

STABILITY IN MAMMILARY COMPARTMENTAL SYSTEMS

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This paper is concerned with the stability of mammillary compartmental system with constant transfer rates and no ingestion of material to any compartment from the outside environment.

1. INTRODUCTION

Compartmental analysis has recently been one of the most widely used mathematical techniques in biological modeling (see for example Jaquez⁴). In this technique a system is divided into "compartments" with laws defining rates of exchange between them, usually exchange of some material. In physiological models^{6,8} the compartments could be suborgans of an organ in the body, whereas in ecological model⁵, the compartments could be populations.

In the usual representation for a compartmental system, a box (or a point) denotes a compartment, and an arrow indicates the transfer of material into or out of a compartment (see Fig. 1). There also may be inputs from the outside environment into one or more compartments (vertical arrows pointing into the tops of boxes) and

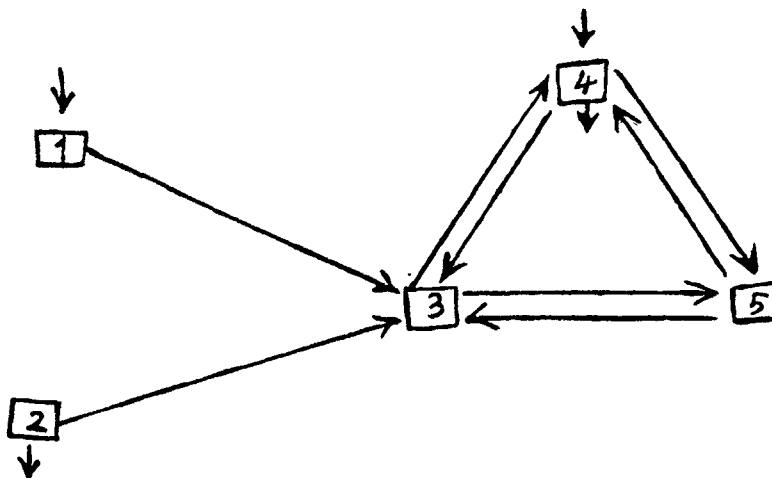


FIG. 1.

there can be excretion of material from some of the compartments to the outside environment (vertical arrows pointing out of the bottoms of boxes). Should there be no exchange of material to the outside environment, the compartmental systems are referred to as closed, otherwise, it is said to be an open system. Realistically, many compartmental systems are open, for some material are lost due excretion, metabolism, etc.

The goal of this article is to investigate the approach to equilibrium point (stability) in mammillary compartmental systems (this will be done in section 3). A mammillary compartmental system has a central compartment called "mother" which exchanges material with all the other, "daughter" compartments, but there is direct exchange between any two of the daughters. Each cycle of length exactly two. Levine² considers an example (a nonlinear closed mammillary compartmental system) of a mammillary compartmental system. He considers the resources R as "mother" and n species as daughters with biomasses N_1, N_2, \dots, N_n which lose biomass to the environment at exponential rates a_1, \dots, a_n respectively. Then, N_1, \dots, N_n obey equations of the form

$$\dot{N}_i = -a_i N_i + f_i \left(K - \sum_{j=1}^n N_j, N_i \right), \quad i = 1, \dots, n$$

$$f_{i1}, f_{i2} > 0$$

where f_i are the ingestion functions from the source R into the compartment i , f_{i1} and f_{i2} denote partial derivatives of f_i with respect to the first and second arguments, and $K = \sum_{i=1}^n N_i + R$ (i.e. the total biomass is constant). Daniel S. Levine shows that the local stability of a positive solution (if it exists) under the condition that the ingestion functions f_i ($i = 1, \dots, n$) are grown slower than linearly with N_i . He derives some propositions concerned with competitive systems. Finally he put the following question: "whether approach to equilibrium occurs for all mammillary systems or more particularly for mammillary systems with structure described in his article?".

2. THE MODEL

Let x_1, \dots, x_n denote the biomass of compartments 1, \dots , n respectively (see for example Fig. 2) with central vertex (mother) compartment 1 which exchanges material with all the other compartments (daughters) such that there is no direct exchange of material between any of two daughters and we assume that there is no input of material from the outside environment. The biomasses x_1, \dots, x_n (here, the variables) obey the equations:

$$\dot{x}_1 = a_{11} x_1 + \sum_{i=1}^{(n-1)} b_i x_{i+1}$$

$$\dot{x}_2 = a_1 x_1 - b_1 x_2 \quad (*)$$

$$\begin{aligned} \dot{x}_3 &= a_2 x_1 - b_2 x_3 \\ \vdots \\ \dot{x}_n &= a_{n-1} x_1 - b_{n-1} x_n \end{aligned}$$

where the transfer components a_i, b_i are nonnegative constants and $\dot{x}_1, \dots, \dot{x}_n$ are the rates of change of biomass of the compartments 1, ..., n respectively. This model has matrix of the form :

