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"An S → E → I epidemic model with varying population size"

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An S→E→I epidemic model with varying population size

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Abstract

An $S \to E \to I$ epidemic model with a general shape of density–dependent mortality and incidence rate is studied analytically and numerically.

The combined effect of a latent period and of varying population size can produce oscillations in this ODE model. When fertility of exposed individuals is the same as that of susceptibles, there is a clear threshold. On the contrary, when both exposed and infectives do not contribute to birth rate, there may exist multiple endemic states also below the threshold.

When the contact rate is independent of population size, the global behaviour is established: all trajectories converge to an equilibrium.

1. Introduction

In a previous paper [12] I analyzed a simple epidemic model, with vertical transmission, an arbitrary density–dependent demography, and a density–dependent contact rate; it was assumed that the disease increased the death rate and/or decreased the birth rate; therefore population size varied with disease prevalence.

The main result of the analysis was that the qualitative conclusions obtained for the constant population model were still valid. There exists a threshold under which the disease-free equilibrium is globally stable; above the threshold there exists also an endemic equilibrium, which is stable and attracts all initial points with $I_0 > 0$. The threshold relates to the disease transmissibility at the demographic equilibrium population size.

A similar model has been studied by Brauer [6], with somewhat different assumptions: he also allows for a generic distribution of the infectious period (before disease-related death occurs); he finds that, while an exponential distribution (the one used in an ODE formulation) always yields (local) stability of the endemic equilibrium, other distributions may render the equilibrium unstable.

Models with varying population size have also been considered by Anderson and May [3], Busenberg *et al.* [7], Busenberg and van der Driessche [8], Andreasen [4], Kretzschmar

[10]. They all assumed that birth and death rates did not depend on population size, and therefore, without epidemics, there would be exponential population growth. Their results are therefore not directly comparable to [12].

The most similar model has been studied by Anderson *et al.* [2] as a model for fox rabies. They assumed that population growth (in absence of epidemics) is logistic, and a standard mass action law term for the incidence rate. The main difference with the model studied in [12] is that they allow for a latent period following infection, i.e. a period in which the animal is not contagious. They found numerically conditions under which the endemic equilibrium is unstable, and there exist stable limit cycles.

The purpose of this paper is to introduce a latent period in the model I considered before, in order to compare the results of [12] with those of Anderson *et al.* [2].

2. Formulation of the model

The population (N) is divided between susceptibles (S), exposed (E) and infectives (I).

As for the demography, I assume non-disease related mortality to be a non-decreasing function, $m(N)$ of total population size; infectives suffer also an additional mortality μ. The fertility of susceptibles is a, that of exposed is $a(1 - \delta_1)$, that of infectives is $a(1 - \delta_2)$, $0 \leq \delta_1 \leq \delta_2 \leq 1$. I assume that all newborns are susceptibles, not allowing therefore for vertical transmission; this is done because in [12] vertical transmission does not change the results, but only make the expressions more complicated. Again for the sake of simplicity, I assume that only mortality (and not also fertility) is density–dependent.

Since it is difficult to study the resulting system for all combinations of δ_1 and δ_2, I will explore in detail only two possible choices, which yield a rather different picture. In the first case, I will assume that exposed individuals have no disease symptoms at all; therefore their fertility is equal to that of susceptible individuals, namely $\delta_1 = 0$. In the second case, I will assume, following Anderson *et al.* [2] and Brauer [5] [6], that both exposed and infected individuals do not contribute at all to the birth rate, namely $\delta_1 = \delta_2 = 1$. I suspect that this second choice is not very realistic; I study it for ease of comparison with other results.

As for the rate of new infections, the probability for a susceptible of getting infected is equal to $\sigma(N)I$ (note that the contact rate per individual $c(N)$ is the equal to $\sigma(N)N$); in case of environmentally transmitted diseases one normally assumes $\sigma(N) \equiv \beta$; for sexually transmitted diseases $\sigma(N) = \beta/N$. Since these are considered to be the extremes, in general one may assume $\sigma(N)$ to be a non-increasing function, while $N\sigma(N)$ is a non-decreasing function (see [9] for the same assumptions). The case $\sigma(N) = \beta/N$ is easier to study, since it leads to a reduction of the dimension of the problem [11], and will be discussed at the end. Here I assume that $c(N)$ is strictly increasing.

The equations resulting from these assumptions are

$$\begin{cases} \dfrac{dS}{dt} = (a - m(N))S + a(1 - \delta_1)E + a(1 - \delta_2)I - \sigma(N)SI \\[2mm] \dfrac{dE}{dt} = \sigma(N)SI - m(N)E - \nu E \\[2mm] \dfrac{dI}{dt} = \nu E - (m(N) + \mu)I \end{cases} \tag{1}$$

where $N = S + E + I$.

The exact assumptions that will be made are:

(H) $a > 0$, $\quad \nu > 0$, $\quad \mu \geq 0$, $\quad 0 \leq \delta_1 \leq \delta_2 \leq 1$, $\quad \mu + a\delta_2 > 0$

$\sigma(N)$ is a non-increasing function, while $c(N) \equiv N\sigma(N)$ is a strictly increasing C^1 function on $(0, \infty)$ such that $\lim_{N \to 0^+} c(N) = 0$.

$m(N)$ is C^1 and non-decreasing on $[0, \infty)$. There exists $(N_1, N_2) \subset (0, \infty)$ such that $m(N)$ is strictly increasing on (N_1, N_2), with $m(N_1) < a < m(N_2)$.

I assumed c and m to be C^1, in order to be able to perform the linearization at equilibria. In the examples, I will also use functions that are only piecewise C^1; it is still possible to perform the linearization, as long as m and c are differentiable at the equilibria.

From the assumptions made on m, it follows that there exists a unique $N^* > 0$ such that $m(N^*) = a$. This is the demographic equilibrium, in absence of the disease.

Summing the three equations in (1), one obtains

$$\frac{dN}{dt} = (a - m(N))N - a\delta_1 E - a\delta_2 I - \mu I \tag{2}$$

One can clearly use, instead of system (1), a system obtained using (2) and any two equations of system (1), remembering that $N = S + E + I$.

Existence and uniqueness of solutions (1) for nonnegative initial data follows from standard results; the fact that $c(N)$ is not assumed to be Lipschitz at $N = 0$ can be handled as in [12]. It is easy to see that the set $\mathcal{A} = \{(S, E, I) : 0 \leq S, E, I, \quad S + E + I \leq N^*\}$ is positively invariant.

