

**NONEXISTENCE OF PERIODIC SOLUTIONS FOR A  
CLASS OF EPIDEMIOLOGICAL MODELS**

**Stavros Busenberg and  
P. van den Driessche**

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# Nonexistence of Periodic Solutions for a Class of Epidemiological Models

Stavros Busenberg<sup>\*</sup>  
Department of Mathematics  
Harvey Mudd College  
Claremont, CA 91711, USA

and

P. van den Driessche<sup>\*\*</sup>  
Department of Mathematics  
University of Victoria  
Victoria, B.C. V8W 3P4, Canada

Dedicated to Kenneth L. Cooke on his 65th birthday, who inspired us both to work in this area.

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**Abstract.**

Disease transmission models are formulated under assumptions that the size of the population varies and the force of infection is of the proportionate mixing type. Conditions are given that rule out the possibility of periodic solutions for such models. Examples are considered and sharp thresholds identified.

## 1. Introduction.

The behaviour of a general S (susceptible), A (asymptomatic), I (infective), S epidemiological model in a population of varying size is governed by a differential equation in  $\mathbb{R}_+^3$ . When the force of infection is of the proportionate mixing type, the nonlinear terms of this equation are homogeneous of degree one and satisfy a balance condition. Moreover, in the linear part, the off-diagonal terms are nonnegative.

We consider a general equation of this form, and give conditions which rule out periodic solutions, including limit cycles, homoclinic orbits and oriented phase polygons. Our method, involving a new technique, extends results of Busenberg and van den Driessche (1990) for an SIR (recovered) S model, in which a generalization of the Bendixson–Dulac criterion is proved.

In certain special cases, the nonexistence of periodic solutions, in combination with analysis of the existence and stability of equilibrium points, provides a complete global analysis of the model.

## 2. Mathematical Formulation.

We consider a differential equation in  $\mathbb{R}_+^3$  of the form

$$x' = Mx + f(x) \quad (2.1)$$

where  $'$  denotes the derivative  $d/dt$ . The  $3 \times 3$  constant matrix  $M = [m_{ij}]$  is assumed to be *essentially nonnegative*, that is the off-diagonal entries of  $M$  are nonnegative, and it is also assumed that at least one is positive. The nonlinear function  $f: \mathbb{R}_+^3 \rightarrow \mathbb{R}_+^3$  is assumed to be continuously differentiable and *homogeneous of degree one*, that is  $f(ax) = af(x)$  for  $a > 0$ , and to have the balance condition  $\sum_{i=1}^3 f_i = 0$ . In the disease transmission models, we are concerned with solutions having nonnegative components  $x_i(t) \geq 0$ , and we also assume that  $(Mx)_i + f_i(x) \geq 0$  when evaluated on  $x_i = 0$ . For  $\sum_{i=1}^3 x_i \neq 0$ , we introduce the normalized variable (see, e.g., Hahn (1967, Section 57), Haderler et al. (1988), Hofbauer and Sigmund (1988), Busenberg and Haderler (1990), Busenberg and van den Driessche (1990))

$$y = x / \sum_{i=1}^3 x_i, \quad (2.2)$$

with  $\sum_{i=1}^3 y_i = 1$ . The normalized variable satisfies

$$\mathbf{y}' = \mathbf{M}\mathbf{y} - (\mathbf{1} \cdot \mathbf{M}\mathbf{y})\mathbf{y} + \mathbf{f}(\mathbf{y}), \quad (2.3)$$

where  $\mathbf{1}$  denotes the vector in  $\mathbb{R}^3$  with every entry equal to one. Clearly, the hyperplane  $S \equiv \left\{ \mathbf{y}: \sum_{i=1}^3 y_i = 1 \right\}$  is invariant under the flow induced by (2.3), since

$$\left[ \sum_{i=1}^3 y_i \right]' = (\mathbf{1} \cdot \mathbf{M}\mathbf{y}) \left[ 1 - \sum_{i=1}^3 y_i \right] + \sum_{i=1}^3 f_i(\mathbf{y}) = 0.$$

