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# THREE-DIMENSIONAL STABLY ADMISSIBLE PREY-PREDATOR MODELS

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## Abstract

This paper deals with the most interesting three dimensional Volterra systems, which have first a sign stable interaction matrix. This matrix is stably admissible too. Then we consider a balanced interaction matrix, which is not sign stable, because it has a cycle, but it is stably admissible, and lost we consider an interesting not stably admissible case.

*Keywords:* sign stability, stably admissibility.

## 1. Introduction

Paper [1] introduces the concept of sign stability, in which case without the exact knowledge of the elements of a matrix we can determine its stability behaviour merely from the sign of its elements. Paper [2] deals with the concept of stably admissible matrices. Applying this we may determine the global asymptotic stability of a solution, or whether some nonconstant periodic solutions occur in Lotka-Volterra systems. We illustrate these concepts by considering a not too complicated population dynamical model. These ideas are of great importance at such models because they may give some information about the future of the system without memory the exact value of the parameters.

## 2. The Survey of the Used References

Let $\mathbf{A}=[a_{ij}]$ be an $n\times n$ real matrix, and its eigenvalues be $\lambda_i$, $i=1,\dots,n$.
**Def 2.1**: $\mathbf{A}$ is called stable, if $Re\lambda_i < 0$, for all $i=1,\dots,n$.
**Def 2.2**: $\mathbf{A}$ is called quasi-stable, if $Re\lambda_i \leq 0$, for all $i=1,\dots,n$, and it has a simple Jordan normal form.

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**Def 2.3**: **A** is called semistable, if $Re\lambda_i \leq 0$, for all $i = 1, \dots, n$.
**Def 2.4**: **A** is called sign stable, sign quasi-stable, sign semistable if each matrix **B** of the same sign-pattern as **A** (sgn $b_{ij}$ =sgn$a_{ij}$ for all $i, j$) is stable, quasi-stable, semistable, respectively.

Let a directed graph $D_{\mathbf{A}}$ and an undirected graph $G_{\mathbf{A}}$ be attached to **A** as follows:

The vertex set of $D_{\mathbf{A}}$ is $V = \{1, \dots, n\}$ and its edge set is $\{(i, j) : i \neq j$ and $a_{ij} \neq 0\}$ . The vertex set of $G_{\mathbf{A}}$ is $V = \{1, \dots, n\}$ and its edge set is $\{\{i, j\} : i \neq j$ and $a_{ij} \neq 0 \neq a_{ji}\}$. Let $R_{\mathbf{A}} = \{i : a_{ii} \neq 0\}$.
**Def 2.5**: We have an $R_{\mathbf{A}}$-colouring of $G_{\mathbf{A}}$ if the next assumptions are valid:

1. each vertex in $R_{\mathbf{A}}$ is black;
2. no black vertex has precisely one white neighbour;
3. each white vertex has at least one white neighbour.

Let $\cup M$ be the set of vertices of edges in $G_{\mathbf{A}}$ which have no common vertex.
**Def 2.6**: $V \setminus R_{\mathbf{A}}$ is called a complete matching if $V \setminus R_{\mathbf{A}} \subset \cup M$ is valid.
**Theorem 2.1**: (Jeffries–Klee–v.d. Driessche) **A** is sign semistable if and only if it satisfies the following conditions:

($\alpha$) $a_{ii} \leq 0$ for all $i$;
($\beta$) $a_{ij}a_{ji} \leq 0$ for all $i \neq j$;
($\gamma$) $D_{\mathbf{A}}$ has no $k \geq 3$ cycle.

($D_{\mathbf{A}}$ has $k \geq 3$ cycle, if $a_{i(1)i(2)} \dots a_{i(k-1)i(k)}a_{i(k)i(1)} \neq 0$ for some sequence of $k \geq 3$ distinct indices $i(1), \dots, i(k)$).
**Theorem 2.2**: (Jeffries–Klee–v.d.Driessche) **A** is sign stable if and only if it satisfies the conditions of Theorem 2.1, and the following two conditions:

($\delta$) in every $R_{\mathbf{A}}$-colouring of the undirected graph $G_{\mathbf{A}}$ all vertices are black;
($\epsilon$) the graph $G_{\mathbf{A}}$ admits a $V \setminus R_{\mathbf{A}}$-complete matching.

