# Global stability of a model for competing predators: an extension of the Ardito & Ricciardi Lyapunov function

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**Abstract**

Sufficient conditions for global stability in a three-dimensional system of ordinary differential equations are formulated in terms of non-positiveness of two real functions.

**Key words** Global stability, competitive exclusion, LaSalle's extension theorem, Lyapunov function.

**Subject classification** 34C35, 58F40, 92D40

# 1 Introduction

The earliest statements of the principle of competitive exclusion can be tracked back to Darwin (1859, sixth ed. 1878), cf. den Boer (1980) and Hardin (1960). Darwin (1859) connected the principle of competitive exclusion to biodiversity, competition should always be most severe between allied forms. Darwin (1859) had obviously limited mathematical tools available, but the ultimate evidence for competition, he took from the fact, that any species would grow exponentially in the absence competition. The simplest mathematical formulations of this principle describe competition for a static limiting resource. This case was modeled already by Volterra (1926). He concluded, in the context of his models, that one of the two competitors drives the other to extinction, under all reasonable biological assumptions. His analysis was later improved by Lotka (1932). Gause (1934) took the results by Volterra (1926) and Lotka (1932) as a basis for his experimental testing of the principle. That is why the principle of competitive exclusion is referred to as "Gause's principle", in the experimental literature. Utida (1957) tried to construct a laboratory system showing violations of the principle of competitive exclusion. Although the models analyzed by Volterra (1926) and Lotka (1932) did not allow for coexistence of any form, Utida (1957), pointed out that nothing in general excludes oscillatory coexistence of two species competing for the same resource. By a proper choice of two parasitoids competing for the same host, he reported experimental oscillatory coexistence for more than 70 generations.

As the above remarks show, local stability is not enough, to ensure competitive exclusion in general. Moreover, the assumption that the resource is constant does not in general hold. The next step was to develop methods giving possibilities to check under what conditions coexistence ensues, and which do allow investigation of models with more complicated resource dynamics. The first mathematically rigorous study of this kind was presented by Hsu, Hubbell and Waltman (1977). Here the supply of the limiting nutrient was assumed to be constant, not the nutrient itself, as in Volterra (1926) and Lotka (1932). Their conclusion was that the principle of competitive exclusion holds, ie in this case we can have neither equilibrium coexistence nor oscillatory coexistence.

In their next study, Hsu, Hubbell and Waltman (1978) introduced and made a careful examination of the following model for competing predators

$$\begin{aligned}\dot{s} &= rs(1 - s/K) - x_0\frac{c_0 s}{s + a_0} - x_1\frac{c_1 s}{s + a_1} \\ \dot{x}_0 &= \left(m_0\frac{c_0 s}{s + a_0} - d_0\right) x_0 \\ \dot{x}_1 &= \left(m_1\frac{c_1 s}{s + a_1} - d_1\right) x_1.\end{aligned} \tag{1}$$

Here $s$ is the prey, $x_0$ and $x_1$ are predators competing for the same prey. The parameter $r$ is the intrinsic growth rate of the prey, $K$ is the carrying capacity for the prey, $c_0$ and $c_1$ are the search rates, $a_0$ and $a_1$ the search rates multiplied by the handling times, see e. g. Holling (1959), $m_0$ and $m_1$ the conversion rates and $d_0$, $d_1$ the death-rates of the predators $x_0$ and $x_1$, respectively. Most of the basic properties of the system (1), including a detailed classification of the stationary points of the system, were examined in Hsu et. al. (1978). Here the resource is not supplied or constant, it reproduces itself.

However, as already noted by Hsu et. al. (1978), parameter values corresponding to non-equilibrium coexistence exist, so the ecological principle of competitive exclusion was violated. In some works this was shown by the singular perturbation argument, see e. g. Muratori and Rinaldi (1989) and Osipov, Söderbacka and Eirola (1986). Keener (1983) used multi-parameter bifurcation analysis to prove oscillatory coexistence for a certain parameter range. R. McGehee and R. A. Armstrong (1977) showed by an elegant construction in a slightly more general case than (1), that coexistence is possible. On the other hand, it should be noted that the range of parameter values giving rise to coexistence is narrow and that the possibility for coexistence decreases with the number of predators competing for the same prey, cf. Coste (1985).