An equilibrium for the system, using as variables (N, E, I), is found as $(N^*, 0, 0)$. The linearization matrix there is

$$A = \begin{pmatrix} -m'(N^*)N^* & -a\delta_1 & -a\delta_2 - \mu \\ 0 & -(m(N^*) + \nu) & \sigma(N^*)N^* \\ 0 & \nu & -(m(N^*) + \mu) \end{pmatrix} \tag{3}$$

whose eigenvalues are $\lambda_1 = -m'(N^*)N^* < 0$ and the eigenvalues of

$$B = \begin{pmatrix} -(m(N^*) + \nu) & \sigma(N^*)N^* \\ \nu & -(m(N^*) + \mu) \end{pmatrix} \tag{4}$$

We have tr $B < 0$, while

$$\det B = (a + \nu)(a + \mu) - \nu\sigma(N^*)N^*$$

If we define

$$R_0 = \frac{\sigma(N^*)N^*}{m(N^*) + \mu} \cdot \frac{\nu}{a + \nu} \tag{5}$$

we have thus the following

Proposition 1

If $R_0 < 1$, the equilibrium $(N^*, 0, 0)$ of system (1) is locally asymptotically stable. If $R_0 > 1, (N^*, 0, 0)$ is unstable.

3. Existence of endemic equilibria.

I now look for the existence of an equilibrium $(\bar{S}, \bar{E}, \bar{I})$ with $\bar{I}, \bar{E}, \bar{S} > 0$. From (1c) we must have

$$\bar{E} = \frac{\mu + m(\bar{N})}{\nu}\bar{I} \tag{6}$$

then, using (6) in (1b)

$$\sigma(\bar{N})\bar{S} = (m(\bar{N}) + \nu)\frac{\mu + m(\bar{N})}{\nu} \tag{7}$$

Finally from (2)

$$\bar{I}/\bar{N} = \frac{(a - m(\bar{N}))\nu}{\nu(\mu + a\delta_2) + a\delta_1(m(\bar{N}) + \mu)} \tag{8}$$

From (6) and (8) we have

$$\bar{S} = \bar{N}\left(1 - \frac{(a - m(\bar{N}))(m(\bar{N}) + \mu + \nu)}{\nu(\mu + a\delta_2) + a\delta_1(m(\bar{N}) + \mu)}\right) \tag{9}$$

Finally (7) yields

$$\sigma(\bar{N})\bar{N} = \frac{(m(\bar{N}) + \mu)(m(\bar{N}) + \nu)\left[\nu(\mu + a\delta_2) + a\delta_1(m(\bar{N}) + \mu)\right]}{\nu\left[\nu(\mu + a\delta_2) + a\delta_1(m(\bar{N}) + \mu) - (a - m(\bar{N}))(m(\bar{N}) + \mu + \nu)\right]} \tag{10}$$

Since we need $\bar{I} > 0$, (8) yields

$$a - m(\bar{N}) > 0 \tag{11}$$

or $\bar{N} < N^*$. Since we need $\bar{S} > 0$, (9) implies

$$(a - m(\bar{N}))(m(\bar{N}) + \mu + \nu) < \nu(\mu + a\delta_2) + a\delta_1(m(\bar{N}) + \mu) \tag{12}$$

As discussed above, I will explore (10) only in two extreme cases: $\delta_1 = 0;\quad \delta_2 = \delta \geq 0;$ or $\delta_1 = \delta_2 = 1$.

In the former case, (10) reduces to

$$\sigma(\bar{N})\bar{N} = F(m(\bar{N})) \tag{13}$$

where

$$F(x) = \frac{(x+\nu)(x+\mu)(\mu+a\delta)}{G(x)} \tag{14}$$

$$G(x) = \nu(\mu+a\delta) - (a-x)(x+\mu+\nu)$$

We have

$$F'(x) = \frac{(\mu+a\delta)}{G(x)^2}$$
$$\times [(2x+\mu+\nu)(\nu(\mu+a\delta)-(a-x)(x+\mu+\nu)) + (x+\mu)(x+\nu)(-2x+a-\mu-\nu)]$$
$$= \frac{(\mu+a\delta)}{G(x)^2} a [-(2x+\mu+\nu)(x+\mu+\nu(1-\delta)) + (x+\mu)(x+\nu)]$$
$$= -\frac{(\mu+a\delta)}{G(x)^2} a [(x+\nu)\nu(1-\delta) + (x+\mu)(x+\mu+\nu(1-\delta))]$$

Therefore $F'(x) < 0$ for $x > 0$.

It is easy to see that the solutions of $G(x) = 0$ are either one positive and one negative; or both negative. Let $\hat{x}$ be the larger one.

If $m(0) > \hat{x}$, we have

$$F(m(0)) > 0 = \lim_{N\to 0+} \sigma(N)N.$$

If $m(0) \le \hat{x}$, there exists $\hat{N} < N^*$ such that $m(\hat{N}) = \hat{x}$. $F(m(N))$ is negative for $0 \le N < \hat{N}$ and

$$\lim_{N\to\hat{N}+} F(m(N)) = +\infty > \sigma(\hat{N})\hat{N}.$$

In either case, there exists a solution of (13) satisfying (11) and (12) if and only if

$$\sigma(N^*)N^* > F(m(N^*)) = \frac{(a+\nu)(a+\mu)}{\nu} \tag{15}$$

Remembering the meaning of R_0, we can state

Proposition 2. Let $\delta_1 = 0$. If $R_0 > 1$, there exists a unique positive equilibrium of (1). If $R_0 \le 1$, there are no positive equilibria.

If $\delta_1 = \delta_2 = 1$, (10) reduces to

$$\sigma(\bar{N})\bar{N} = F(m(\bar{N})) \tag{16}$$

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where

$$F(x) = \frac{\mu\nu + a(x + \mu + \nu)}{\nu} \qquad (17)$$

is increasing. In this case, it is easy to construct instances in which (16) has multiple solutions (see Fig. 1): let

$$\sigma(N) = \beta; \quad m(N) = \begin{cases} b_0 & \text{for } N \leq N_0 \\ b_0 + \kappa(N - N_0) & \text{for } N > N_0 \end{cases}$$

Then, if $0 \leq b_0 < a$, $a\kappa > \beta\nu > 0$, $\frac{(a+\mu)(a+\nu)}{\beta\nu} - \frac{a-b_0}{\kappa} > N_0 > \frac{\mu(a+\nu)+a(b_0+\nu)}{\beta\nu}$, there exist two solutions of (16) with $N \in (0, N^*)$.
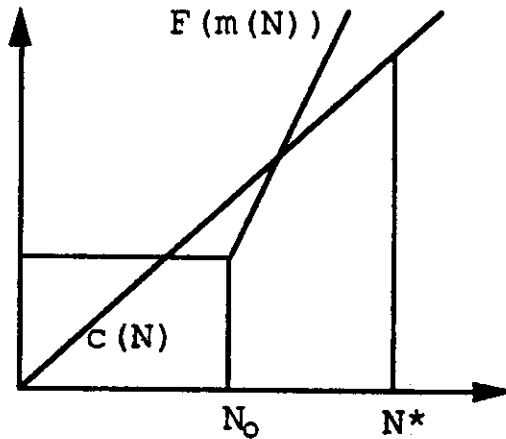
Fig. 1. Possible plot of $c(N)$ and $F(m(N))$ when $\sigma(N)$ and $m(N)$ are defined as above. The two intersections (both with $N < N^*$) correspond the two endemic equilibria of the system.