We now write (2.3) in component form for  $i = 1, 2, 3$ :

$$y_i' = (\mathbf{M}\mathbf{y})_i - (\mathbf{1} \cdot \mathbf{M}\mathbf{y})y_i + f_i(y_1, y_2, y_3). \quad (2.4)$$

On  $S$  we can write the first equation of (2.4) in the following alternate forms:

$$y_1' = f_{12}(y_1, y_2) + f_1(y_1, y_2, 1-y_1-y_2) = f_{13}(y_1, y_3) + f_1(y_1, 1-y_1-y_3, y_3), \quad (2.5)$$

where

$$\begin{aligned} f_{12}(y_1, y_2) \equiv & (m_{11}-m_{13})y_1 + (m_{12}-m_{13})y_2 + m_{13} - y_1[(m_{11}+m_{21}+m_{31}-m_{13}-m_{23}-m_{33})y_1 \\ & + (m_{12}+m_{22}+m_{32}-m_{13}-m_{23}-m_{33})y_2 + m_{13}+m_{23}+m_{33}]. \end{aligned} \quad (2.6)$$

In (2.5) the first equation is in terms of  $y_1$  and  $y_2$  only, whereas the second equation is in terms of  $y_1$  and  $y_3$  only, and  $f_1$  contains the

homogeneous terms. The function  $f_{13}$  is defined from  $f_{12}$  by interchanging subscripts 2 and 3. Similarly we can write

$$y'_2 = f_{23}(y_2, y_3) + f_2(1-y_2-y_3, y_2, y_3) = f_{21}(y_1, y_2) + f_2(y_1, y_2, 1-y_1-y_2) \quad (2.7)$$

where

$$\begin{aligned} f_{23} = & (m_{22}-m_{21})y_2 + (m_{23}-m_{21})y_3 + m_{21} - y_2[(m_{12}+m_{22}+m_{32}-m_{11}-m_{21}-m_{31})y_2 \\ & + (m_{13}+m_{23}+m_{33}-m_{11}-m_{21}-m_{31})y_3 + m_{11}+m_{21}+m_{31}], \end{aligned} \quad (2.8)$$

and  $f_{21}$  is defined from  $f_{23}$  by interchanging subscripts 3 and 1;

$$y'_3 = f_{31}(y_1, y_3) + f_3(y_1, 1-y_1-y_3, y_2) = f_{32}(y_2, y_3) + f_3(1-y_2-y_3, y_2, y_3) \quad (2.9)$$

where

$$\begin{aligned} f_{31} = & (m_{31}-m_{32})y_1 + (m_{33}-m_{32})y_3 + m_{32} - y_3[(m_{11}+m_{21}+m_{31}-m_{12}-m_{22}-m_{32})y_1 \\ & + (m_{13}+m_{23}+m_{33}-m_{12}-m_{22}-m_{32})y_3 + m_{12}+m_{22}+m_{32}], \end{aligned} \quad (2.10)$$

and  $f_{32}$  is defined from  $f_{31}$  by interchanging subscripts 1 and 2.

Now let  $S^+ \equiv S \cap \mathbb{R}_+^3$ ,  $S^0 \equiv S^+ - \partial S^+$ , and define  $g$  on  $S^0$  so its transpose  $g^T$  is given by

$$\begin{aligned}
g^T \equiv & \left[ \frac{1}{y_1 y_3} f_{31}(y_1, y_3) + \frac{1}{y_1 y_3} f_3(y_1, 1-y_1-y_3, y_3) - \frac{1}{y_1 y_2} f_{21}(y_1, y_2) \right. \\
& - \frac{1}{y_1 y_2} f_2(y_1, y_2, 1-y_1-y_2), \quad \frac{1}{y_1 y_2} f_{12}(y_1, y_2) + \frac{1}{y_1 y_2} f_1(y_1, y_2, 1-y_1-y_2) \\
& - \frac{1}{y_2 y_3} f_{32}(y_2, y_3) - \frac{1}{y_2 y_3} f_3(1-y_2-y_3, y_2, y_3), \quad \frac{1}{y_2 y_3} f_{23}(y_2, y_3) \\
& \left. + \frac{1}{y_2 y_3} f_2(1-y_2-y_3, y_2, y_3) - \frac{1}{y_1 y_3} f_{13}(y_1, y_3) - \frac{1}{y_1 y_3} f_1(y_1, 1-y_1-y_3, y_3) \right].
\end{aligned} \tag{2.11}$$