Despite that the region of the parameter space, where oscillatory coexistence is allowed for, is narrow in the model (1) it is difficult to verify extinction and global stability for large areas of the parameter space of the model (1). Some answers to this question were given by Hsu (1978)[13], Hsu et. al. (1978), Kustarov (1986), Lindström (1994)[21] and Lindström (1994)[22]. The above papers contain sufficient (graphical) conditions for global stability or extinction of one of the predators in the model (1). This approach is continued in this paper. Sufficient criteria for global stability are stated, which are graphical and easy to use. Moreover, they are valid for considerably larger regions of the parameter space than all corresponding theorems given earlier.

# 2 Model

We consider the following model for competing predators

$$\begin{aligned} \dot{s} &= h(s) - x_0 f_0(s) - x_1 f_1(s) \\ \dot{x}_0 &= x_0 \psi_0(s) \\ \dot{x}_1 &= x_1 \psi_1(s). \end{aligned} \tag{2}$$

Here $s$ denotes the prey density, $x_0$ and $x_1$ are the densities of the specialist predators feeding on the same prey $s$. This is a generalized version of the model treated by Hsu et. al. (1978).

We shall analyze the model (2) qualitatively under the following general conditions, which will be assumed throughout the paper:

(A–I) The functions $h$, $f_0$, $f_1$, $\psi_0$ and $\psi_1$ are $C^1[0, \infty)$.

(A–II) There exists a constant $K$, $K > 0$, such that $h$ satisfies $h(s) > 0$ if $0 < s < K$ and $h(s) < 0$ if $s < 0$ or $s > K$

(A–III) The functions $f_0$ and $f_1$ are increasing and have unique zeros at $s = 0$.

(A–IV) The functions $\psi_0$ and $\psi_1$ are increasing and there exist $\lambda_i$ such that $\psi_i$ satisfy $\psi_i(s) < 0$ if $0 < s < \lambda_i$ and $\psi_i(s) > 0$ if $s > \lambda_i$ for $i = 0, 1$. Moreover, we assume that $\lambda_0 < \lambda_1 < K$.

**Remark 1** We note that the most usual specific forms of the functions included in the model (2) are $h(s) = rs(1 - s/K)$, $f_i(s) = \frac{c_i s}{s + a_i}$, $\psi_i(s) = m_i f_i(s) - d_i$, $i = 1, 2$. The functions $f_i$, $i = 1, 2$ as given in this remark are specialist predator functional responses, cf. Holling (1959).

If (A-I)-(A-IV) are valid, the solutions remain positive and bounded, see e. g. Lindström (1994)[21]. Put

$$F_0(s) = \frac{h(s)}{f_0(s)} \text{ and } F_1(s) = \frac{h(s)}{f_1(s)}. \tag{3}$$

We deduce that exactly four equilibria exist, and they are given by $(0,0,0)$, $(K,0,0)$, $(\lambda_0, F_0(\lambda_0), 0)$, $(\lambda_1, 0, F_1(\lambda_1))$, i.e. no interior equilibria exist, hence this model excludes equilibrium coexistence of the predators. The origin is a saddle point and the equilibrium $(K,0,0)$ is a saddle point. If $F_0'(\lambda_0) < (>)0$ then some neighborhood of the point $(\lambda_0, F_0(\lambda_0), 0)$ in the $(s, x_0)$-coordinate plane belongs to the (un)stable manifold of the equilibrium $(\lambda_0, F_0(\lambda_0), 0)$. If $F_1'(\lambda_1) < (>)0$ then some neighborhood of the equilibrium $(\lambda_1, 0, F_1(\lambda_1))$ in the $(s, x_1)$-coordinate plane belongs to the (un)stable manifold of the equilibrium point $(\lambda_1, 0, F_1(\lambda_1))$. The equilibrium $(\lambda_0, F_0(\lambda_0), 0)$ has at least a one-dimensional stable manifold in the interior of $\mathbf{R}_+^3$. The equilibrium $(\lambda_1, 0, F_1(\lambda_1))$ has at least a one-dimensional unstable manifold in the interior of $\mathbf{R}_+^3$.

