

**BIFURCATIONS IN A SYSTEM MODELLING HANTAVIRUS
EPIDEMICS I:
TRANSCRITICAL BIFURCATION**

By

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Abstract. In this paper, a simple mathematical model is studied that describes the dynamic of Hantavirus epidemics in a rodent population. Sensitivity analysis is performed on an epidemic threshold value and it is then used to show that at its critical value a transcritical bifurcation takes place. This bifurcation is forward: a super-threshold endemic equilibrium exists, the global asymptotic stability of which is also shown.

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1. Introduction

There are situations in many disciplines which can be described, at least up to a crude first approximation, by a simple system of first order differential equations. Such are for example epidemic models where the population is divided into some groups such as susceptibles who can catch the disease and infectives who have the disease and can transmit it. Therefore, as it is usual in some of these models, we make the following assumptions (cf. [9], [8]):

- all newborns are susceptible and the birth rate is proportional to the total density of the population, because all individuals contribute equally to the procreation;
- the population is “well stirred”, meaning that every individual has an equal chance to meet any other member of the population;
- the gain in the infective class is at a rate proportional to the member of infectives and susceptibles;
- the incubation period is short enough to be negligible; that is a susceptible who contracts the disease is infective right away;
- the infection is chronic, infectives do not die of it and infectives do not loose there infectiousness probably for their whole life.

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Studies of the dynamical properties of such models usually consist of finding constant equilibrium solutions, and then carry out a linearized analysis to determine their stability with respect to small disturbances.

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In [1] the following simple mathematical model is proposed to study the Hantavirus epidemics of a mice population:

$$(1) \quad \left. \begin{aligned} \dot{M}_S &= F_1(M_S, M_I) := bM - cM_S - \frac{M_S M}{K} - aM_S M_I, \\ \dot{M}_I &= F_2(M_S, M_I) := -cM_I - \frac{M_I M}{K} + aM_S M_I. \end{aligned} \right\}$$

Here the dot means differentiation with respect to time t ; $M_S(t) \geq 0$ and $M_I(t) \geq 0$ are the numbers or densities of susceptible and infected mice, $M(t) = M_S(t) + M_I(t)$ denotes the total population, respectively. $a > 0$, $b > 0$, $c > 0$ and $K > 0$ are the infection rate (the measure of the effectiveness of the infection between the two groups), the birth rate, the death rate and the carrying capacity of the environment, respectively.

In [3] a short analysis of the dynamical properties of system (1) was given (by using a Liapunov function) and two non-standard finite difference schemes were used for the simulation of (1).

The aim of the present paper is to give a detailed analysis of dynamical properties of (1) (by using other methods than it was used in [3]). We perform a sensitivity analysis on the so called basic reproduction number and show that transcritical bifurcation takes place.

2. The model

We shall present some results, including the positivity and boundedness of solutions, furthermore existence and stability of equilibria.

First of all, Picard–Lindelöf’s Theorem guarantees that solutions of the initial value problem for system (1) exist locally and are unique.

We show now that interior of the positive quadrant of the phase space $[M_S, M_I]$ is an invariant region.

LEMMA 2.1. *All solutions of (1) with positive initial conditions $M_S(0) > 0$, $M_I(0) > 0$ remain positive for all $t \geq 0$ in their domain of existence.*

PROOF. Let us assume contrary to the statement that there exists $t > 0$ at which $M_S(t)$ or $M_I(t)$ is equal to zero. Denote

$$t^* := \min \{t > 0 : M_S(t) \cdot M_I(t) = 0\},$$

then

- assuming that $M_I(t^*) = 0$, it follows that $M_S(t) \geq 0$ ($t \in [0, t^*]$). If we define

$$C := \min \left\{ aM_S(t) - \frac{M_S(t) + M_I(t)}{K} - c : t \in [0, t^*] \right\}$$

then for $t \in [0, t^*]$, $\dot{M}_I(t) \geq CM_I(t)$. Therefore

$$M_I(t^*) > M_I(0) \exp(Ct^*) > 0,$$

which is a contradiction. Thus $M_I(t) > 0$ for all $t \geq 0$.