Note that  $g$  on  $S$  is equal to  $y \times (My - (\underline{1} \cdot My)y + f(y))/(y_1 y_2 y_3)$ . Then  $\nabla \times g$  is composed of two terms, one involving the functions  $f_{ij}$  coming from the linear part of (2.1) and the other involving the functions  $f_i$  coming from the nonlinear homogeneous part of (2.1). We call these  $\nabla \times g_M$  and  $\nabla \times g_f$ , respectively, and have the following results, the first of which simply collects two relations we need in the sequel.

### Lemma 2.1

Using definitions and assumptions above,

$$\nabla \times g_M \cdot \underline{1} = - \left[ \frac{\frac{m_{13}}{2}}{y_1 y_2} + \frac{\frac{m_{23}}{2}}{y_1 y_2} + \frac{\frac{m_{32}}{2}}{y_1 y_3} + \frac{\frac{m_{12}}{2}}{y_1 y_3} + \frac{\frac{m_{21}}{2}}{y_2 y_3} + \frac{\frac{m_{31}}{2}}{y_2 y_3} \right], \tag{2.12}$$

and



$$\nabla \times g_f \cdot \underline{1} = \frac{f_2 y_3 (y_2 - y_1) + f_3 y_2 (y_3 - y_1)}{y_1^2 y_2^2 y_3^2} + \frac{\frac{\partial f_2}{\partial y_2} - \frac{\partial f_2}{\partial y_1} + \frac{\partial f_3}{\partial y_3} - \frac{\partial f_3}{\partial y_1}}{y_1 y_2 y_3}. \quad (2.13)$$

**Proof:** As  $\underline{1} = (1, 1, 1)$ , the term  $\nabla \times g_{\mathbf{M}} \cdot \underline{1}$  is computed by adding the terms of  $\nabla \times g$  involving the functions  $f_{ij}$  from (2.11). Performing these simple but lengthy computations and collecting terms gives  $\nabla \times g_{\mathbf{M}} \cdot \underline{1}$  as in (2.12). Similarly for the nonlinear terms, and using the fact that  $f_1 = -f_2 - f_3$ , gives (2.13). ■

### Theorem 2.2

Assume that  $\mathbf{M} = [m_{ij}]$  has  $m_{ij} \geq 0$  for  $i \neq j$ , with at least one strict inequality; and  $f: \mathbb{R}_+^3 \rightarrow \mathbb{R}_+^3$  is continuously differential, homogeneous of degree 1 with  $f_1 + f_2 + f_3 = 0$ . If on  $S^0$

$$f_2 y_3 (y_2 - y_1) + f_3 y_2 (y_3 - y_1) + y_1 y_2 y_3 \left[ \frac{\partial f_2}{\partial y_2} - \frac{\partial f_2}{\partial y_1} + \frac{\partial f_3}{\partial y_3} - \frac{\partial f_3}{\partial y_1} \right] \leq 0, \quad (2.14)$$

then there are no periodic solutions of the system (2.3), namely

$y' = \mathbf{M}y - (\underline{1} \cdot \mathbf{M}y)y + f(y)$ , in  $S^0$ . Moreover, if  $(\mathbf{M}y)_i - (\underline{1} \cdot \mathbf{M}y)y_i + f_i(y)$  evaluated at  $y_i = 0$  is nonnegative for  $i = 1, 2, 3$ , and is positive for at least one  $i$ , then this result holds in the invariant region  $S^+$ .