# 3 Extinction

According to the principle of competitive exclusion, one of the predators goes extinct for large regimes of parameter values in the system (2). The most important theorems giving sufficient conditions for extinction of one of the predators can be stated as follows:

**Theorem 1** *Let* (A-I)-(A-IV) *hold and assume that there exist* $\alpha > 0$ *and* $\beta > 0$ *such that*

$$\beta\psi_1(s) - \alpha\psi_0(s) < 0 \tag{4}$$

*when* $0 < s < K$, *is satisfied, then the specialist predator* $x_1$ *becomes extinct, except for initial conditions in the* $(s, x_1)$*-co-ordinate-plane and the* $(x_0, x_1)$*-co-ordinate-plane.*

The above theorem was originally proved by Kustarov (1986). A shorter proof than the original one is presented in Lindström (1994)[21]. In fact, if we consider the model (1) and put $\alpha = \frac{1}{d_0}$ and $\beta = \frac{1}{d_1}$, it can be seen that the above theorem contains the preliminary extinction results, theorem 3.4 and theorem 3.6, in Hsu et. al. (1978).

The above theorem implies that it is possible to reduce the system to a two-dimensional predator-prey model of the form (5) provided that the conditions given in the theorem hold, but not that the cycles disappear. Then we can make use of the results presented in section 4.

## 4 Two-dimensional global stability

In section 3 some sufficient conditions for extinction of one of the predators in system (2) was given. In this case the system (2), reduces to the following two-dimensional system:

$$\begin{aligned} \dot{s} &= f_0(s)(F_0(s) - x_0) \\ \dot{x}_0 &= x_0\psi_0(s). \end{aligned} \tag{5}$$

Here $F_0(s) = h(s)/f_0(s)$, as in (3). That is, a three dimensional global stability problem has been reduced to a two-dimensional one. Since 1980, the global stability problems of the system (5) have been considered in a large number of papers. Loosely speaking, systems like (5) possess global stability when $F_0$ decreases enough. A trivial result, which usually is contained in the more advanced global stability results states that, if $F_0$ is decreasing, then the system (5) is globally asymptotically stable in the positive quadrant. In order to obtain this result, the first integral

$$\int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds' + \int_{F_0(\lambda_0)}^{x_0} \frac{x_0' - F_0(\lambda_0)}{x_0'} dx_0' \tag{6}$$

of the separable system

$$\begin{aligned} \dot{s} &= f_0(s)(F_0(\lambda_0) - x_0) \\ \dot{x}_0 &= x_0\psi_0(s), \end{aligned}$$

can be used as a Lyapunov function. Similarly, one conclude, that if

$$(F_0(s) - F_0(\lambda_0))\,(s - \lambda_0) < 0, \; s \neq \lambda_0,$$

then the system (5) is globally stable in the first quadrant. This result was already included in the early results by Hsu (1978)[14][1] and Harrison (1979) and and can be regarded as an extension of the classical Rosenzweig-MacArthur graphical criterion for local stability, cf. Rosenzweig and MacArthur (1963).

The first remarkable extension of this result, was the mirror-image criterion, by Cheng, Hsu and Lin (1981). This theorem can be stated as follows.