Note that multiple solutions can not occur when $\sigma(N) \equiv \beta$ and $m(N) = b_0 + \kappa N$, the case considered in [2]; in this case, in fact, both sides of (16) are straight lines, and, if they do not coincide, they have at most one point in common.

One can study this as a bifurcation in the strength of infection, parametrized by a real variable β. Let

$$H(\beta, N) = \beta c(N) - F(m(N));$$

for a given value of β a value of $N \in (0, N^*)$ such that $H(\beta, N) = 0$ is an endemic equilibrium for (1). It is clear that, for all $N > 0$, $\beta(N) = \frac{F(m(N))}{c(N)}$ is positive and solves $H(\beta(N), N) = 0$. We therefore have a function $\beta(N)$ defined on $(0, +\infty)$, such that $\lim_{N \to 0+} \beta(N) = +\infty$. If $\beta'(N) < 0$ for all N, we can then invert the function and obtain that for each $\beta \in (\frac{F(m(N^*))}{c(N^*)}, +\infty)$ we have a unique solution in $(\hat{N}, N^*)$ of $H(\beta, N) = 0$. Otherwise, if there are $N < N^*$ such that $\beta'(N) > 0$, there can be no global inversion (see Fig. 5). Summarizing we can state that

Proposition 3. Let $\delta_1 = \delta_2 = 1$. If $R_0 > 1$, there exists at least one positive equilibrium of (1). If $R_0 \leq 1$, there may or may not be positive equilibria.

4. Local stability of the endemic equilibria

We now study the (local) stability of the endemic equilibria.

First consider the case $\delta_1 = 0$; $\delta_2 = \delta \geq 0$. We now use as variables (N, S, I); the linearization matrix at $(\bar{N}, \bar{S}, \bar{I})$ is

$$\begin{pmatrix} a - m(\bar{N}) - m'(\bar{N})\bar{N} & 0 & -(\mu + a\delta) \\ a - m'(\bar{N})\bar{S} - \sigma'(\bar{N})\bar{S}\bar{I} & -m(\bar{N}) - \sigma(\bar{N})\bar{I} & -a\delta - \sigma(\bar{N})\bar{S} \\ \nu - m'(\bar{N})\bar{I} & -\nu & -(m(\bar{N}) + \mu + \nu) \end{pmatrix}$$

The characteristic polinomial of A is, after a change of sign,

$$z^3 + a_1 z^2 + a_2 z + a_3.$$

After some computations we find

$$a_1 = m'(\bar{N})\bar{N} + B$$
$$a_2 = m'(\bar{N})\bar{N}B + C$$
$$a_3 = m'(\bar{N})\bar{N}C + \gamma D$$

with

$$B = \frac{a(a-b)[b + \mu + \nu(1-\delta)]}{\nu(\mu + a\delta) - (a-b)(b+\mu+\nu)} + 2b + \mu + \nu > 0$$

$$C = \frac{a(a-b)[\nu(1-\delta)(2b+\mu+\nu) + (b+\mu)^2]}{\nu(\mu + a\delta) - (a-b)(b+\mu+\nu)} > 0$$

$$D = (a-b)(b+\mu)(b+\nu) > 0$$

where

$$\gamma = \frac{\bar{N}c'(\bar{N})}{c(\bar{N})},$$

$b = m(\bar{N})$, $c(N) = N\sigma(N)$. From the assumptions that $c(N)$ is increasing, while $\sigma(N)$ is non-increasing, we see that for all N, $0 \leq \gamma \leq 1$.

From these expressions, it is clear that a_1, a_2, and a_3 are positive. The (local) stability of $(\bar{N}, \bar{S}, \bar{I})$ depends only on the sign of $a_1 a_2 - a_3$. Setting, for ease of notation, $\alpha = m'(\bar{N})\bar{N}$, we have

$$a_1 a_2 - a_3 = \alpha^2 B + \alpha B^2 + BC - \gamma(a-b)(b+\mu)(b+\nu) \tag{18}$$

This expression is not definite in sign; therefore, according to the parameters values, $(\bar{N}, \bar{S}, \bar{I})$ may be either stable or unstable.

How does $a_1 a_2 - a_3$ depend on the parameters? It is clear that, as α increases, so does $a_1 a_2 - a_3$ (a stronger density-dependence of the mortality renders stable the endemic equilibrium); while, as γ increases, $a_1 a_2 - a_3$ decreases (the shape of $\sigma(N)$ therefore

influences the stability); at the limit of $\gamma = 0$, $(\bar{N}, \bar{S}, \bar{I})$ is always stable. The dependence on the other parameters is less clear, and has been explored through numerical evaluations of (18).