- assuming that $M_S(t^*) = 0$, it follows that

$$\begin{aligned} \dot{M}_S(t^*) &= bM(t^*) - cM_S(t^*) - \frac{M_S(t^*)M(t^*)}{K} - aM_S(t^*)M_I(t^*) = \\ &= bM_I(t^*) > 0. \end{aligned}$$

Since $M_S(0) > 0$, for $M_S(t^*) = 0$ we must have $\dot{M}_S(t^*) \leq 0$, which is a contradiction. Thus $M_S(t) > 0$ for all $t \geq 0$. ■

We shall consider system (1) restricted to \mathbb{R}_+^2 and prove that all solutions stay bounded in $t \in [0, +\infty)$ which implies the existence of solutions for every $t > 0$.

LEMMA 2.2. *System (1) is dissipative, i.e. all solutions are bounded.*

PROOF. We define the function $\sigma(M_S, M_I) := M_S + M_I$. The time derivative along a solution of (1) is

$$(2) \quad \dot{\sigma}(M_S, M_I) = \dot{M}_S + \dot{M}_I = M \left(b - c - \frac{M}{K} \right).$$

Thus, if $b \leq c$ or if $b > c$ but $M_S + M_I > K(b - c)$ then this derivative is negative. This means that the trajectories of the restricted system cross the line $\sigma(M_S, M_I) = L$ from outside to inside if $L > 0$ is sufficiently large. ■

REMARK 2.1. Equation (2) has the same character as the logistic equation for M . Thus, for every positive initial $\varphi(0)$ the solution

$$\varphi(t) = \frac{K(b - c)\varphi(0)}{\varphi(0) + [K(b - c) - \varphi(0)]e^{-(b-c)t}} \quad (t \in [0, +\infty))$$

of (2) is positive and tends to $K(b - c)$ or to 0 if $b > c$ or $b < c$, respectively.

On the boundary of the positive quadrant the system (1) has two equilibrium points: the trivial equilibrium $(0, 0)$ for all parameter values and the uninfected equilibrium $(K(b - c), 0)$ provided that

$$(3) \quad b > c.$$

A standard stability analysis based on the Jacobian

$$J(M_S, M_I) := \frac{1}{K} \begin{pmatrix} K(b - c) - 2M_S - (1 + aK)M_I & bK - (1 + aK)M_S \\ (aK - 1)M_I & (aK - 1)M_S - cK - 2M_I \end{pmatrix}$$

shows that $(0, 0)$ is stable iff the inequality (3) doesn't hold (i.e. when the birth rate is not higher than the death rate, the whole mice population may die) and (3) with $K \leq b/a(b - c)$ imply the stability of the uninfected equilibrium, respectively. In fact,

$$J(0, 0) = \begin{pmatrix} b - c & b \\ 0 & -c \end{pmatrix}, \text{ resp } J(K(b - c), 0) = \begin{pmatrix} c - b & c + aK(c - b) \\ 0 & -b - aK(c - b) \end{pmatrix}$$

has the eigenvalues $b - c$, c resp. $c - b$, $-b - aK(c - b)$.

Based on the next generation approach (c.f. [5]) a value $\mathcal{R}_0 := aK(1 - c/b)$ is in [3] introduced for the so called basic reproductive number which has for this model the following interpretation: “ \mathcal{R}_0 is the number of infected mice resulting from each infected mouse during its infected lifetime”. To examine the sensitivity of \mathcal{R}_0 to each of its parameters we calculate the normalized sensitivity indices (cf. [4])

$$\begin{aligned} \Psi_a &= \frac{a}{\mathcal{R}_0} \cdot \frac{\partial \mathcal{R}_0}{\partial a} = \frac{a}{aK(1 - c/b)} \cdot K(1 - c/b) = 1, \\ \Psi_b &= \frac{b}{\mathcal{R}_0} \cdot \frac{\partial \mathcal{R}_0}{\partial b} = \frac{b}{aK(1 - c/b)} \cdot \frac{aKc}{b^2} = \frac{c}{b - c}, \\ \Psi_c &= \frac{c}{\mathcal{R}_0} \cdot \frac{\partial \mathcal{R}_0}{\partial c} = \frac{c}{aK(1 - c/b)} \cdot \left(-\frac{aK}{b}\right) = \frac{c}{c - b}, \\ \Psi_K &= \frac{K}{\mathcal{R}_0} \cdot \frac{\partial \mathcal{R}_0}{\partial K} = \frac{K}{aK(1 - c/b)} \cdot a(1 - c/b) = 1. \end{aligned}$$