[1] See Hofbauer and So (1990) and Kuang (1990), for essential corrections regarding other results in this work

**Theorem 2 (Mirror image criterion)** *Consider the system* (5). *Let* $F_0$ *be given by* (3), *let* (A-I)-(A-IV) *hold and assume*

(M–I) *We have*

$$\frac{d}{ds}\left(\frac{h(s)}{f_0(s)}\right) < 0$$

*for all* $s$, $\lambda_0 \leq s \leq K$,

(M–II) *and*

$$\frac{h(2\lambda_0 - s)}{f_0(2\lambda_0 - s)} \leq \frac{h(s)}{f_0(s)}$$

*for all* $s$, $\max(0, 2\lambda_0 - K) \leq s \leq \lambda_0$.

(M–III) *Moreover,* $\psi_0(s) = m_0 f_0(s) - d_0$ *and*

$$\frac{d_0}{f_0(s)} - m_0 > m_0 - \frac{d_0}{f_0(2\lambda_0 - s)}$$

*for all* $s$, $\lambda_0 \leq s < \min(2\lambda_0, K)$

*Then* $(\lambda_0, F_0(\lambda_0))$ *is globally asymptotically stable for the system* (5) *in the interior of the first quadrant.*

A small error can be detected in the first condition, (A-I), of the original formulation of the theorem. This is followed by a false conclusion in one of the examples, see e. g. Arnold (1973), pp 14-15, and Ardito and Ricciardi (1995). The error was removed in the next formulation of the theorem, Liou and Cheng (1988). The characteristic assumptions of the theorem are the assumptions (M-I), (M-II) and (M-III). Condition (M-I) states that $F_0$ must be decreasing in the region $\lambda_0 < s < K$. The geometric meaning of (M-II) is that, if we take the mirror image of $F_0$ in the region $\lambda_0 < s < K$ with respect to $s = \lambda_0$, then $F_0$ in the region $0 < s < \lambda_0$ is above the mirror image of $F_0$ in the region $\lambda_0 < s < K$. The condition (M-III) can be replaced by a more restrictive condition, that is, $f_0(s)$ is concave. Hence the theorem works well, if the functional response is of the type given in remark 1.

The theorem is proved using comparison of the system (5) to a reference system which has the same prey isocline in the region $\lambda_0 < s < K$ and the mirror image of this prey isocline as prey isocline in the region

$\max(0, 2\lambda_0 - K) \leq s \leq \lambda_0$. Some improved variants of this theorem were presented in Liou and Cheng (1988) and Kuang (1990) and these proofs were based on comparison to a corresponding reference system with closed trajectories. The problem with these extensions is that the conditions are not easy to verify, but the authors prove that their extensions contain the mirror image criterion, Theorem 2. The "mirror image criterion" works badly if the functional response is not of concave type. An alternative criterion for global stability was therefore presented in Cheng et al. (1981). Here, another technique of proof was used. Possible limit cycles must enclose $(\lambda_0, F_0(\lambda_0))$, and since the divergence integrated along the limit cycle is negative, it cannot exist, since $(\lambda_0, F_0(\lambda_0))$ is locally stable. The theorem follows, because the solutions are positive and bounded.

Quite recently, Ardito and Ricciardi (1995) made an essential contribution in unifying these two-dimensional global stability theorems. Their idea was the use of the Lyapunov function,

$$\begin{aligned} V(s, x_0) \quad = \quad & \frac{\exp(\gamma x_0)}{\gamma F_0(\lambda_0)} \exp\left(\gamma \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds'\right) - \\ & \int_{F_0(\lambda_0)}^{x_0} \frac{\exp(\gamma x_0')}{x_0'} dx_0' - \frac{\exp(\gamma F_0(\lambda_0))}{\gamma F_0(\lambda_0)}. \end{aligned} \tag{7}$$

One of the key ideas in the next section is to multiply the Lyapunov function (7) with $F_0(\lambda_0)$ and rewrite it as

$$\begin{aligned} V(s, x_0) \quad = \quad & \int_{F_0(\lambda_0)}^{x_0} \frac{x_0' - F_0(\lambda_0)}{x_0'} \exp(\gamma x_0') dx_0' + \\ & \int_{x_0}^{x_0 + \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds'} \exp(\gamma x_0') dx_0'. \end{aligned} \tag{8}$$