In Fig. 2 I show how the minimum α necessary to render (18) positive depends on $D = \frac{1}{\mu}$, the average length of the infectious period before death and $L = \frac{1}{\nu}$, the average length of the latent period, for fixed values of a, δ, γ and $b = m(\bar{N})$. Note that $c(\bar{N})$ varies with D and L, since by (13) we have $c(\bar{N}) = F(m(\bar{N}))$. It appears that when L and D differ, the endemic equilibrium tends to be always stable, while when L and D are similar, a relevant density–dependence is necessary for stability.
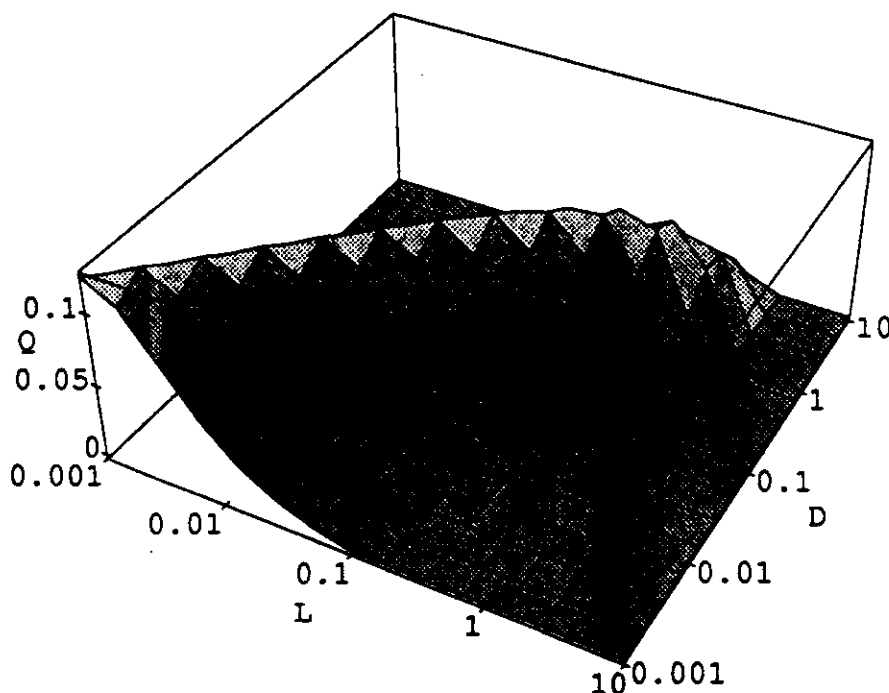

Fig. 2. The minimum $Q=\frac{\alpha}{b}\geq 0$ such that (18) is greater or equal to 0, vs. $L=\frac{1}{\nu}$ and $D=\frac{1}{\mu}$. The other parameter values are $a=0.15$, $b=0.1$, $\delta=0.9$, $\gamma=1$.

In Fig. 3 I again show the stability region, assuming however that $c(N) = \beta N$, and $m(N) = b_0 + \frac{a-b_0}{K}N$ (logistic demography with carrying capacity K). For fixed values of a, b_0, δ, β and μ, we show how the stability of the endemic equilibrium varies with ν and K. It appears, as shown also by Anderson et al. that a large K tends to destabilize the endemic equilibrium, although this does not occur for all values of ν. For a fixed value of K one can note again that the endemic equilibrium tends to be unstable when $L = \frac{1}{\nu} \approx D = \frac{1}{\mu}$, while it becomes stable when L becomes either larger or smaller. We already know [12] that in the limit $L = 0$, the endemic equilibrium is always stable.
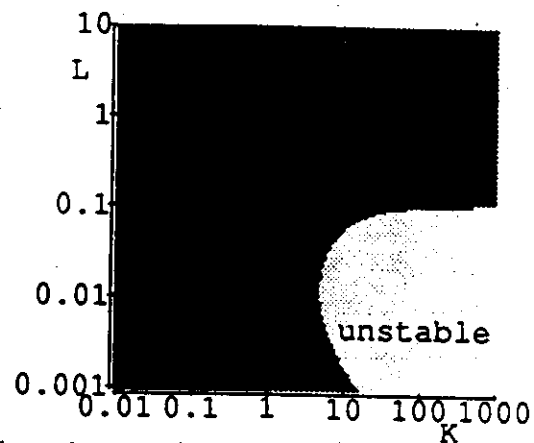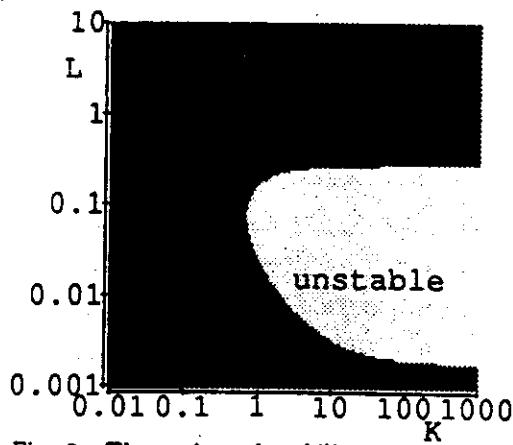
Fig. 3. The region of stability of the endemic equilibrium of system (1). We assume $\sigma(N)\equiv\beta$, and $m(N)=b_0+(a-b_0)N/K$. On the x-axis K; on the y-axis $L=1/\nu$. In the black region of (K,L) values, there is no endemic equilibrium; in the darker grey part the endemic equilibrium exists and is stable; in the lighter part the endemic equilibrium is unstable.

Parameter values are $\beta=80$, $a=1$, $b_0=0.5$, $\delta=0.9$. On the left part of the figure we have $\mu=7$, i.e. $D=0.143$; on the right part $\mu=73$, i.e. $D=0.0137$.

When $\delta_1 = \delta_2 = 1$ (the case considered by Anderson et al.), the characteristic polynomial of the linearization matrix at the endemic equilibrium is (after a change of sign):

$$z^3 + a_1 z^2 + a_2 z + a_3$$

with

$$a_1 = \alpha + B$$
$$a_2 = \alpha B - C(1 - \gamma)$$
$$a_3 = -\alpha C + \gamma D$$

where

$$B = 2b + \mu + \nu > 0$$
$$C = \frac{a(b + \mu)(b + \nu)(a - b)}{a(b + \mu + \nu) + \mu\nu} > 0$$
$$D = (a - b)(b + \mu)(b + \nu) > 0$$
$$\alpha = m'(\bar{N})\bar{N}$$
$$b = m(\bar{N})$$
$$\gamma = \frac{c'(\bar{N})\bar{N}}{c(\bar{N})}$$

Finally we have

$$a_1 a_2 - a_3 = \alpha^2 B + \alpha\left(B^2 + \gamma C\right) - \left(BC(1 - \gamma) + \gamma D\right)$$

Note first that $a_3 > 0$ is equivalent to $\frac{d}{dN}\frac{F(m(N))}{c(N)}|_{N=\bar{N}} > 0$ (remember that by definition $F(m(\bar{N})) = c(\bar{N})$). Therefore the parts going backwards of the bifurcation diagram (see Fig. 5) are always unstable, while in the parts going forward we have $a_3 > 0$.