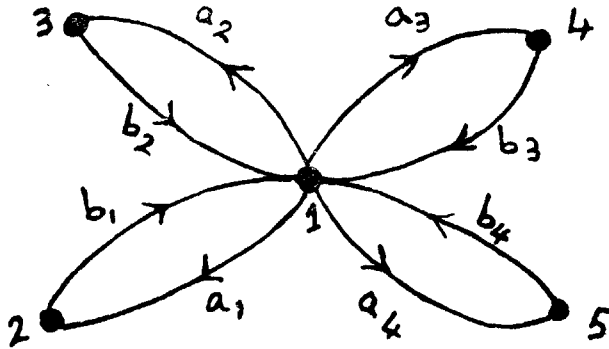


FIG. 2. A mammillary system with five compartments.

$$A = \begin{bmatrix} a_{11} & b_1 & b_2 & \dots & b_{n-1} \\ a_1 & -b_1 & 0 & \dots & 0 \\ a_2 & 0 & -b_2 & \dots & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ a_{n-1} & 0 & 0 & \dots & -b_{n-1} \end{bmatrix} \quad \dots(2.1)$$

where $a_{11} = -\sum_{i=1}^{(n-1)} a_i$, if the system (*) is closed and $a_{11} = -[a_{01} + \sum_{i=1}^{(n-1)} a_i]$ if the

system (*) is open, a_{01} is an excretion of material (biomass) from compartment a 1 (mother) to the outside environment. In the case of open mammillary compartmental systems, the trivial solution is locally asymptotically stable as shown in the following theorem :

3. THEOREM

Theorem— The trivial solution of mammillary compartmental system (*) is locally asymptotically stable if there exists an excretion of material from some of the compartments to the outside environment (that is if the system is open).

PROOF : The eigenvalues of the matrix A (2.1) are real because each of its cycle is of length which does not exceed two (in this case each cycle of length exactly two) (see H. Anderson¹, p. 61). Such matrix must have nonnegative off diagonal elements,

then if the determinants of its principal minors alternate in sign, the eigenvalues of A have negative real parts⁷, but they are originally real¹, then we can deduce that the eigenvalues of A are real and negative. Consequently, the trivial solution of the system (*) is locally asymptotically stable. To verify this we restrict ourselves (for simplicity) to the mammary system with five compartments (see Fig. 2), its matrix has the form:

$$A = \begin{bmatrix} a_{11} & b_1 & b_2 & b_3 & b_4 \\ a_1 - b_1 & 0 & 0 & 0 & 0 \\ a_2 & 0 - b_2 & 0 & 0 & 0 \\ a_3 & 0 & 0 - b_3 & 0 & 0 \\ a_4 & 0 & 0 & 0 - b_4 \end{bmatrix} \quad \dots(3.1)$$

where $a_{11} = - \sum_{i=1}^4 a_i$ if the system is closed, let d_1, d_2, d_3, d_4, d_5 denote the determinants of the principal minors of A respectively. If the system is closed the verification of the stability is difficult since $d_5 = |A| = 0$ (in this case : $d_1 < 0, d_2 > 0, d_3 < 0, d_4 > 0, d_5 = |A| = 0$). For this reason, we assume that there exists an excretion of material from some of the compartments to the outside environment, for obtaining $d_5 < 0$ to conclude that the trivial solution is locally asymptotically stable. Thus, the following procedure restrict to check the sign of the principal minors of A in (3.1) (under the assumption that a_i, b_i and $a_{0i}, (i = 1, 2, \dots, n)$ are positive constants, where a_{0i} is an excretion of material from compartment, i , to the outside environment) :

(i) The case of an excretion $a_{01} > 0$ of material from the compartment 1 to the outside environment (see Fig. 3), in this case $a_{11} = -a_{01} - \sum_{i=1}^4 a_i$. One can show that the determinant of the principal minors of the matrix A are :

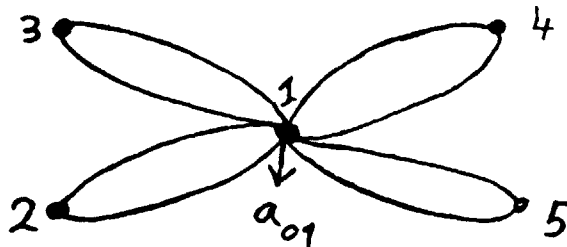


FIG. 3. A five vertices mammary systems with all excretion in compartment 1.

$$d_1 = a_{11} = - [a_{01} + \sum_{i=1}^4 a_i] < 0$$

$$d_2 = [a_2 + a_3 + a_4 + a_{01}] b_1 > 0$$

$$d_3 = - [a_3 + a_4 + a_{01}] b_1 b_2 < 0$$

$$d_4 = [a_4 + a_{01}] b_1 b_2 b_3 > 0$$

$$d_5 = |A| = -a_{01} b_1 b_2 b_3 b_4 < 0.$$

(ii) In the case of an excretion a_{02} of material from compartment 2 to the outside environment (see Fig. 4). In this case, the matrix A has the form :

$$A = \begin{bmatrix} a_{11} & b_1 & b_2 & b_3 & b_4 \\ a_1 - b_1 - a_{02} & 0 & 0 & 0 & 0 \\ a_2 & 0 & -b_2 & 0 & 0 \\ a_3 & 0 & 0 & -b_3 & 0 \\ a_4 & 0 & 0 & 0 & -b_4 \end{bmatrix} \quad \dots(3.2)$$