For the values of the parameters used in this model, the sensitivity indices Ψ_a resp. Ψ_K are unit (which means that an increase in a or K of 1% will result in an increase on \mathcal{R}_0 1%), $\Psi_b = -\Psi_c$. Furthermore, since both of the indices Ψ_b , Ψ_c are functions of the parameters, these sensitivity indices will change as the parameter values change.

Clearly, the uninfected boundary equilibrium is locally asymptotically stable if $\mathcal{R}_0 < 1$ holds; whereas if $\mathcal{R}_0 > 1$ then it is unstable. Thus, \mathcal{R}_0 is a threshold parameter for this model. The following analysis of the local center manifold yields the existence and local stability of a super-threshold endemic equilibrium for \mathcal{R}_0 near one.

Let denote by A the Jacobian of $\mathbf{F} := \text{col}(F_1, F_2)$ evaluated at the critical value $K^* := b/(a(b-c))$ (i.e. when $\mathcal{R}_0 = 1$) and at the equilibrium point $(K^*(b-c), 0)$, i.e.

$$A := \begin{bmatrix} c-b & c-b \\ 0 & 0 \end{bmatrix}.$$

Clearly, the zero eigenvalue of A is simple, the other eigenvalue of A is negative and the vectors

$$\mathbf{q} := \begin{bmatrix} -1 \\ 1 \end{bmatrix}, \quad \mathbf{p} := \begin{bmatrix} 0 \\ 1 \end{bmatrix}$$

are right and left nullvectors of A , i.e. $A\mathbf{q} = \mathbf{0}$, $A^T\mathbf{p} = \mathbf{0}$ such that $\mathbf{p}^T\mathbf{q} \equiv \langle \mathbf{p}, \mathbf{q} \rangle = 1$. Let

$$\alpha := \frac{\langle \mathbf{p}, \mathbf{B}(\mathbf{q}, \mathbf{q}) \rangle}{2}, \quad \beta := \langle \mathbf{p}, \tilde{\mathbf{B}}(\mathbf{q}) \rangle$$

where the functions $\mathbf{B} : \mathbb{R}^2 \times \mathbb{R}^2 \rightarrow \mathbb{R}^2$, $\tilde{\mathbf{B}} : \mathbb{R}^2 \rightarrow \mathbb{R}^2$ are given by

$$B_i(\mathbf{x}, \mathbf{y}) := \sum_{j,k=1}^2 \frac{\partial^2 F_i(\boldsymbol{\xi}, K^*)}{\partial \xi_j \partial \xi_k} \Bigg|_{\boldsymbol{\xi}=(K^*(b-c),0)} x_j y_k \quad (i \in \{1, 2\}),$$

$$\tilde{B}_i(\mathbf{x}) := \sum_{j=1}^2 \frac{\partial^2 F_i(\boldsymbol{\xi}, K^*)}{\partial \xi_j \partial K} \Bigg|_{\boldsymbol{\xi}=(K^*(b-c),0)} x_j \quad (i \in \{1, 2\}).$$

All second derivatives of F_i are the following:

$$\frac{\partial^2 F_1(\boldsymbol{\xi}, K^*)}{\partial M_S \partial M_I} \Bigg|_{\boldsymbol{\xi}} = \frac{1}{K^*} - a = \frac{\partial^2 F_1(\boldsymbol{\xi}, K^*)}{\partial M_I \partial M_S} \Bigg|_{\boldsymbol{\xi}},$$

$$\frac{\partial^2 F_1(\boldsymbol{\xi}, K^*)}{\partial M_S^2} \Bigg|_{\boldsymbol{\xi}} = \frac{2}{K^*}, \quad \frac{\partial^2 F_1(\boldsymbol{\xi}, K^*)}{\partial M_I^2} \Bigg|_{\boldsymbol{\xi}} = 0,$$