As for a_2 and $a_1 a_2 - a_3$, they are both indefinite in sign, and their dependence on the parameters appears rather intricate. The only clear thing is that the endemic equilibrium becomes stable, with increasing $\alpha = m'(\bar{N})\bar{N}$, the strength of the density–dependence at $\bar{N}$. The dependence on γ is instead unclear. If $\gamma = 1$ (the case considered in Anderson *et al.*), then $a_2 > 0$ and destabilization may occur only through $a_1 a_2 - a_3$ becoming negative (under some conditions a classical Hopf bifurcation); on the other hand, if $\gamma < 1$, the situation is certainly more complicated.

In order to see graphically the possible cases, I assume, analogously to Fig. 3, a logistic demography with carrying capacity K. In Fig. 4 I show the regions of the plane (K,L) where zero, one or two endemic equilibrium exist (L is the length of the latent period).
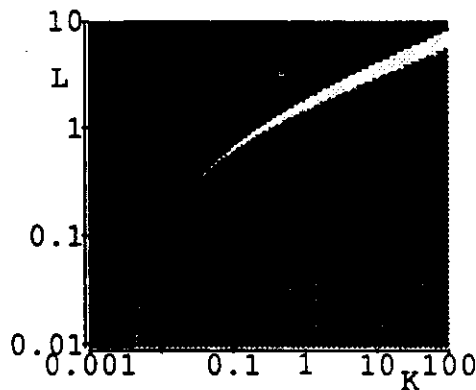

Fig. 4. The region of existence of endemic equilibria of system (1). We assume $\sigma(N)=\beta N^{1/4}$, and $m(N)= b_0+(a-b_0)N/K$. On the x-axis K; on the y-axis $L=1/\nu$. In the black region of (K,L) values, there is no endemic equilibrium; in the darker grey part there is one endemic equilibrium; in the lighter part there are two endemic equilibria. Parameter values are $\beta=10$, $a=2$, $b_0=0.25$, $\mu=0.5$.

The parameters for Figs. 4 and 5 have been chosen so as to give rise to multiple endemic equilibria with a logistic demography; if mortality had been chosen as in Fig. 1, multiple equilibria would arise more easily.

In Fig. 5, for two values of L, I show the bifurcation diagram of the equilibria with varying K. As seen above, when there are two endemic equilibria, the larger one is always unstable ($a_3 < 0$). The stability of the smaller one depends on the parameter values. In the left part of Fig. 5, at the bend of the branch of endemic equilibria, the real positive eigenvalue (remember that on the backward part $a_3 < 0$) of the linearization matrix at the equilibrium crosses into the negative half plane; for a while the equilibrium is locally stable; further on the endemic equilibrium loses stability with a couple of eigenvalues crossing the imaginary axis. In the right part of Fig. 5, at the bend of the branch a second real eigenvalue crosses into the positive half plane; the lower endemic equilibrium is always
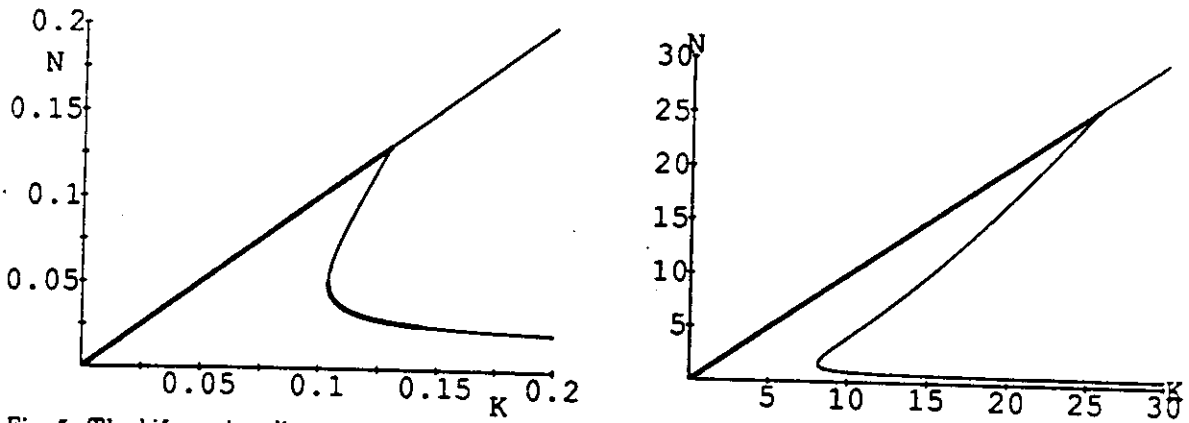
unstable.

Fig. 5. The bifurcation diagram of the equilibria of system (1) with varying K, the carrying capacity of a logistic demography. The straight line corresponds to the equilibrium without infectives ($N=K$); the line branching off is the line of endemic equilibria. The thick part of the lines corresponds to a locally stable equilibrium; the thin part to an unstable equilibrium. In the left part of the graph L (the length of the latent period) is 0.7; in the right part of the graph L is 4. Other parameter values as in Fig. 4.

In Fig. 6 I show more extensively how the stability of the endemic equilibrium (the smaller one when there are two of them) depends on K and L. In the right part of the figure parameter values are as in Fig. 4. In the left part of the figure parameter values are as in Fig. 3, in order to allow a comparison. Clearly the stability region is about the same as in Fig. 3 for small values of L; for large values of L, this case gives rise to a much larger region of instability.
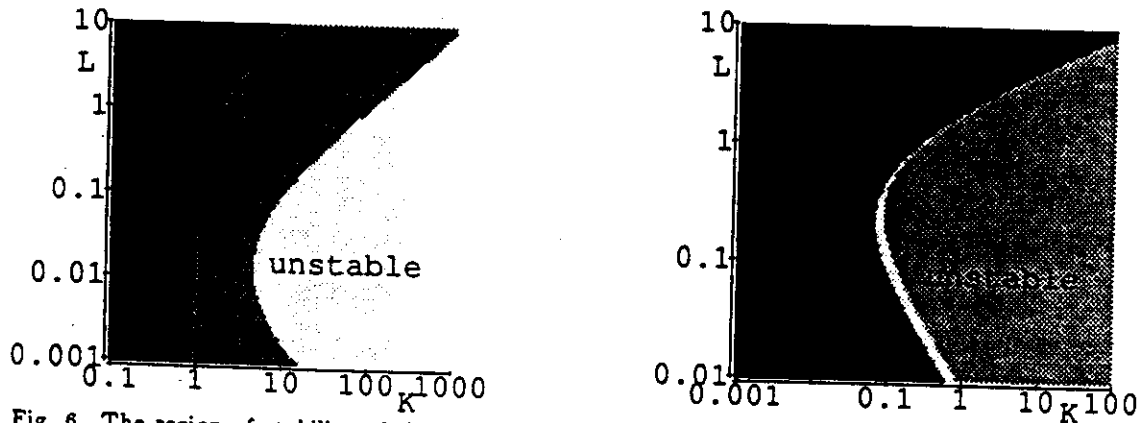

Fig. 6. The region of stability of the endemic equilibrium of system (1) (the lower one when there are two of them). We assume $m(N)=b_0+(a-b_0)N/K$. In the black regions there are no endemic equilibria. In the darker grey region the endemic equilibrium is stable. In the two lighter regions the endemic equilibrium is unstable; in the lightest one $a_1a_2-a_3<0$, but $a_2>0$; in the intermediate grey (present only in the right half) both a_2 and $a_1a_2-a_3$ are negative. In the left part of the figure parameters are as in Fig. 3b. In the right part as in Fig. 4.