This Lyapunov-function reduces to the Lyapunov function (6) when $\gamma = 0$. Global stability results based on (8) are better than the mirror image criterion, Cheng et. al. (1981), and its improved variants, Liou and Cheng (1988) and Kuang (1990) because of three reasons. First it removes the somehow non-essential condition, (M-III). Secondly, the total time-derivative of (8), with respect to (5) is given by

$$\dot{V} = \exp(\gamma x_0) \exp\left(\gamma \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds'\right) \psi_0(s) \left(F_0(s) - \overline{F}_0(s)\right), \tag{9}$$

where

$$\overline{F}_0(s) = F_0(\lambda_0) \exp\left(-\gamma \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds'\right), \tag{10}$$

so the basic criterion for global stability is that there exists a $\gamma \leq 0$ such that

$$(F_0(s) - \overline{F}_0(s))(s - \lambda_0) < 0, \quad s \neq \lambda_0.$$

This is a purely geometrical criterion, which is much easier to check than the criteria in the improved variants of the mirror-image theorem, Liou and Cheng (1988) and Kuang (1990). Thirdly, the Lyapunov function is explicit and not implicitly given by the strictly two-dimensional comparison method. Therefore, this Lyapunov function can be extended into three-dimensions, although it is not too evident how this should be done. In the next section I shall show how this extension was made.

# 5 Main theorem

The main theorem of this paper is stated as follows.

**Theorem 3** *Let* $F_0$ *be given by* (3) *and* $\overline{F}_0$ *be given by* (10)*, let* (A-I)-(A-IV) *hold and assume there exist* $\alpha > 0$*,* $\beta > 0$ *and* $\gamma \geq 0$ *such that*

(L–I) $\left(F_0(s) - \overline{F}_0(s)\right)(s - \lambda_0) < 0,\ s \neq \lambda_0.$

(L–II) $\alpha\psi_1(s)f_0(s) - \beta\psi_0(s)f_1(s) + \alpha\gamma h(s)\psi_0(s) < 0$

*holds for* $0 < x < K$*. Then the equilibrium* $(\lambda_0, F_0(\lambda_0), 0)$ *is globally asymptotically stable, except for initial conditions in the* $(s, x_1)$*-coordinate plane and the* $(x_0, x_1)$*-coordinate plane.*

**Remark 2** In Lindström (1994)[21] and Lindström (1994)[22] I proved the above theorem in the special case $\gamma = 0$. This theorem was proved using a three dimensional variant of the Lyapunov function (6) and LaSalle's extension theorem, cf. LaSalle (1960) and Hale (1969). In Lindström (1994)[21], I showed that this theorem contains the first partial answers given by Hsu (1978)[13], as alluded to in section 1. Furthermore, I showed, that there exist parameter values of the system (1), such that Kustarov's theorem, theorem 1, does not apply, but theorem 3 applies.

**Proof** The key idea is to extend the Lyapunov function (8) and write the extension in the following form

$$\begin{aligned} V(s, x_0, x_1) &= \int_{F_0(\lambda_0)}^{x_0} \exp(\gamma x_0') \frac{x_0' - F_0(\lambda_0)}{x_0'} dx_0' + \\ & \int_{x_0}^{x_0 + \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds'} \exp(\gamma x_0') dx_0' + \\ & \int_{x_0 + \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')}}^{x_0 + \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds' + \frac{\alpha}{\beta} x_1} \exp(\gamma x_0') dx_0' \end{aligned} \tag{11}$$