$$\frac{\partial^2 F_2(\boldsymbol{\xi}, K^*)}{\partial M_S \partial M_I} \Bigg|_{\boldsymbol{\xi}} = a - \frac{1}{K^*} = \frac{\partial^2 F_2(\boldsymbol{\xi}, K^*)}{\partial M_I \partial M_S} \Bigg|_{\boldsymbol{\xi}},$$

$$\left. \frac{\partial^2 F_2(\xi, K^*)}{\partial M_S^2} \right|_{\xi} = 0, \quad \left. \frac{\partial^2 F_2(\xi, K^*)}{\partial M_I^2} \right|_{\xi} = -\frac{2}{K^*};$$

resp.

$$\left. \frac{\partial^2 F_1(\xi, K^*)}{\partial M_S \partial K} \right|_{\xi} = \frac{2(b-c)}{K^*}, \quad \left. \frac{\partial^2 F_1(\xi, K^*)}{\partial M_I \partial K} \right|_{\xi} = \frac{b-c}{K^*},$$

$$\left. \frac{\partial^2 F_2(\xi, K^*)}{\partial M_S \partial K} \right|_{\xi} = 0, \quad \left. \frac{\partial^2 F_2(\xi, K^*)}{\partial M_I \partial K} \right|_{\xi} = \frac{b-c}{K^*}.$$

Hence

$$\alpha = -a < 0 \quad \text{and} \quad \beta = \frac{b-c}{K^*} > 0.$$

As a consequence (cf. Theorem 4 in [6]) there exists for $\delta > 0$ such that for $1 < \mathcal{R}_0 < \delta$ system (1) has at least one locally asymptotically stable endemic equilibrium, i.e. a transcritical bifurcation takes place which is forward meaning that there is a transfer of stability from the infection-free steady state to the endemic equilibrium, and vice versa (cf. [2]). The interior equilibria are the intersections of the susceptibles null-cline

$$M_I = h_1(M_S) := \frac{K(b-c)M_S - M_S^2}{(aK+a)M_S - bK}$$

and the infecteds null-cline

$$M_I = h_2(M_S) := (aK-1)M_S - cK$$

(c.f. Fig. 1). The intersection $(\overline{M}_S, \overline{M}_I) := (b/a, K(b-c) - b/a)$ lies in the interior of the positive quadrant if and only if

$$(4) \quad b > c \quad \text{and} \quad K > \frac{b}{a(b-c)}.$$

The Jacobian

$$J(\overline{M}_S, \overline{M}_I) = \frac{1}{a\overline{K}} \begin{pmatrix} a^2 K^2 (c-b) + b(aK-1) & -b \\ b(1-2aK) + acK - a^2 K^2 (c-b) & acK - b(aK-1) \end{pmatrix}$$

of \mathbf{F} evaluated at $(\overline{M}_S, \overline{M}_I)$ has the eigenvalues $c-b$ and $b+aK(c-b)$ (cf. [3]) which proves again that $(\overline{M}_S, \overline{M}_I)$ is locally asymptotically stable if $\mathcal{R}_0 > 1$ i.e. (4) holds.

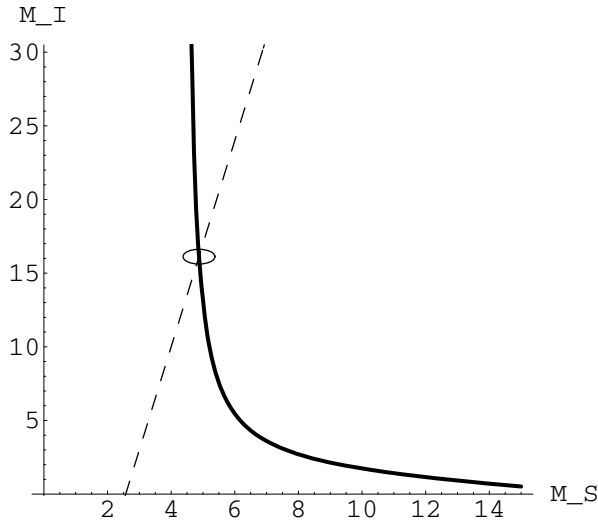


Fig. 1. The zero isoclines (dashed: h_2 , bold: h_1) and the endemic equilibrium of system (1) (MATHEMATICA[®])