5. Numerical simulations

In order to have more information about the behaviour of the solutions of (1), numerical solutions of system (1) have been obtained with an adaptive Runge–Kutta algorithm.
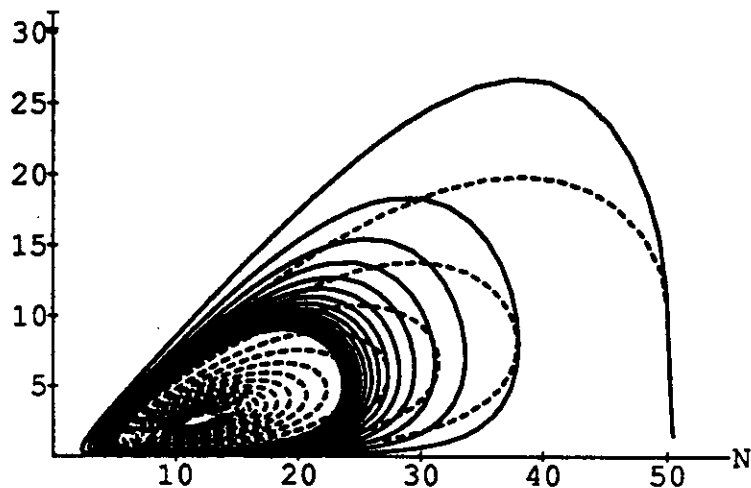

Fig. 7. Numerical solutions of system (1) with $\delta_1=0$. We used $m(N)=0.1$ for $N<50$; $m(N)=0.1(N-49)$ for $N\geq50$; $c(N)=\beta N^\gamma$. The solid line is obtained with $\gamma=1$, $\beta=0.025$. The dashed line with $\gamma=1/2$, $\beta=0.085940$. Other parameter values are $a=0.15$, $\mu=0.1$, $\nu=1$, $\delta_2=0.9$.
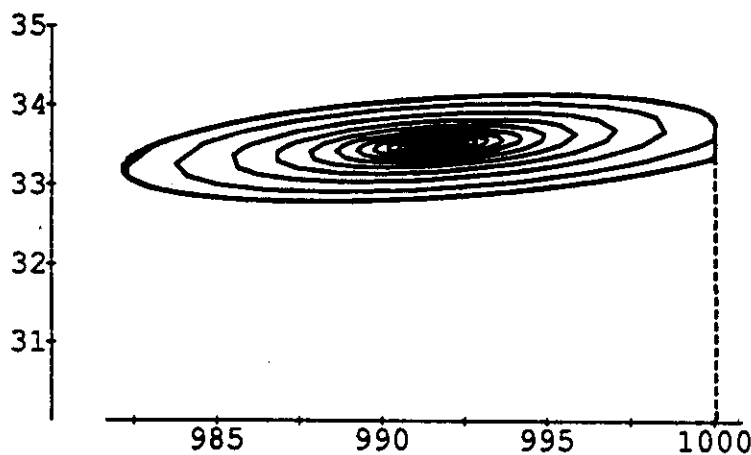

Fig. 8. Numerical solutions of system (1) with $\delta_1=\delta_2=1$. We used $m(N)=0.1$ for $N<1000$; $m(N)=0.1(N-999)$ for $N\geq1000$; $c(N)=0.047N^{1/2}$. Other parameter values are $a=0.15$, $\mu=1$, $\nu=0.5$, $\delta_2=0.9$. The solid line is obtained starting from $(N,S,I)=(991.6,884.4,33.5)$. The dashed line starting from $(1000.2,937.8,19.3)$. Not shown is the trajectory starting from $(1000.2,937.9,19.2)$ which apparently converges to the disease free equilibrium $(1000.5,1000.5,0)$

In Fig. 7 I show some results in the case $\delta_1 = 0$. The two trajectories shown (starting from the same initial value) correspond to the case $\gamma = 1$ and $\gamma = 1/2$; β has been adjusted so as to give rise to the same endemic equilibrium. When $\gamma = 1$ the equilibrium is unstable, and the trajectory apparently converges to a limit cycle. When $\gamma = 1/2$ the equilibrium

is stable and the trajectory converges to the equilibrium in weakly damped oscillations. Note that in this example $m(N)$ has been chosen as in Fig. 1; at the endemic equilibrium there is no density–dependence.

In Fig. 8 we have $\delta_1 = \delta_2 = 1$. $m(N)$ is as in Fig. 1; other parameters have been chosen so as to give rise to two equilibria, both unstable as in Fig. 5b. The two trajectories shown start from very close to the two endemic equilibria; apparently both approach the same limit cycle, one from the inside, the other one from the outside. Note that, although the system is tridimensional, the trajectories appear to be adequately described by the projections on the plane (N, I).

6. The case when the contact rate is independent of population size

When $\sigma(N) = \frac{\beta}{N}$, or $c(N) \equiv \beta$, the dimension of system (1) can be reduced, as noted by May et al. [11] and Busenberg and Van der Driessche [8]. In fact, let

$$\phi = \frac{I}{N} \qquad \theta = \frac{E + I}{N}.$$

System (1) can be rewritten as

$$\begin{cases} \dot{N} = N\left[a - m(N) - a\delta_1\theta - (\mu + a(\delta_2 - \delta_1))\phi\right] \\ \dot{\theta} = (\beta - \mu)\phi(1 - \theta) - a\theta(1 - \delta_1\theta - (\delta_2 - \delta_1)\phi) \\ \dot{\phi} = -\mu\phi(1 - \phi) + \nu(\theta - \phi) - a\phi(1 - \delta_1\theta - (\delta_2 - \delta_1)\phi) \end{cases} \tag{30}$$

The second and third equation of (30) do not depend on N; therefore one can study a bidimensional system in the variables θ and ϕ.