**Theorem 2.3**: (Jeffries–Klee–v.d.Driessche) The sufficient condition of **A** to be a sign quasi-stable matrix is that **A** satisfies the conditions of Theorem 2.1 and **A** is skew-symmetric in the sense that

($\beta^*$) sgn $a_{ji}$= −sgn $a_{ij}$ for all $i \neq j$
(thus $a_{ij}a_{ji} = 0$ if and only if $a_{ij} = a_{ji} = 0$ for all $i \neq j$.)

The proof of these theorems can be found in [1]. We consider the Volterra system:

$$\dot{x_i} = x_i(c_i + \sum_{j=1}^{n} a_{ij}x_j), : x_i(0) > 0, : (i = 1 \dots, n), \tag{2.1}$$

where $c_i$ and $a_{ij}$ are real constants. Assume that:

$$a_{ii} \leq 0, \text{and} a_{ij}a_{ji} < 0 \quad \text{if} \quad (i-j)a_{ij} \neq 0, (i,j = 1\ldots,n). \tag{2.2}$$

We suppose that there exists a positive equilibrium point $E = (e_i)$ such that:

$$c_i + \sum_{j=1}^{n} a_{ij}e_j = 0, (i = 1\ldots,n).$$

It means that the system (2.1) has the following linearization at $E$:

$$\dot{x_i} = e_i \sum_{j=1}^{n} a_{ij}x_j.$$

(Condition (2.2) means that the $D_{\mathbf{A}}$ and the $G_{\mathbf{A}}$ graphs of the matrix **A** are the same.)
**Def 2.7**: $\tilde{\mathbf{A}}$ is a perturbation of **A**, if $\tilde{a}_{ii} \leq 0$ and $\tilde{a}_{ij} = 0$ for $i \neq j$ if and only if $a_{ij} = 0$; the perturbation is small if

$$\max_{i,j} =| \tilde{a}_{ij} - a_{ij} |$$

is small.
**Def 2.8**: The matrix **A** is admissible if there exists $p_i > 0$ such that $(p_i a_{ij}) \leq 0$, i.e. the matrix $(p_i a_{ij})$ is negative semidefinite and, in addition,

$$\sum_{i=1}^{n}\sum_{j=1}^{n} p_i a_{ij} w_i w_j = 0 \Longrightarrow a_{ii}w_i = 0, : i = 1\ldots,n, (w_1,\ldots,w_n) \in \mathbf{R}^n.$$

The matrix **A** is stably admissible if every matrix $\tilde{\mathbf{A}}$ obtained by a sufficiently small perturbation of **A** is admissible.

Let us denote a cycle $a_{i(1)i(2)}\cdots a_{i(k-1)i(k)}a_{i(k)i(1)} \neq 0$ of the graph $G_{\mathbf{A}}$ of the matrix **A** by $[i(1), i(2), \ldots, i(k)]$.
**Def 2.9**: The cycle $[i(1), i(2), \ldots, i(k)]$ of the matrix **A** is balanced if

$$| a_{i(1)i(2)}\cdots a_{i(k-1)i(k)}a_{i(k)i(1)} |=| a_{i(2)i(1)}\cdots a_{i(k)i(k-1)}a_{i(1)i(k)} | .$$

**Def 2.10**: The matrix **A** is balanced if its cycles are all balanced.

Now we colour the vertices of graph $G_{\mathbf{A}}$ which belong to the set $R_{\mathbf{A}}$ black but omit the $R_{\mathbf{A}}$-colouring of the graph.

**Def 2.11**: An edge which directly connects two black dots is called a strong link.

See the proof of the following theorems in [2].

**Theorem 2.4**: (Redheffer–Zhiming) If the matrix **A** is stably admissible then every cycle in its graph must contain at least one strong link. Conversely, if a balanced matrix **A** has this property then it is stably admissible.

**Def 2.12**: We have the reduced graph $R_{\mathbf{A}}$ of matrix **A** if the following colouring process is continued till the colours of the vertices cannot be changed any more.