This Lyapunov function is positive. Moreover, by (A-I), it is radially unbounded with respect to $(\lambda_0, F_0(\lambda_0), 0)$ in all directions essential after that boundedness of solutions has been proved. The total time-derivative with respect to the system (2) is given by

$$\begin{aligned} \dot{V} &= x_0 \psi_0(s) \exp(\gamma x_0) \frac{x_0 - F_0(\lambda_0)}{x_0} + \\ & x_0 \psi_0(s) \exp(\gamma x_0) \left( \exp\left( \gamma \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds' \right) - 1 \right) + \\ & x_0 \psi_0(s) \exp(\gamma x_0) \exp\left( \gamma \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds' \right) \left( e^{\gamma \frac{\alpha}{\beta} x_1} - 1 \right) + \\ & f_0(s) \left( F_0(s) - x_0 - x_1 \frac{f_1(s)}{f_0(s)} \right) \exp(\gamma x_0) \exp\left( \gamma \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds' \right) \frac{\psi_0(s)}{f_0(s)} + \\ & f_0(s) \left( F_0(s) - x_0 - x_1 \frac{f_1(s)}{f_0(s)} \right) \exp(\gamma x_0) \exp\left( \gamma \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds' \right) \cdot \\ & \left( e^{\gamma \frac{\alpha}{\beta} x_1} - 1 \right) \frac{\psi_0(s)}{f_0(s)} + x_1 \psi_1(s) \exp(\gamma x_0) \exp\left( \gamma \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds' \right) \frac{\alpha}{\beta} e^{\gamma \frac{\alpha}{\beta} x_1}. \end{aligned}$$

We reorganize this expression and get,

$$\begin{aligned} \dot{V} &= \exp(\gamma x_0) \exp\left( \gamma \int_{\lambda_0}^{s} \frac{\psi_0(s')}{f_0(s')} ds' \right) \cdot \left( \left( F_0(s) - \overline{F}_0(s) \right) \psi_0(s) + \right. \\ & x_0 \psi_0(s) \left( e^{\gamma \frac{\alpha}{\beta} x_1} - 1 \right) - x_1 \frac{f_1(s)}{f_0(s)} \psi_0(s) + F_0(s) \left( e^{\gamma \frac{\alpha}{\beta} x_1} - 1 \right) \psi_0(s) - \\ & \left. x_0 \left( e^{\gamma \frac{\alpha}{\beta} x_1} - 1 \right) \psi_0(s) - x_1 \frac{f_1(s)}{f_0(s)} \left( e^{\gamma \frac{\alpha}{\beta} x_1} - 1 \right) \psi_0(s) + x_1 \psi_1(s) \frac{\alpha}{\beta} e^{\gamma \frac{\alpha}{\beta} x_1} \right) \end{aligned}$$

$$
\begin{aligned}
&= \exp(\gamma x_0)\exp\left(\gamma\int_{\lambda_0}^{s}\frac{\psi_0(s')}{f_0(s')}ds'\right)\cdot\Bigg(\left(F_0(s)-\overline{F}_0(s)\right)\psi_0(s)+ \\
&\quad x_1\psi_1(s)\frac{\alpha}{\beta}e^{\gamma\frac{\alpha}{\beta}x_1}-x_1\frac{f_1(s)}{f_0(s)}\psi_0(s)e^{\gamma\frac{\alpha}{\beta}x_1}+\frac{h(s)}{f_0(s)}\left(e^{\gamma\frac{\alpha}{\beta}x_1}-1\right)\psi_0(s)\Bigg) \\
&= \exp(\gamma x_0)\exp\left(\gamma\int_{\lambda_0}^{s}\frac{\psi_0(s')}{f_0(s')}ds'\right)\cdot\Bigg(\left(F_0(s)-\overline{F}_0(s)\right)\psi_0(s)+ \\
&\quad \frac{x_1e^{\gamma\frac{\alpha}{\beta}x_1}}{\beta f_0(s)}\left(\alpha f_0(s)\psi_1(s)-\beta f_1(s)\psi_0(s)+\frac{e^{\gamma\frac{\alpha}{\beta}x_1}-1}{x_1e^{\gamma\frac{\alpha}{\beta}x_1}}\beta h(s)\psi_0(s)\right)\Bigg) \\
&\le \exp(\gamma x_0)\exp\left(\gamma\int_{\lambda_0}^{s}\frac{\psi_0(s')}{f_0(s')}ds'\right)\cdot\Bigg(\left(F_0(s)-\overline{F}_0(s)\right)\psi_0(s)+ \\
&\quad \frac{x_1e^{\gamma\frac{\alpha}{\beta}x_1}}{\beta f_0(s)}\left(\alpha f_0(s)\psi_1(s)-\beta f_1(s)\psi_0(s)+\gamma\alpha h(s)\psi_0(s)\right)\Bigg) \le 0.
\end{aligned}
$$