**Proof:** The nonexistence of periodic solutions (including closed orbits, homoclinic loops and oriented phase polygons) follows from Theorem 4.1 of Busenberg and van den Driessche (1990). We check the conditions there, namely  $g \cdot (\mathbf{M}y - (\underline{1} \cdot \mathbf{M}y)y + f(y)) = 0$ , and (by Lemma (2.1), (2.14) and the assumptions on  $\mathbf{M}$ ) we have  $\nabla \times g \cdot \underline{1} = \nabla \times g_{\mathbf{M}} \cdot \underline{1} + \nabla \times g_f \cdot \underline{1} < 0$ .

The fact that  $S$  is invariant has already been established, while the invariance of  $\mathbb{R}_+^3$  follows from the fact that (2.3) and assumptions on  $M$  and  $f$  ensure that  $y'_1$  evaluated at  $y_1 = 0$  is nonnegative. If, in addition, one of these terms is strictly positive, then the boundary  $\partial S^+$  is not a phase polygon for the system, and the nonexistence of closed orbits in  $S^+$  is established. ■

**Remark:** The balance condition,  $\sum_{i=1}^3 f_i = 0$ , which occurs naturally in the epidemiological models we consider, is needed only to obtain a simpler form (2.13) for  $\nabla \times g_f \cdot \underline{1}$ . Conditions other than (2.14) are needed when this does not hold. As  $M$  is assumed to be essentially nonnegative with at least one negative off-diagonal entry,  $\nabla \times g_M \cdot \underline{1}$  is strictly negative by (2.12).

### 3. A General Epidemiological Model

We consider a model of disease transmission in a nonconstant population  $N$  divided into three groups, susceptibles, asymptomatics (infectives *without* symptoms) and infectives (infectives *with* symptoms), the numbers in each class being given by  $S$ ,  $A$ ,  $I$ , respectively, thus  $N = S + A + I$ . For a discussion of the role of asymptomatic individuals in a constant population model, see Cooke (1982). Our model is given schematically in figure 1, and all parameters are assumed nonnegative.

Figure 1

Births from each class are included, thus  $b_{SS}S + b_{AS}A + b_{IS}I$  is the number of newborns entering the susceptible class, where  $b_{SS}$ ,  $b_{AS}$ ,  $b_{IS}$  are all assumed positive. Vertical transmission is also included with  $b_{AA}A + b_{IA}I$  newborns entering  $A$  and  $b_{II}I + b_{AI}A$  entering  $I$ ; the parameters  $b_{SS}$ ,  $b_{AS}$ ,  $b_{IS}$ ,  $b_{AA}$ ,  $b_{IA}$ ,  $b_{II}$ ,  $b_{AI}$  are birth rates, the first subscript denoting the parent class and the second subscript denoting the class of the offspring. The disease free death rate is  $d$ , and excess per capita death rates  $\delta$ ,  $\epsilon$  are assumed in  $A$ ,  $I$ , respectively. Recoveries from  $A$ ,  $I$  are at rates  $c_A$ ,  $c_I$  respectively. There is also the possibility of passing from asymptomatic to infective at rate  $p$ , and in the opposite direction at a rate  $q$ . The force of infection is of the proportionate mixing type, with  $\lambda_A$ ,  $\lambda_I$  the effective per capita contact rate of infective individuals in class  $A$ ,  $I$  respectively. The rate at which susceptibles become infected is thus  $\lambda_A SA/N + \lambda_I SI/N$ . Proportions  $\alpha, \beta \in [0,1]$  of those

infected by asymptomatics, infectives, respectively, pass directly into the infective class. This model includes many epidemiological models previously studied in the literature, for example it includes the SIRS model of Busenberg and van den Driessche (1990); some special cases and previous work will be discussed in the next section.