1. All vertices of graph $G_{\mathbf{A}}$ which belong to $R_{\mathbf{A}}$ are black.

2. Suppose that vertex $i$ is 'black' • or 'plus' $\oplus$ , and all vertices adjacent to $i$ are • except the single vertex $j$. Then we colour $j$ to • .

3. Suppose there is a • or a $\oplus$ at $i$ and a • or a $\oplus$ at the vertex adjacent to $i$ except for a single vertex $j$ adjacent to $i$. Then we put $\oplus$ at $j$.

4. Suppose $i$ is 'white' ∘, and we have a • or a $\oplus$ at each vertex $j$ adjacent to $i$. Then we put a $\oplus$ at $i$.

(Preference is always given to • when there is a choice between • and $\oplus$. See the meaning of this colouring in [1] and [4].)

**Theorem 2.5**: (Redheffer–Zhiming) If the graph $R_{\mathbf{A}}$ of some stably admissible matrix **A** has • or $\oplus$ at every vertex, then the solutions of system (2.1) have a limit as $t \to \infty$ which may depend on the initial conditions. If every vertex has • , the limit is independent of the initial conditions. In neither case can there be a limit a cycle, a nonconstant periodic solution, or a strange attractor.

(It is easy to see that Theorem 2.5 gives global asymptotic stability.)

## 3. The General Model

Consider the following three dimensional predator-prey system:

$$\left.\begin{aligned} \dot{x} &= xF(x, y_1, y_2, K) \\ \dot{y_1} &= y_1 G_1(x, y_1, y_2) \\ \dot{y_2} &= y_2 G_2(x, y_1, y_2) \end{aligned}\right\} \tag{3.1}$$

where $F, G_i \in C^1$: $(i = 1, 2)$ and $y_i(t)$ is the quantity of predator $i$ at time $t, (i = 1, 2)$ and assume that the two predators are competing for the prey $x(t)$. (Denote $F_x(x, y_1, y_2, K) = \partial F(x, y_1, y_2, K)/\partial x$,etc.) The natural rules induce the following conditions: Assume that there exists a positive equilibrium point $E = (x_0, y_{10}, y_{20})$ namely $F(E, K) = G_i(E) = 0, i = 1, 2.$ and that

$$(x - K)F(x, 0, 0, K) < 0, x \neq K, F_{yi}(x, y_1, y_2, K) < 0, x > 0 (i = 1, 2), \tag{3.2}$$

$$G_i(0, y_1, y_2) < 0, G_{iyi}(x, y_1, y_2) \leq 0, G_{1x}(x, y_1, y_2) > 0, G_{2x}(x, y_1, y_2) > 0, \tag{3.3}$$

$$(x, y_1, y_2) \in Int\mathbf{R}^3_+, (i = 1, 2),$$

$$F(0, 0, 0, K) > 0, F(K, 0, 0, K) = 0. \tag{3.4}$$

(See in [3]). Linearize the system (3.1) in the equilibrium point $E$. The coefficient matrix $\mathbf{A}$ of the linear system is: (all functions are to be taken at $E$).

$$\mathbf{A} = \begin{bmatrix} x_0 F_x & x_0 F_{y1} & x_0 F_{y2} \\ y_{10} G_{1x} & y_{10} G_{1y1} & y_{10} G_{1y2} \\ y_{20} G_{2x} & y_{20} G_{2y1} & y_{20} G_{2y2} \end{bmatrix} \tag{3.5}$$

Our problem is under what conditions will the matrix $\mathbf{A}$ be stable, namely what can we say about the behaviour of solutions. The characteristic polynomial is:

$$\begin{aligned} D(\lambda) = {} & \lambda^3 - \lambda^2[x_0 F_x + y_{10} G_{1y1} + y_{20} G_{2y2}] \\ & -\lambda[x_0 y_{10}(F_{y1} G_{1x} - F_x G_{1y1}) + x_0 y_{20}(F_{y2} G_{2x} - F_x G_{2y2}) + \\ & y_{10} y_{20}(G_{1y2} G_{2y1} - G_{1y1} G_{2y2})] - \det \mathbf{A}. \end{aligned} \tag{3.6}$$

