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Prelude to Hopf Bifurcation in an Epidemic Model: Analysis of a Characteristic Equation Associated with a Nonlinear Volterra Integral Equation

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Abstract. We discuss a simple deterministic model for the spread, in a closed population, of an infectious disease which confers only temporary immunity. The model leads to a nonlinear Volterra integral equation of convolution type. We are interested in the bifurcation of periodic solutions from a constant solution (the endemic state) as a certain parameter (the population size) is varied. Thus we are led to study a characteristic equation. Our main result gives a fairly detailed description (in terms of Fourier coefficients of the kernel) of the traffic of roots across the imaginary axis. As a corollary we obtain the following: if the period of immunity is longer than the preceding period of incubation and infectivity, then the endemic state is unstable for large population sizes and at least one periodic solution will originate.

Key words: Epidemic model – Temporary immunity – Nonlinear Volterra integral equation – Characteristic equation – Hopf bifurcation

1. A Simple Deterministic Epidemic Model

Consider a population divided into two classes S and I. The class S consists of those individuals who are susceptible to a certain infectious disease and the class I of those who experience the consequences of an infection. We distinguish the members of I according to the time elapsed since they were infected. In particular, let $i(t, \tau)$ denote the density, at time t, of those members of I which have class-age τ. We assume that:

(i) The population is demographically closed and all changes are due to the infection mechanism. In other words,

$$S(t) + I(t) = N, \tag{1.1}$$

where N denotes the population size.

(ii) The interaction of infectives and susceptibles is of "mass-action" type, with a weighted average over the age-structured class of infectives. More precisely, there exists a nonnegative function $A(\tau)$, describing the infective "force" of an individual which was infected τ units of time ago, such that

$$i(t,0) = S(t)\int_0^\infty A(\tau)i(t,\tau)\,d\tau. \tag{1.2}$$

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(iii) The infective "force" reduces to zero after a finite time: there exists a least positive number $\tau_1 < \infty$ such that the support of A is contained in $[0, \tau_1]$.

(iv) The disease confers only temporary immunity: there exists a number $\tau_2 \geqslant \tau_1$, such that every infected individual becomes susceptible again exactly τ_2 units of time after its contagion.

On account of (iv) we can rewrite (1.1) as

$$S(t) + \int_0^{\tau_2} i(t, \tau)\, d\tau = N. \tag{1.3}$$

Noting that $i(t, \tau) = i(t - \tau, 0)$ and eliminating $S(t)$ from (1.2) and (1.3) we obtain

$$i(t, 0) = \left(N - \int_0^{\tau_2} i(t - \tau, 0)\, d\tau\right) \int_0^{\tau_1} A(\tau) i(t - \tau, 0)\, d\tau, \tag{1.4}$$

which upon the transformation of variables

$$\begin{aligned} x(t) &= \frac{\tau_2}{N} i(\tau_2 t, 0), \\ b(t) &= \tau_2 A(\tau_2 t) \left(\int_0^{\tau_2} A(\tau)\, d\tau\right)^{-1}, \\ \gamma &= N \int_0^{\tau_2} A(\tau)\, d\tau \end{aligned} \tag{1.5}$$

leads to

$$x(t) = \gamma \left(1 - \int_0^1 x(t - \tau)\, d\tau\right) \int_0^1 b(\tau) x(t - \tau)\, d\tau. \tag{1.6}$$

We remark that this and similar models have been discussed before in the literature. In particular we refer to [1, 8, 12, 13, 14, 15, 16, 17, 19] and the references given there.

2. A Nonlinear Volterra Integral Equation

Let $b\colon \mathbb{R} \to \mathbb{R}$ be a nonnegative and measurable function such that its support is contained in $[0, 1]$ and

$$\int_0^1 b(\tau)\, d\tau = 1. \tag{2.1}$$

The nonlinear autonomous (i.e., translation invariant) Volterra integral equation

$$x(t) = \gamma \left(1 - \int_{t-1}^t x(\tau)\, d\tau\right) \int_{t-1}^t b(t - \tau) x(\tau)\, d\tau \qquad (2.2) = (1.6)$$

admits the constant solutions

$$\bar{x}_1 = 0, \qquad \bar{x}_2 = 1 - \gamma^{-1}. \tag{2.3}$$

If we (formally) linearize the equation about such a constant solution and if we, subsequently, substitute the function $\exp(\lambda t)$, we obtain an equation for λ which is called the *characteristic equation*. The location of the roots of the characteristic equation in the complex plane (as well as the variation of this location with variations in γ) yields information about the qualitative behaviour of solutions of (2.2) near the constant solution. In order to make this statement more precise it is advantageous to have a theory which associates with (2.2) a nonlinear semigroup of operators on some function space such that, for instance, the principle of linearized stability and the Hopf bifurcation theorem can be derived in a standard manner. In [6] a specific semigroup construction has been introduced (see [5] for the linear case). A detailed elaboration of some qualitative items within that context is in preparation [7].