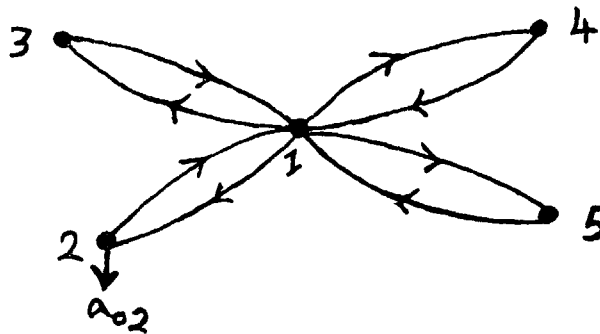


FIG. 4. A five vertices mammillary system with excretion of material from compartment 2 to the outside environment.

where $a_{11} = -\sum_{i=1}^4 a_i$. One can show that the determinants of the principal minors of A are

$$d_1 = a_{11} = -\sum_{i=1}^4 a_i < 0$$

$$d_2 = [a_2 + a_3 + a_4] (b_1 + a_{02}) + a_1 a_{02} > 0$$

$$d_3 = -[a_3 b_1 + a_4 b_1 + (a_1 + a_3 + a_4) a_{02}] b_2 < 0$$

$$d_4 = [(a_1 + a_4) a_{02} + a_4 b_1] b_2 b_3 > 0$$

$$d_5 = |A| = -a_1 a_{02} b_2 b_3 b_4 < 0.$$

(iii) In the case of an excretion $a_{03} > 0$ of material from the compartment 3 to the outside environment the determinant d_1, d_2 of the first and the second principal minors are the same as in the case of closed system i.e. $d_1 = a_{11} < 0$, $d_2 = (a_2 + a_3 + a_4) b_1 > 0$ then it remains to check the sign of the determinant of the other principal minors. The matrix A in the case has the form :

$$A = \begin{bmatrix} a_{11} & b_1 & b_2 & b_3 & b_4 \\ a_1 & -b_2 & 0 & 0 & 0 \\ a_2 & 0 & -b_2 - a_{03} & 0 & 0 \\ a_3 & 0 & 0 & -b_3 & 0 \\ a_4 & 0 & 0 & 0 & -b_4 \end{bmatrix}$$

$$d_3 = -[a_3 b_2 + a_4 b_2 + a_2 a_{03} + a_3 a_{03} + a_4 a_{03}] b_1 < 0$$

$$d_4 = [a_4 b_2 + a_2 a_{03} + a_4 a_{03}] b_1 b_3 > 0$$

$$d_5 = |A| = -a_2 a_{03} b_1 b_3 b_4 < 0$$

(iv) If there exists an excretion a_{04} of material from compartment 4 to the outside environment it suffices to examine the sign of d_4, d_5 . The matrix A in this case has the form :

$$A = \begin{bmatrix} a_{11} & b_1 & b_2 & b_3 & b_4 \\ a_2 & -b_1 & 0 & 0 & 0 \\ a_2 & 0 & -b_2 & 0 & 0 \\ a_3 & 0 & 0 & -b_3 - a_{04} & 0 \\ 0 & 0 & 0 & 0 & -b_4 \end{bmatrix}$$

One can show :

$$d_4 = [a_4 b_3 + a_4 a_{04} + a_3 a_{04}] b_1 b_2 > 0$$

$$d_5 = |A| = -a_3 a_{04} b_1 b_2 b_4 < 0.$$

(v) Finally, if there exists an excretion $a_{05} > 0$ of material from compartment 5 to the outside environment, the determinants d_1, d_2, d_3, d_4 are the same as in the closed case then it suffices to check the sign of the determinant of the last principal minor :

$$d_5 = -a_4 a_{05} b_1 b_2 b_2 < 0.$$

Thus, we observe that in each of the previous case the sign of the determinants of the principal minors of the coefficient matrix A alternate in sign then the eigenvalues of A have negative real parts⁷, but the eigenvalues of A are originally real¹, then it follows that the eigenvalues of A are real and negative proving the local stability of the trivial solution for mammillary system with five compartments, it is plausible to generate this result to the mammillary systems with n compartments.

4. DISCUSSION

In this paper we discussed the stability of mammillary compartmental system (with constant transfer rates) :

$$\dot{x} = Ax$$

with no ingestion of material to any compartment from the outside environment. It remains to study the stability of mammillary compartmental system with nonzero ingestion of material, b_i , into any compartment, i , from the outside environment, the dynamics of this system with constant flow rate are based on a differential equation of the form :

$$\dot{x} = Ax + b$$

where x and b are $n \times 1$ column vectors, A is $n \times n$ compartmental matrix. We leave this study to a future work.

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