Again I study (30) in the two cases: $\delta_1 = 0$, and $\delta_1 = \delta_2 = 1$.

When $\delta_1 = 0$, the system to be studied is:

$$\begin{cases} \dot{\theta} = (\beta - \mu)\phi(1 - \theta) - a\theta(1 - \delta\phi) \\ \dot{\phi} = -\mu\phi(1 - \phi) + \nu(\theta - \phi) - a\phi(1 - \delta\phi) \end{cases} \tag{31}$$

and one has to study it in the triangle $T = \{(\phi, \theta) : 0 \le \phi \le \theta \le 1\}$.

In T the first of (31) yields $\dot{\theta} \le (\beta - \mu - a)\phi(1 - \theta)$. Therefore, if $\beta < a + \mu$, all solutions converge to $(0, 0)$.

Assume then $\beta \ge a + \mu$. The examination of the phase plane is enough to find out the behaviour of the solutions. In fact $\dot{\theta} = 0$ is equivalent to

$$\theta = \frac{(\beta - \mu)\phi}{a + (\beta - \mu - a\delta)\phi} \stackrel{\text{def}}{=} \theta_1(\phi)$$

while $\dot{\phi} = 0$ is equivalent to

$$\theta = \frac{\phi(a + \mu + \nu - (\mu + a\delta)\phi)}{\nu} \stackrel{\text{def}}{=} \theta_2(\phi)$$

Moreover we have $\dot\theta > [<] 0$ for $\theta < [>] \theta_1(\phi)$; $\dot\phi > [<] 0$ for $\theta > [<]\theta_2(\phi)$. See Fig. 9.

As for the relative position of $\theta_1(\phi)$ and $\theta_2(\phi)$, we first note that

$$\theta_1(0) = \theta_2(0) = 0 \qquad \theta_1(1) = \frac{\beta - \mu}{\beta - \mu + a(1-\delta)} < 1 < \frac{\nu + a(1-\delta)}{\nu} = \theta_2(1)$$

We first look for endemic equilibria, i.e. $\phi > 0$ such that $\theta_1(\phi) = \theta_2(\phi)$. Such ϕ would satisfy $Q(\phi) = 0$ where

$$Q(\phi) = -(\beta-\mu-a\delta)(\mu+a\delta)\phi^2+[(\beta - \mu - a\delta)(a + \mu + \nu) - a(\mu + a\delta)] \phi+a(a+\mu+\nu)-\nu(\beta-\mu).$$

Since $Q(1) = a(1 - \delta)(\beta - \mu + \nu + a(1 - \delta)) > 0$, while $\lim_{\phi\to\infty} Q(\phi) = -\infty$, there exists at least one solution of $Q(\phi) = 0$ in $(1,\infty)$. Since Q is a second-degree polynomial, there exists at most one solution of $Q(\phi) = 0$ in $(0,1)$.

Therefore, if $Q(0) < 0$, that is equivalent to $\beta\nu > (a + \mu)(a + \nu)$, or $\theta_1'(0) > \theta_2'(0)$, there exists one solution in $(0,1)$ of $\theta_1(\phi) = \theta_2(\phi)$, i.e. an endemic equilibrium for (31). Note that the equilibrium is necessarily in T, since $\theta_1(\phi) < 1$, while $\theta_2(\phi) > \phi$ for all $0 < \phi < 1$.

If $\theta_1'(0) \le \theta_2'(0)$, or $Q(0) \ge 0$, it follows that there is no endemic equilibrium.

Global convergence to the endemic equilibrium in the first case, to $(0,0)$ in the second case is then easily established by considering the phase plane (see Fig. 9).
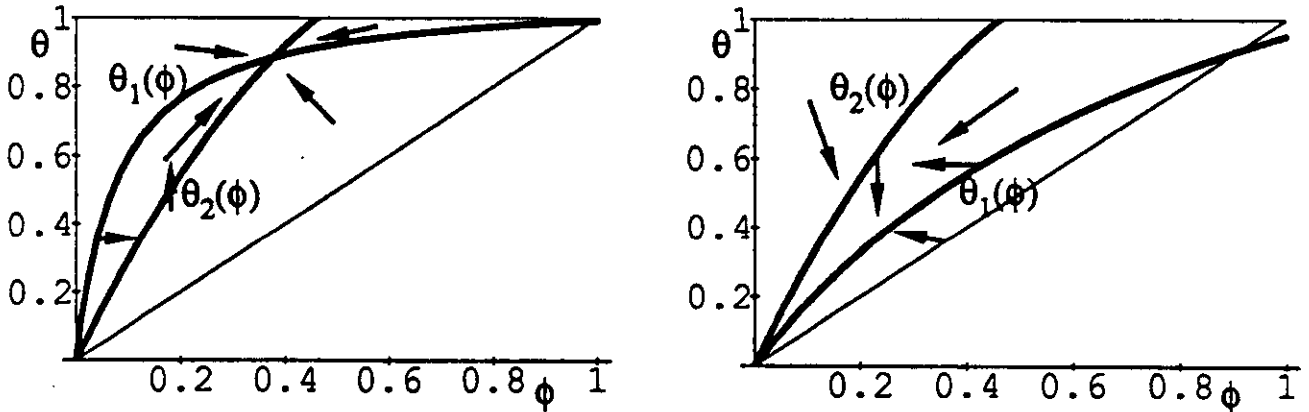

Fig. 9. The phase plane of system (31). In a) $\beta\nu>(a+\mu)(a+\nu)$; in b) $\beta\nu\le(a+\mu)(a+\nu)$

The behaviour of N then follows from the first of (30). If $\beta\nu \le (a+\mu)(a+\nu)$, N tends to N^*. If $\beta\nu > (a+\mu)(a+\nu)$, let $\bar\phi$ be the solution in $(0,1)$ of $Q(\phi) = 0$. If $a \le m(0)+(\mu+a\delta)\bar\phi$, N tends to 0; otherwise it tends to the solution $\bar N$ of $m(N) = a - (\mu + a\delta)\bar\phi$.