Equality holds in the last inequality if and only if $s=\lambda_0$ and $x_1=0$. On this line, only the equilibrium point $(\lambda_0, F_0(\lambda_0), 0)$ is invariant with respect to the flow (2). In the second last inequality we used the fact that

$$
\frac{e^{\gamma\frac{\alpha}{\beta}x_1}-1}{x_1e^{\gamma\frac{\alpha}{\beta}x_1}} \le \frac{\gamma\alpha}{\beta}
$$

and in the last inequality we used the conditions, (L-I) and (L-II), of the theorem. The theorem follows by LaSalle's extension theorem, cf. LaSalle (1960) and Hale (1969). □

# 6 Example

In this section we apply the theorem to some specific parameter values in the system (1). It was pointed out Lindström (1994)[21], that condition (L-II) is always satisfied for the system (1), if $\gamma=0$. In Keener (1983), it was shown that the system (1), with sequence of linear transformations, can be rewritten as

$$
\begin{aligned}
\dot{s} &= s(1-s)-\frac{sx_0}{a_0+s}-\frac{sx_1}{a_1+s} \\
\dot{x_0} &= m_0\left(\frac{s-\lambda_0}{s+a_0}\right)x_0
\end{aligned} \tag{12}
$$

$$\dot{x_1} = m_1 \left( \frac{s - \lambda_1}{s + a_1} \right) x_1,$$

hence only six parameters can be important. We choose these six parameters as $a_0 = 0.1$, $a_1 = 0.6$, $m_0 = 1.0$, $m_1 = 3.0$, $\lambda_0 = 0.5$ and $\lambda_1 = 0.6$. In this case theorem 1 cannot be applied, since $\psi_0(s)$ and $\psi_1(s)$ intersect at two points in the interval $0 < s < 1$, see figure 1(a). This means that the extinction results in Hsu et. al. (1978) do not apply either. The expression $F_0(s) - F_0(\lambda_0)$ changes sign twice in the interval $0 < s < 1$, too, so the results in Lindström (1994)[21] and Lindström (1994)[22] do not apply either, see figure 1(b). Since the results in Hsu (1978)[13] were included in the above results, they do not apply either. However, if we choose $\gamma = 1.8$, the expression $F_0(s) - \overline{F}_0(s)$ changes sign once in the interval $0 < s < 1$, figure 1(c). The choice $\alpha = 1$ and $\beta = 3$ shows that $\alpha$ and $\beta$ can be chosen so that the conditions of theorem 3 still are valid, figure 1(d). Hence the equilibrium point $(\lambda_0, F(\lambda_0), 0)$ of system (12) is globally stable in the positive octant if $a_0 = 0.1$, $a_1 = 0.6$, $m_0 = 1.0$, $m_1 = 3.0$, $\lambda_0 = 0.5$ and $\lambda_1 = 0.6$.

# 7 Summary

We have stated and proved a new theorem for global stability of the model (2) in this paper. The starting point was the two dimensional Lyapunov function (7), originally presented by Ardito and Ricciardi (1995). The Lyapunov function (7) is rewritten in a specific way, so that it is easy to see the geometric meaning of it. After this, it is extended into three dimensions and applied to (2). The result is two basic sufficient conditions for global stability of the system (2) in the positive octant. These conditions are purely geometrical, hence easy to check. At the end of the paper we apply the result to a specific example.