Let us denote the coefficients of the constant, linear and quadratic terms of the characteristic polynomial by $a_0$, $a_1$, $a_2$, respectively. The Hurwitz determinant of the polynomial is:

$$\begin{aligned} a_2 a_1 - a_0 = {} & x_0^2 y_{10} F_x(F_{y1} G_{1x} - F_x G_{1y1}) + x_0^2 y_{20} F_x(F_{y2} G_{2x} - F_x G_{2y2}) \\ & + x_0 y_{20}^2 G_{1y1}(F_{y1} G_{1x} - F_x G_{1y1}) + y_{10}^2 y_{20} G_{1y1}(G_{1y1} G_{2y1} - G_{1y1} G_{2y2}) \\ & + x_0 y_{20}^2 G_{2y2}(F_{y2} G_{2x} - F_x G_{2y2}) + y_{10} y_{20}^2 G_{2y2}(G_{1y1} G_{2y1} - G_{1y1} G_{2y2}) + \\ & x_0 y_{10} y_{20}(-F_x G_{1y1} G_{2y2} - F_x G_{1y1} G_{2y2} + F_{y1} G_{1y2} G_{2x} + F_{y2} G_{1x} G_{2y1}) \end{aligned} \tag{3.7}$$

Finally, $\mathbf{A}$ is stable (according to the well-known Hurwitz criteria) if and only if:

$$a_0, a_1, a_2 > 0$$

and the Hurwitz determinant

$$a_2 a_1 - a_0 > 0. \tag{3.8}$$

Now, we shall proceed to the study of concrete models. We start with the easiest but biologically meaningful matrix **A**, and then treat a more complicated case. We are going to study the stability conditions in all cases using the methods of Section 2.

## 4. The Stability Behaviour of the Different Models

In this section first we will present the matrix **A** with its graph, then we are going to reach the conclusions and support them with the study of Hurwitz criteria.

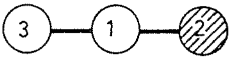
4.1 Let the system be:

$$\left.\begin{aligned} \dot{x} &= xF(y_1, y_2) \\ \dot{y_1} &= y_1 G_1(x, y_1) \\ \dot{y_2} &= y_2 G_2(x) \end{aligned}\right\} \tag{4.1}$$

This is the simplest model, which is biologically rational. This model can have a positive equilibrium point $E$. There is no intraspecific competition in prey, no interspecific competition between predators, no intraspecific competition in $G_2$, because $F, G_i, G_2$ is independent of $x, y_j (j \neq i), y_2$ respectively. The coefficient matrix **A** of the system linearized at $E$ is:

$$\mathbf{A} = \begin{bmatrix} 0 & x_0 F_{y1} & x_0 F_{y2} \\ y_{10} G_{1x} & y_{10} G_{1y1} & 0 \\ y_{20} G_{2x} & 0 & 0 \end{bmatrix}$$

The graph $D_{\mathrm{A}} = G_{\mathrm{A}}$ is:




It is easy to see that the matrix **A** satisfies the conditions of Theorem 2.2, hence $A$ is sign stable. (Of course the case $G_{1y1} = 0$ and $G_{2y2} \neq 0$ is the same.) By the way, if the characteristic polynomial is denoted by $D(\lambda) = \lambda^3 + c_2\lambda^2 + c_1\lambda + c_0$, it can easily be seen from (3.6) that $c_i > 0, c_i \in$

**R**, and the Hurwitz determinant (3.7) is also positive. This means that the system has a stable focus or a stable node. The graph $R_{\mathbf{A}}$ of the matrix **A** is:


We get this by applying first, the second point of Definition 2.12 to vertex 2 then to vertex 1. Thus, we can apply the Theorem 2.5 and see that $E$ is a globally asymptotically stable equilibrium point of the linear system, furthermore, it is globally asymptotically stable of the nonlinear system if it is a Volterra one.