Summarizing the results about the local stability of the two essential equilibria we can establish the following: If (3) holds then $(K(b - c), 0)$ is stable along the M_S -direction and stable or unstable along the M_I -direction according as $K \leq$ or $> b/(a(b - c))$. Thus, if $(\overline{M}_S, \overline{M}_I)$ does not exist, then $(K(b - c), 0)$ is an attractor or sink. But if $(\overline{M}_S, \overline{M}_I)$ exists, then $(K(b - c), 0)$ is a saddle point with ingoing trajectories on the M_S -axis. The phase portrait of system (1) for given values $a = 0.2$, $b = 0.9$, $c = 0.45$ and $K = 10$ resp. $K = 50$ is shown in Fig. 2.

By showing that system (1) admits no periodic orbits we extend the local stability result to a global one.

LEMMA 2.3. *The system (1) has no limit cycle in the positive quadrant of the phase plane.*

PROOF. Let define the function h by

$$h(M_S, M_I) := \frac{1}{M_S \cdot M_I} \quad (M_S > 0, M_I > 0).$$

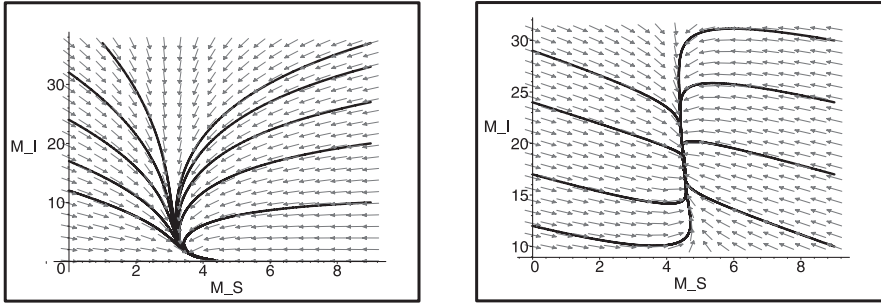


Fig. 2. Phase portraits of the system (1) for $K < b/(a(b - c))$ in left-hand graph and $K > b/(a(b - c))$ in the right-hand graph (MAPLE[®])

Then, we have

$$\begin{aligned} (\operatorname{div}(\mathbf{h}\mathbf{F})) (M_S, M_I) &= (\partial_1(\mathbf{h}F_1)) (M_S, M_I) + (\partial_2(\mathbf{h}F_2)) (M_S, M_I) = \\ &= -\frac{b}{M_S} - \frac{1}{KM_I} - \frac{1}{KM_S} < 0. \end{aligned}$$

Therefore by the Dulac's negative criterion (see e.g. [7]) system (1) has no limit cycle in the positive quadrant of the $[M_S, M_S]$ plane. ■

Thus, we can summarize our results in the following:

THEOREM 2.1. *If*

1. $b \leq c$ then system (1) has only the trivial equilibrium which is globally asymptotically stable;
2. $b > c$ and
 - (a) $K < b/(a(b - c))$ then apart from the trivial (unstable) one there is only the uninfected equilibrium $(K(b - c), 0)$ which is globally asymptotically stable;
 - (b) $K \geq b/(a(b - c))$ then a new (endemic) equilibrium (\bar{M}_S, \bar{M}_I) bifurcates from $(K(b - c), 0)$

$$((\bar{M}_S, \bar{M}_I) = (K(b - c), 0)$$

as $K = b/(a(b - c))$ by a forward transcritical bifurcation and the new equilibrium becomes the globally asymptotically stable one as $K > b/(a(b - c))$, whereas $(K(b - c), 0)$ is a repeller as $K > b/(a(b - c))$.

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In a subsequent paper we are going to study what happens if delay is introduced into the system. It will be shown that at the critical value Poincaré–

Andronov–Hopf bifurcation takes place: a small amplitude periodic solution occurs.

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