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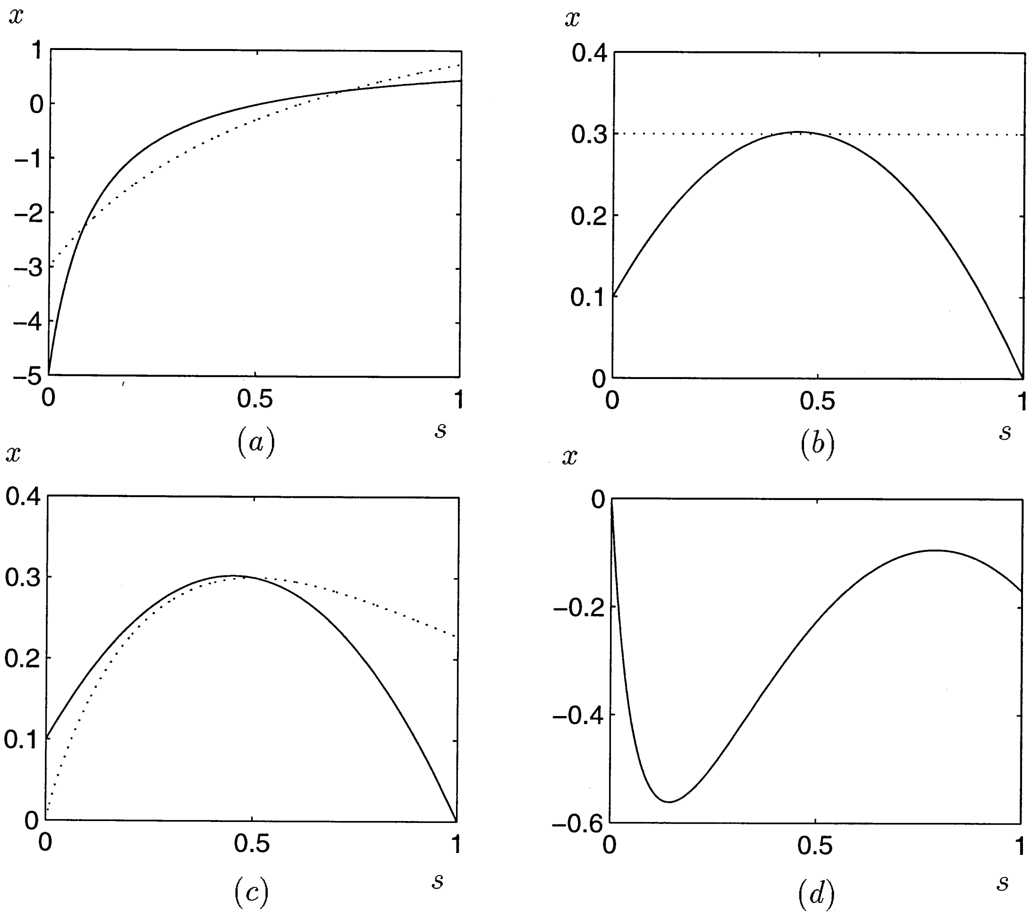


Figure 1: The system (12) is considered and the parameters are given by $a_0 = 0.1$, $a_1 = 0.6$, $m_0 = 1.0$, $m_1 = 3.0$, $\lambda_0 = 0.5$ and $\lambda_1 = 0.6$. (a) The functions $x = \psi_0(s)$ (solid) and $x = \psi_1(s)$ (dotted) intersect at two points. (b) The functions $x = F_0(s)$ (solid) and $x = F_0(\lambda_0)$ (dotted) intersect at two points, too. (c) If $\gamma = 1.8$, then the functions $x = F_0(s)$ (solid) and $\overline{F}_0(s)$ (dotted) intersect each other once. (d) If $\gamma = 1.8$, $\alpha = 1$ and $\beta = 3$, the the function $x = \alpha f_0(s)\psi_1(s) + f_1(s)\psi_0(s) + \gamma\alpha h(s)\psi_0(s)$ is strictly negative in the unit interval.