The above hypotheses lead to the following model equations, an example of system (2.1), for the nonnegative variables:

$$S' = b_{SS}S + b_{AS}A + b_{IS}I - dS - \lambda_A SA/N - \lambda_I SI/N + c_A A + c_I I, \quad (3.1)$$

$$A' = b_{AA}A + b_{IA}I + (1-a)\lambda_A SA/N + (1-\beta)\lambda_I SI/N - (d+\delta+c_A)A - pA + qI, \quad (3.2)$$

$$I' = b_{AI}A + b_{II}I + a\lambda_A SA/N + \beta\lambda_I SI/N - (d+\epsilon+c_I)I + pA - qI, \quad (3.3)$$

giving

$$N' = b_{SS}S + (b_{AS}+b_{AA}+b_{AI}-\delta)A + (b_{IS}+b_{IA}+b_{II}-\epsilon)I - dN. \quad (3.4)$$

Given initial data which are nonnegative, we can easily show that nonnegative solutions are defined for all time  $t \geq 0$ , thus the model is well posed.

We are interested in solutions with the total population  $N$  varying, thus we work with proportions in the three epidemiological classes, namely the normalized variables of section 2,  $s \equiv S/N = y_1$ ,  $a \equiv A/N = y_2$ ,  $i \equiv I/N = y_3$ . The feasibility region is  $S^+ \equiv \{s \geq 0, a \geq 0, i \geq 0, s + a + i = 1\}$ . We note that the linear part of these equation has nonnegative off-diagonal entries, with  $m_{12} = b_{AS} + c_A$  and  $m_{13} = b_{IS} + c_I$  both positive, as assumed for matrix  $M$  in section 2. Also the nonlinear terms satisfy the assumptions

there, in particular the homogeneity and balance condition. The proportion equations are:

$$s' = b_{SS}s + b_{AS}a + b_{IS}i - \lambda_A sa - \lambda_I si + c_A a + c_I i \quad (3.5)$$

$$-s[b_{SS}s + (b_{AS}+b_{AA}+b_{AI}-\delta)a + (b_{IS}+b_{IA}+b_{II}-\epsilon)i],$$

$$a' = b_{AA}a + b_{IA}i + (1-a)\lambda_A sa + (1-\beta)\lambda_I si - (\delta+c_A)a \quad (3.6)$$

$$- pa + qi - a[b_{SS}s + (b_{AS}+b_{AA}+b_{AI}-\delta)a + (b_{IS}+b_{IA}+b_{II}-\epsilon)i],$$

$$i' = b_{AI}a + b_{II}i + a\lambda_A sa + \beta\lambda_I si - (\epsilon+c_I)i \quad (3.7)$$

$$+ pa - qi - i[b_{SS}s + (b_{AS}+b_{AA}+b_{AI}-\delta)a + (b_{IS}+b_{IA}+b_{II}-\epsilon)i].$$

Note that the disease free death rate  $d$  does not occur in these. We use our previous theorem to show the nonexistence of periodic solution for this disease transmission model.

### Theorem 3.1

The model system (3.5)–(3.7) has no periodic solutions in  $S^+$ .

*Proof:* The condition (2.14) of theorem 2.2 reduces to

$$sai[-a\lambda_A sa/i - (1-\beta)\lambda_I si/a]$$

which is certainly  $\leq 0$  in  $S^0$  as all parameters are nonnegative and  $a, \beta \in [0,1]$ . The conditions for invariance of  $S^+$  are easily checked. We need to consider the boundary  $\partial S^+$ . But  $s'(0,a,i) = (b_{AS}+c_A)a + (b_{IS}+c_I)i$  which is positive by our assumptions on the birth rates. Similarly,  $a'(s,0,i)$  and  $i'(s,a,0)$  are non-negative. Thus the boundary cannot be a phase polygon for the system, and we have eliminated all periodic solutions. ■

We now investigate the disease free equilibrium (DFE), namely  $(s,a,i) = (1,0,0)$ . We find that the following threshold parameters are important:

$$R_{0A} = \frac{(1-a)\lambda_A}{c_A + p + \delta + b_{SS} - b_{AA}}, \quad R_{0I} = \frac{\beta\lambda_I}{c_I + q + \epsilon + b_{SS} - b_{II}}. \quad (3.8)$$

We make the biologically reasonable assumption that  $b_{SS} > \{b_{AA}, b_{II}\}$  so that the denominators do not vanish. For the A class,  $R_{0A}$  gives a measure of the relative strength of the disease transmission via contacts versus dilution through recovery, transfer into I, excess death, or relative increase in the S population by births and is thus a *disease reproduction number*; whereas  $R_{0I}$  gives a similar measure for the I class. These parameters play an important role in the following result.