Consider now system (30) when $\delta_1 = \delta_2 = 1$. The resulting system is

$$\begin{cases} \dot\theta = (1 - \theta)\,[(\beta - \mu)\phi - a\theta] \\ \dot\phi = -\mu\phi(1 - \phi) + \nu(\theta - \phi) - a\phi(1 - \theta) \end{cases} \qquad (32)$$

As above, we find the isoclines. $\dot\theta = 0$ is equivalent to

$$\theta = 1 \quad \text{or} \quad \theta = \frac{\beta - \mu}{a}\phi \overset{\text{def}}{=} \theta_1(\phi)$$

while $\dot\phi = 0$ is equivalent to

$$\theta = \frac{\phi(a + \nu + \mu(1 - \phi))}{a\phi + \nu} \overset{\text{def}}{=} \theta_2(\phi)$$

We have $\theta_2(0) = 0$, $\theta_2(1) = 1$, and θ_2 concave. Moreover, if $\nu \geq \mu$, θ_2 is increasing on $[0,1]$; if $\mu > \nu$, $\theta_2(\nu/\mu) = 1$, $\theta_2(\phi) < 1$ for $0 \leq \phi < \nu/\mu$, $\theta_2(\phi) > 1$ for $\nu/\mu < \phi < 1$.

It follows that if $\theta_1'(0) \geq \theta_2'(0)$, or $\beta\nu \geq (a+\mu)(a+\nu)$, $\theta_1(\phi) > \theta_2(\phi)$ for all $0 < \phi \leq 1$, and the phase plane is as in Fig. 10a. From all initial points except $(0,0)$ the solutions converge to $(1,1)$ if $\nu \geq \mu$; to $(\nu/\mu, 1)$ if $\nu < \mu$.

If $(a+\mu)(a+\nu) > \beta\nu > \mu\nu + a\max\{\mu,\nu\}$, there exists an endemic equilibrium which is a saddle point (Fig. 10b). Depending on the starting point, a different equilibrium is approached: there exists a separatrix line, starting from which solutions converge to the endemic equilibrium; starting below that line solutions converge to $(0,0)$; starting above to $(1,1)$ if $\nu \geq \mu$, to $(\nu/\mu, 1)$ if $\nu < \mu$.

Finally, if $\beta\nu \leq \mu\nu + a\max\{\mu,\nu\}$, in T $\theta_1(\phi)$ is always below $\theta_2(\phi)$, and we have global convergence to $(0,0)$ except from the line $\theta = 1$ (Fig. 10c).
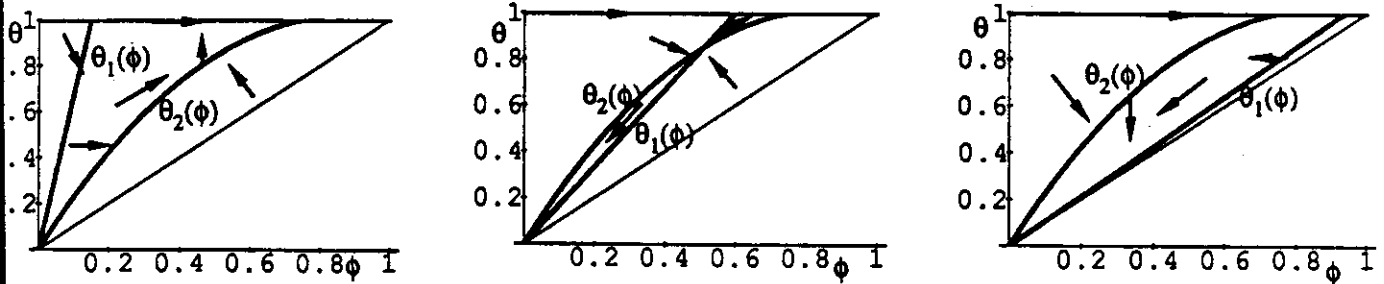

Fig. 10. The phase plane of system (32). In a) $\beta\nu \geq (a+\mu)(a+\nu)$; in b) $(a+\mu)(a+\nu) > \beta\nu > \mu\nu + a\max\{\mu,\nu\}$; in c) $\beta\nu \leq \mu\nu + a\max\{\mu,\nu\}$

The behaviour of N follows from the first of (30). When (ϕ, θ) converge to $(0,0)$, N tends to N^*. When (ϕ, θ) converge to $(1,1)$ or $(\nu/\mu, 1)$, N tends to 0. In the nongeneric case that N converges to the endemic equilibrium $(\bar\phi, \bar\theta)$, N tends to 0, if $a(1 - \bar\theta) \leq m(0) + \mu\bar\phi$; otherwise it tends to the solution $\bar N$ of $m(N) = a(1 - \bar\theta) - \mu\bar\phi$.

7. Discussion

In this paper I have analyzed an ODE model for a disease without recovery, with a latent period and with variable population size: demographic parameters depend on epidemic state.

It appears that this model, as already noted by Anderson et al. can produce either convergence to an equilibrium (with or without infectives), or oscillations. This in contrast

both with models without latent period [12], and with constant population size (see for instance [1]). Although neither the latent period, nor variable population size, can produce by themselves oscillations in an ODE model (but see [6]), their combination can.

Another aspect resulting from this work is the qualitative difference between the case where fertility of exposed (but not infective) individuals is equal to that of susceptibles to the case where it is reduced. In the first case we have a clear threshold, below which the disease-free equilibrium is stable, and no endemic equilibrium exists; and above which the disease-free equilibrium is unstable, and a unique endemic equilibrium exists. Building a bifurcation diagram, the branch of endemic equilibria inherits the (local) stability from the disease-free equilibrium; destabilization may occur only with two conjugate eigenvalues crossing the imaginary axis. On the other hand, when fertility of exposed and infective individuals is zero (as assumed in [2] and [6]) the threshold phenomenon is weaker: below the threshold the disease-free equilibrium is stable; above it is unstable, and there exists an endemic equilibrium. However, the endemic equilibrium needs not be unique, and it may exist also below the threshold. Multiple equilibria do not arise if mortality and the contact rate per individual are linear with population size (as in [2]), but may arise as soon as one of these assumptions is relaxed.

Summarizing, the model with $\delta_1 = 0$, which appears to be more respondent to the biology, gives rise to a picture similar to that of most epidemic models, with also the possibility of oscillations. The dynamics of the model with $\delta_1 = \delta_2 = 1$ appears to be more complicated for certain parameter values, and is probably not completely captured by the few simulations presented in Fig. 8; further analysis of the qualitative behaviour would probably be interesting. Note, however, that when the latent period is not very large, the two models do not differ sensibly (see Fig. 3b and 4a).

The different behaviour of the two cases shows clearly when contact rate is independent of population size (Section 6). When $\delta_1 = 0$, one again has a threshold, with global convergence to the disease free equilibrium below the threshold, to the endemic equilibrium above. When $\delta_1 = \delta_2$, the endemic equilibrium exists only in an intermediate range of values and is always unstable; from almost all initial values has convergence either to the disease free equilibrium, or to zero population.

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