)\) it is necessary that

\[-g(0) + cp(k) > 0 \quad \text{and} \quad -h(0) + dq(k) > 0 \]  

(3.5.)
as it implies increase of predator population \(y\) and predator population \(z\).

**Persistence Criteria:**

In section 3, we have given necessary conditions for existence of equilibria \((x^*, y^*, 0)\) and \((\hat{x}, 0, \hat{z})\), and criteria for their global asymptotic stability.

In this section, we shall assume global stability of these equilibria and obtain persistence criteria for the system (2.1.).

First, we prove the following two lemmas:

**Lemma 4.1.** The equilibrium \((x^*, y^*, 0)\) in the interior of the \(x\)-\(y\) plane is unstable in the positive direction orthogonal to \(x\)-\(y\) plane if

\[-h(0) + dq(x^*) > 0 \quad \text{or} \quad -h(0) + d\alpha p(x^*) > 0 . \]

**Proof:**

The proof is immediate upon computing the variational matrix \(V(x^*, y^*, 0)\) of system (2.1.) about \((x^*, y^*, 0)\).

We have:

\[
\begin{bmatrix}
    f(x^*) + x^* f'(x^*) - y^* p'(x^*) & -p(x^*) & -q(x^*) \\
    cy^* p'(x^*) & -g(y^*) + cp(x^*) - y^* g'(y^*) & 0 \\
    0 & 0 & -h(0) + dq(x^*)
\end{bmatrix}
\]

Thus if \(-h(0) + dq(x^*) > 0 \quad \text{or} \quad -h(0) + d\alpha p(x^*) > 0 , \) we have the result.

**Lemma 4.2.** The equilibrium \((\hat{x}, 0, \hat{z})\) in the interior of the \(x\)-\(z\) plane is unstable in the positive direction orthogonal to \(x\)-\(z\) plane if

\[-g(0) + cp(\hat{x}) > 0 . \]

**Proof:**

The proof is immediate upon computing the variational matrix \(V(\hat{x}, 0, \hat{z})\) of the system (2.1.) about \((\hat{x}, 0, \hat{z})\).
Now to apply persistence criteria to our system (2.1.), we have to check hypotheses (B1)-(B4) of theorem 4.1. in Freedman and Waltman (Freedman & Waltman, 1984) and boundedness of solutions.

We have:

\[ F(x, y, z) = f(x) - y \frac{p(x)}{x} - z \frac{q(x)}{x} \]
\[ G_1(x, y, z) = -g(y) + cp(x) \]
\[ G_2(x, y, z) = -h(z) + dq(x) , \]

therefore; condition (B1) is trivially satisfied due to (A1)-(A6). Also notice that 

\[ p(0) = 0, \quad p'(x) > 0, \]

implies \( p(x) \) is a strictly increasing positive function. Similarly \( q(x) \). Condition (B2) is true due to (A1).

\[ F(0,0,0) = f(0) > 0, \quad F(k,0,0) = f(k) = 0, \]
\[ \frac{\partial f}{\partial x}(x,0,0) = f'(x) \leq 0 . \]

Satisfying (B3), there are no equilibria on y-axis or z-axis or in y-z plane, for if we suppose that there exists an equilibrium \((0, y, z)\) in y-z plane which is given by: \( g(y_i) = 0 \) and \( h(z_i) = 0 \), then this contradicts conditions (A5) and (A6), and satisfying (B4) each predator can, on the prey, i.e. there exist points \((x^*, y^*, 0)\) and \((\hat{x}, 0, \hat{z})\) such that (2.2.) and (2.3.) hold. Also see remark 3.2.. Moreover, we require;

(B5): Boundedness of solutions of system (2.1.). We suppose that the functions \( f(x) \), \( p(x) \), \( q(x) \), \( g(y) \) and \( h(z) \) are sufficiently smooth so that the solution to the initial value problem (2.1.) exists, is unique and continuable for positive values of \( t \). Regarding boundedness of solution, see Freedman and Waltman (Freedman & Waltman, 1977; Freedman & Waltman, 1984).