### Theorem 3.2

The system (3.5)–(3.7) always has the DFE. If  $b_{AI} + a\lambda_A + p > 0$  and  $b_{IA} + (1-\beta)\lambda_I + q > 0$ , then it is the only equilibrium with either  $a$  or  $i$  equal to 0. In this case, the DFE is locally asymptotically stable in  $S^+$

if  $R_{0A} < 1$ ,  $R_{0I} < 1$ , and

$$(1-R_{0A})(1-R_{0I}) > \frac{(b_{AI}+a\lambda_A+p)(b_{IA}+(1-\beta)\lambda_I+q)}{(c_A+p+\delta+b_{SS}-b_{AA})(c_I+q+\epsilon+b_{SS}-b_{II})} . \quad (3.9)$$

**Proof:** Setting the derivatives in (3.5)–(3.7) to zero, gives the three nonlinear equations which must hold at an equilibrium point. From (3.7), when  $i = 0$ ,  $(b_{AI}+a\lambda_A+p)a = 0$ , and from (3.6) when  $a = 0$ ,  $(b_{IA}+(1-\beta)\lambda_I+q)i = 0$ . Thus when both parameter sums are positive, that is, at least one of each set  $\{b_{AI}, a\lambda_A, p\}$  and  $\{b_{IA}, (1-\beta)\lambda_I, q\}$  strictly positive, we see that, at an equilibrium,  $a = 0$  implies  $i = 0$  and conversely.

Local stability of the DFE is governed by the eigenvalues of the Jacobian matrix

$$\begin{bmatrix} b_{AA}+(1-a)\lambda_A & b_{IA}+(1-\beta)\lambda_I+q \\ -(\delta+c_A+p+b_{SS}) & \\ b_{AI}+a\lambda_A+p & b_{II}+\beta\lambda_I \\ & -(\epsilon+c_I+q+b_{SS}) \end{bmatrix}, \quad (3.10)$$

since the third eigenvalue is  $-b_{SS}$  which is negative. Thus, using (3.8), if  $R_{0A} < 1$  and  $R_{0I} < 1$ , the main diagonal entries, and hence the trace of the matrix, are negative. Condition (3.9) is then equivalent to the determinant being positive. These trace and determinant conditions are necessary and sufficient for the matrix to be stable, hence the DFE is locally asymptotically stable under the stated conditions. ■

The first two conditions of the theorem are simply that the disease reproduction number for each class is less than one, whereas inequality (3.9) is a coupled condition.

We have already ruled out periodic solutions, so to establish global stability of the DFE, we need to rule out the possibility of an endemic equilibrium  $(s^*, a^*, i^*)$  in  $S^+$  with  $i^* > 0$ . We consider now some important special cases.



#### 4. Examples.

##### Example 4.1. SIRS model.

Identifying the class  $A$  with a recovered class  $R$ , and setting  $b_{SS} = b_{AS} = b_{IS} = b > 0$ ,  $b_{AA} = b_{AI} = b_{II} = b_{IA} = 0$ ,  $p = c_I = \lambda_A = 0$ ,  $\beta = 1$ ,  $\lambda_I$ ,  $c_A$ ,  $q > 0$ , we obtain an SIRS model with no vertical transmission. A complete global analysis is given in Busenberg and van den Driessche (1990). Here it suffices to state that, in this case,  $R_{0A} = 0$ , and the determinant condition (3.9) reduces to  $R_{0I} = \lambda_I/(q+\epsilon+b) < 1$ . Although  $b_{AI} + a\lambda_A + p = 0$ , the equilibrium point  $(\bar{s}, 0, \bar{a})$  with  $\bar{a} = (\delta+c_A+b)/\delta > 1$  is outside  $S$ . We are able to rule out an endemic equilibrium, and to prove that the DFE is globally asymptotically stable in  $S^+$  iff  $R_{0I} \leq 1$ . When  $R_{0I} > 1$ , there is a unique endemic proportion equilibrium, which is globally asymptotically stable in  $S^+ - \{(1,0,0)\}$ ; thus the reproduction number  $R_{0I}$  gives a sharp threshold.