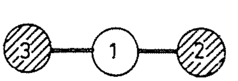
4.2 Let the system be now:

$$\left.\begin{aligned} \dot{x} &= xF(y_1, y_2) \\ \dot{y_1} &= y_1 G_1(x, y_1) \\ \dot{y_2} &= y_2 G_2(x, y_2) \end{aligned}\right\} \tag{4.2}$$

There is no intraspecific competition in prey and no interspecific competition between predators apart from the fact that they both eat the same prey. The coefficient matrix **A** of the system linearized at $E$ is:

$$\mathbf{A} = \begin{bmatrix} 0 & x_0 F_{y1} & x_0 F_{y2} \\ y_{10} G_{1x} & y_{10} G_{1y1} & 0 \\ y_{20} G_{2x} & 0 & y_{20} G_{2y2} \end{bmatrix}$$

The graph $D_{\mathbf{A}} = G_{\mathbf{A}}$ is:




It is easy to see that we can say the same as in case 4.1. (All vertices of the graph $R_{\mathbf{A}}$ are black: we have to apply the 2 nd point of Definition 2.12 to vertex 2 or 3 of the graph $G_{\mathbf{A}}$.)

**4.3** Let the system be:

$$\left.\begin{aligned} \dot{x} &= xF(x, y_1, y_2) \\ \dot{y_1} &= y_1 G_1(x, y_1) \\ \dot{y_2} &= y_2 G_2(x) \end{aligned}\right\} \tag{4.3}$$

There is no interspecific competition between predators. The coefficient matrix $\mathbf{A}$ of the system linearized at $E$ is:

$$\mathbf{A} = \begin{bmatrix} x_0F_x & x_0F_{y1} & x_0F_{y2} \\ y_{10}G_{1x} & y_{10}G_{1y1} & 0 \\ y_{20}G_{2x} & 0 & 0 \end{bmatrix}$$

(See the detailed study of this case by Ljapunov function in [3]). The graph $D_{\mathbf{A}} = G_{\mathbf{A}}$ is:


The matrix $\mathbf{A}$ is sign stable in this case. It would be sign stable also if we had $G_{1y1} = 0$ and $G_{2y2} \neq 0$.

(It is easy to see that the matrices in case 4.1 and 4.2 are also sign stable). All vertices of the graph $R_{\mathbf{A}}$ of the matrix $\mathbf{A}$ are black: apply the 2nd point of Definition 2.12 to the vertex 1 of the graph $G_{\mathbf{A}}$. Thus the solutions are globally asymptotically stable if it is a Volterra system. Thus we get the following theorems:

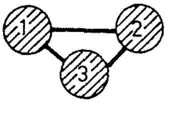
**Theorem 4.1:** If the system (3.1) satisfies the conditions (3.2)–(3.4) and $F_x \leq 0, G_{1y1}^2 + G_{2y2}^2 > 0$ and the graph $D_{\mathbf{A}} = G_{\mathbf{A}}$ has not got any cycle then (3.5) is sign stable. Furthermore, if the system is a Volterra one then $E$ is globally asymptotically stable.

**Theorem 4.2:** A system satisfies the Theorem 4.1 if it is a (4.1) or a (4.2) or a (4.3).

Remark: There are some other systems which satisfy the Theorem 4.1, but these three are the most important according to their graphs.

The matrix $\mathbf{A}$ occurring in case 4.1–4.3 are stably admissible (see Theorem 2.4). We may get some other stably admissible cases when the graph $G_{\mathbf{A}}$ has a cycle. Let us consider these cases:

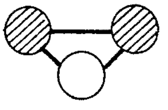
**4.4** Let the system be the most general, thus the coefficient matrix $\mathbf{A}$ of the linear system is (3.5) where $G_{1y2}G_{2y1} < 0$. The graph $D_{\mathbf{A}} = G_{\mathbf{A}}$ is:




Here we cannot satisfy condition ($\gamma$) of Theorem 2.1, i.e. this cannot be a sign semistable case. In order to guarantee some stability (which of course depends on the effective values of the elements of the matrix) let $\mathbf{A}$ be balanced, therefore:

$$| F_{y1}G_{1y2}G_{2x} |=| G_{1x}G_{2y1}F_{y2} | . \qquad (4.4)$$

Then from (3.6) we get: $D(\lambda) = \lambda^3 + c_2\lambda^2 + c_1\lambda - \det \mathbf{A}$, where $c_i > 0, c_i \in \mathbf{R}$, $i = 1,2$. It is easy to see that the det **A**¡0 if (4.4) is satisfied. Also there holds the Hurwitz criterion (3.8). Thus **A** is stable in this case (but not signstable). Since the matrix **A** is stably admissible, then, because of Theorem 2.5, the equilibrium point of (3.1) is globally asymptotically stable, if the system is a Volterra one. The same holds if $F_x \neq 0$ and $G_{1y1} \neq 0$ but $G_{2y2} = 0$, or $F_x \neq 0$ and $G_{2y2} \neq 0$ but $G_{1y1} = 0$, or $F_x = 0$ and $G_{iyi} \neq 0 (i = 1,2)$. In these cases the matrix $A$ remains stably admissible because the graph $G_{\mathbf{A}}$ - after colouring its vertices which belong to set $R_{\mathbf{A}}$ – has a strong link. Thus we get the following graph:



But we can colour the white vertex of this graph black, if we apply the 2nd point of Definition 2.12. Then applying Theorem 2.5, we get the previous result, i.e.:

**Theorem 4.3:** If the system (3.1) satisfies the conditions (3.2)–(3.4) $F_x \leq 0$ and (4.4), and two out of the quantities $F_x, G_{1y1}, G_{2y2}$ do not vanish, then $E$ is a globally asymptotically stable equilibrium point if the system is a Volterra one.

We worked out the biologically possible stably admissible cases. We shall examine one more matrix which is not stably admissible, nevertheless we can guarantee stability under certain conditions.

**4.5** Let the coefficient matrix **A** of the system linearized at $E$ be:

$$\mathbf{A} = \begin{bmatrix} x_0F_x & x_0F_{y1} & x_0F_{y2} \\ y_{10}G_{1x} & y_{10}G_{1y1} & y_{10}G_{1y2} \\ y_{20}G_{2x} & 0 & y_{20}G_{2y2} \end{bmatrix} \qquad (4.5)$$

and $\delta = y_{10}G_{1y2} \neq 0$. We want to illustrate that the stability, obviously, depends on that how small $| \delta |$ remains. It is clear from (3.6) that: $D(\lambda) = \lambda^3 + c_2\lambda^2 + c_1\lambda - \det\mathbf{A}(\delta)$, where $c_i > 0$, $c_i \in \mathbf{R}$, $i = 1,2$. It is easy to see that if $\delta > 0$ then det $\mathbf{A}(\delta) < 0$. Then the stability depends on whether the Hurwitz determinant is positive or not. If $\delta < 0$ then the Hurwitz determinant (3.7) is positive. Then the stability depends on the condition det $\mathbf{A}(\delta) < 0$. Thus, we get from these two conditions about $\delta$ the following theorem.

**Theorem 4.4:** The matrix (4.5) satisfying the conditions (3.2)-(3.4) is stable if $\delta_1 < \delta < \delta_2$, and $\delta_1 < 0, \delta_2 > 0$, where:

$$\delta_1 = y_{10}\frac{1}{F_{y1}G_{2x}}[G_{1y1}G_{2x}F_{y2} + G_{2y2}G_{1x}F_{y1} + G_{2y2}G_{1y1}F_x],$$

$$\delta_2 = -\frac{1}{x_0 y_{20}}\frac{1}{F_{y1}G_{2x}}[(x_0F_x + y_{10}G_{1y1})(y_{10})$$

$$\{x_0(F_{y1}G_{1x} - F_xG_{1y1}) - y_{20}(G_{1y1}G_{2y2})\}+$$

$$(x_0F_x + y_{20}G_{2y2})(y_{20})\{x_0(F_{y2}G_{2x} - F_xG_{2y2}) - y_{10}(G_{1y1}G_{2y2})\}].$$

Corollary: If $\delta = \delta_1$ then $\det A = 0$, there is an eigenvalue $\lambda_1 = 0$. If $\delta = \delta_2$, then the Hurwitz determinant is equal to zero, then the real part of the complex conjugate rootpair vanishes. Thus in case $\delta = \delta_2$ an Andronov-Hopf bifurcation occurs.

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