We state and prove the main theorem.

**Theorem 4.1.:** Let (B1)-(B5) hold. Let \( \frac{xf(x)}{p(x)} \) be a strictly decreasing function and

\[ -g(0) + cp(\hat{x}) > 0 \quad \text{and} \quad -h(0) + d\alpha p(x^*) > 0 . \]  

Then the system (2.1.) persists.

**Proof:**

By (B5) solutions are bounded.
By Remark 3.1. the equilibrium \((0,0,0)\) is unstable along the \(x\)-axis and unstable manifold of \((k,0,0)\) is two dimensional. Conditions \((4.1)\) follow from Lemmas 4.1. and 4.2.. Non-existence of limit cycles follows from Lemmas 3.1. and 3.2.

This completes the proof.

Remark 4.1.:

From \((A4)\), we have
\[
\alpha = \frac{q(x)}{p(x)} = \text{rate of prey consumption per predator } z \text{ at prey density } x.
\]

Thus, if we consider \(\alpha\) as a parameter then, the system \((2.1)\) will persist provided
\[
\alpha > \frac{h(0)}{dp(x^*)}.
\]

Remark 4.2.:

We have discussed persistence criteria for a system modelling the interaction of two competing predator populations living exclusively on a common prey. But in the same way, the persistence criteria can be obtained for the system modelling interactions between two prey populations and one predator population, that is,
\[
\begin{align*}
\dot{x} &= xf(x) - zq(x) \\
\dot{y} &= yg(y) - zr(y) \\
\dot{z} &= z[-h(z) + d_1q(x) + d_2r(y)]
\end{align*}
\]
and for three-level food web, that is
\[
\begin{align*}
\dot{x} &= xf(x) - yp(x) - zq(x) \\
\dot{y} &= y[-g(y) + cp(x)] - zr(y) \\
\dot{z} &= z[-h(z) + d_1q(x) + d_2r(y)]
\end{align*}
\]

For construction of Lyapunov functions for the systems \((4.2)\) and \((4.3)\) see [1].

Example 4.1.:

To illustrate theorem 4.1., consider the system with the Holling type II functional response.
\[
\begin{align*}
\dot{x} &= x(1-x) - y \frac{2x}{1+x} - z \alpha \frac{2x}{1+x} \\
\dot{y} &= y[-(1+y) + \frac{33}{16} \frac{2x}{1+x}] \\
\dot{z} &= z[-(1+z) + \frac{11}{9} \alpha \frac{2x}{1+x}]
\end{align*}
\]
Here, \( k = 1 \), \( \frac{xf(x)}{p(x)} = \frac{1 - x^2}{2} \).

Thus \( \frac{xf(x)}{p(x)} \) is a strictly decreasing function for \( x > 0 \).

\[
(x^*, y^*, 0) = \left( \frac{1}{2}, \frac{3}{8}, 0 \right)
\]

\[
p(x^*) = p\left( \frac{1}{2} \right) = \frac{2}{3}
\]

\[
\alpha > \frac{h(0)}{dp(x^*)} = \frac{27}{22}. \text{ Thus take } \alpha = 2
\]

\[
(\hat{x}, 0, \hat{z}) = \left( \frac{1}{3}, 0, \frac{2}{9} \right).
\]

To check condition (4.1.)

\[
-g(0) + cp(\hat{x}) = -\left( -\frac{33}{16} \times \frac{1}{2} \right) = \frac{1}{32} > 0
\]

\[
-h(0) + dcp(x^*) = -1 + \frac{11}{9} \times 2 \times \frac{2}{3} = -1 + \frac{44}{27} = \frac{17}{27} > 0
\]

Theorem 4.1. applies and hence the system (4.4.) is persistent.

**CONCLUSION**

Positivity of system solutions was utilized to represent the concept of system persistence by giving sufficient conditions imposed upon the mathematical model, leaving the door open for further alternative methods. Hence we have a set of measures that can be taken to preserve the ecosystem and resist extinction.

**REFERENCES**