Hadeler and Busenberg (1990) consider a generalization of this SIRS model which includes vertical transmission in the infective class ( $b_{II} > 0$ ), with the biologically reasonable assumptions that the birth rates satisfy  $b_{SS} \geq b_{AS} \geq b_{IS} + b_{II}$ . They also assume that disease related death in the infective class is at least as large as that in the removed class, that is  $\epsilon \geq \delta$ . The above sharp threshold result continues to hold, with the parameter  $R_{0I}$  defined in (3.8) modified by the vertical transmission term.

For an SIR model with permanent immunity the parameter  $c_A$  is zero, and our results so modified hold in this special case.

Example 4.2. SEIS model.

We can obtain an SEIS model by identifying  $A$  with an exposed (but not yet infectious) class  $E$ , and setting  $q = c_A = \lambda_A = \beta = 0$ ,  $\lambda_I$ ,  $c_I$ ,  $p > 0$ . As in the SIRS model, we neglect vertical transmission and assume that the birth rate in each class is equal to  $b > 0$ . For this model, which was shown in Busenberg and van den Driessche (1990) to have no periodic solutions, we see that both parameters in (3.8) are zero. Theorem 3.2 gives that the DFE, which is the only equilibrium on  $\partial S^+$ , is locally asymptotically stable in  $S^+$  if

$$1 > \frac{\lambda_I}{(b+c_I+\epsilon)} - \frac{p}{(b+p+\delta)} .$$

If this inequality is reversed, then the DFE is unstable. If  $p \rightarrow \infty$ , that is the average exposed period  $1/p \rightarrow 0$ , the model reduces to an SIS model, with the above inequality then becoming  $1 > \lambda_I/(b+c_I+\epsilon)$ .

The corresponding SEI model, in which there is no cycling back into the susceptible class, is obtained from the SEIS model by setting  $c_I$  equal to zero. This is analysed by Mena Lorca (1988, section 5.7) under the additional assumption that there is no disease related death in the exposed class ( $\delta = 0$ ). The sharp threshold result is obtained with reproduction number  $\lambda_I p / [(b+\epsilon)(b+p)]$ .

For diseases with no recovery and no latent class the correct model is an SI one. This can be obtained from our SEIS model by letting  $p \rightarrow \infty$  and  $c_I = 0$ . Pugliese (1990) considers this model with a general shape of density dependent natural mortality and incidence rate and some vertical transmission. The sharp threshold result is also obtained in this case with reproduction number  $(\lambda_I + b_{II})/(b+\epsilon)$ . Brauer (1989) formulates a model for universally

fatal diseases including nonlinear population dynamics and a distribution of infective periods which generalizes our average infective period  $1/\epsilon$ . A linear analysis again gives a sharp threshold.

Example 4.3. Simplified SIAS model.

Consider equations (3.1) – (3.3) with no vertical transmission, no possibility of moving directly between groups A and I (i.e.  $b_{AA} = b_{AI} = b_{II} = b_{IA} = p = q = 0$ ) and  $\alpha = \beta$ . The resulting model corresponds to the SIAS model in a population of constant size considered by Cooke (1982). Making the additional assumption that the birth rate in each class is equal to  $b > 0$ , we obtain from (3.8) the threshold parameters

$$R_{0A} = \frac{(1-\alpha)\lambda_A}{c_A + \delta + b} , \quad R_{0I} = \frac{\alpha\lambda_I}{c_I + \epsilon + b} .$$

Thus, for  $\alpha \in (0,1)$  and  $\lambda_A, \lambda_I > 0$ , theorem 4.1 shows that the DFE is locally asymptotically stable in  $S^+$  if  $R_{0A} + R_{0I} < 1$ . This sum corresponds to the sharp threshold found by Cooke (1982).

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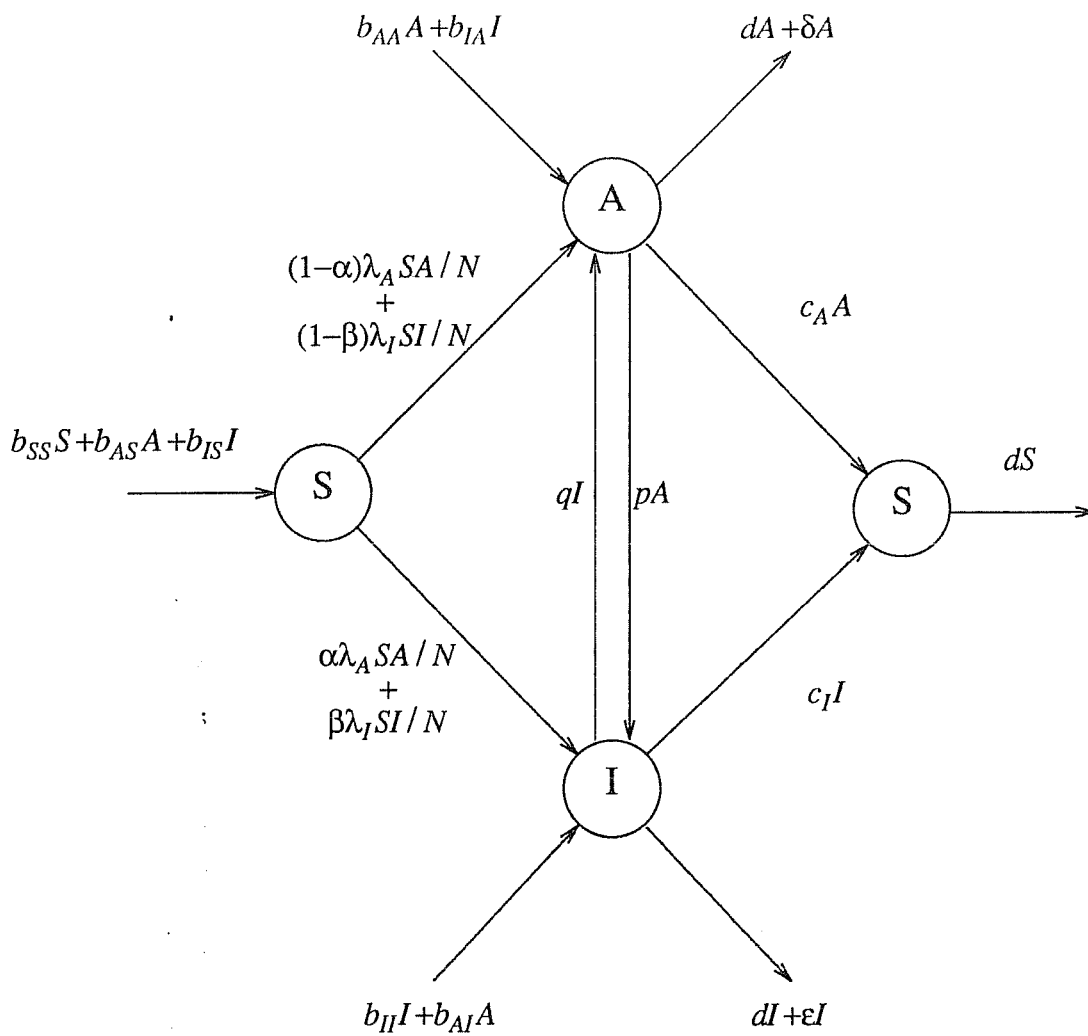


Figure 1.