However, we note that other approaches are possible and, in fact, have been studied in the literature. In particular the Hopf bifurcation theorem has drawn a lot of attention, see [2, 3, 4, 8, 9, 10, 11, 20]. As we will indicate more clearly later, the present paper forms a good combination with Gripenberg [8].

The characteristic equations corresponding to $\bar{x}_1$ and $\bar{x}_2$ are, respectively,

$$\gamma\bar{b}(\lambda) = 1, \tag{2.4}$$

$$\bar{b}(\lambda) + (1-\gamma)\frac{1-e^{-\lambda}}{\lambda} = 1. \tag{2.5}$$

Here $\bar{b}$ denotes the Laplace transform of b:

$$\bar{b}(\lambda) = \int_0^1 e^{-\lambda\tau} b(\tau)\,d\tau. \tag{2.6}$$

If $0 < \gamma < 1$ all roots of (2.4) lie in the left half plane (l.h.p.). Indeed, by the nonnegativity of b, all roots satisfy $\operatorname{Re}\lambda \leqslant \zeta$, where ζ is the unique real root and if $\gamma < 1$ then $\zeta < 0$. Similarly, one deduces that for $\gamma < 1$ (2.5) has at least one root, viz. a real one, in the right half plane (r.h.p.). If γ passes through one, $\bar{x}_1$ and $\bar{x}_2$ intersect each other, the real root of (2.4) moves into the r.h.p. (and will stay there for all $\gamma > 1$), the real root of (2.5) moves into the l.h.p. and, at least for $\gamma > 1$ but $\gamma - 1$ small, *all* roots of (2.5) lie in the l.h.p. Consequently, if γ passes through one bifurcation and exchange of (linearized) stability takes place.

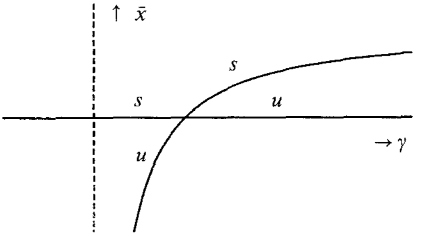

Fig. 1. The graph of $\bar{x}_1$ and $\bar{x}_2$

In the epidemic model $\bar{x}_2$ corresponds to the state in which the disease is endemic. As the population size reaches a critical value (i.e., as γ passes through one) this state becomes positive, and thus biologically meaningful, and at the same time it takes over the stability of the state $\bar{x}_1$ in which the disease is absent from the population. This is the well-known threshold phenomenon.

The following question naturally arises: does the endemic state $\bar{x}_2$ retain its stability as γ is further increased? First of all, we observe that $\lambda = 0$ is a solution of (2.5) if and only if $\gamma = 1$ (note that $\bar{b}(0) = 1$). Consequently, stability will be lost if and only if a pair of complex conjugated roots crosses the imaginary axis (note that nonreal roots occur in conjugated pairs and that no roots can enter the r.h.p. from infinity). Such a crossing will, presumably, be attended with a Hopf bifurcation (i.e., the origination of a periodic solution). In the next section we shall study the traffic of roots of (2.5) across the imaginary axis when γ increases.

3. Imaginary Roots: The Main Result

Putting $\lambda = x + iy$ and splitting (2.5) into its real and its imaginary part we obtain the system of two real equations

$$f_i(x, y, \gamma) = 0, \qquad i = 1, 2, \tag{3.1}$$

where by definition

$$f_1(x, y, \gamma) = \int_0^1 b(\tau) e^{-x\tau} \cos(y\tau)\, d\tau + (1 - \gamma) \int_0^1 e^{-x\tau} \cos(y\tau)\, d\tau - 1, \tag{3.2}$$

$$f_2(x, y, \gamma) = -\int_0^1 b(\tau) e^{-x\tau} \sin(y\tau)\, d\tau - (1 - \gamma) \int_0^1 e^{-x\tau} \sin(y\tau)\, d\tau. \tag{3.3}$$

In search for purely imaginary roots we concentrate on solutions with $x = 0$ and $y \neq 0$.

Suppose $(0, y, \gamma)$ is a solution of (3.1). We note that necessarily $y \neq 2n\pi$, $n \in \mathbb{Z} \backslash \{0\}$, since for those values of y

$$f_1(0, y, \gamma) = \int_0^1 b(\tau) \cos(y\tau)\, d\tau - 1 < 0.$$

So we can use the second equation to express γ in terms of y:

$$\gamma = 1 + \frac{\int_0^1 b(\tau) \sin(y\tau)\, d\tau}{\int_0^1 \sin(y\tau)\, d\tau}. \tag{3.4}$$

Substitution of this expression into the first equation yields an equation for y alone

$$K(y) = 0, \tag{3.5}$$

where by definition

$$K(y) = -1 + \frac{\int_0^1 b(\tau) \cos(y\tau)\, d\tau \int_0^1 \sin(y\tau)\, d\tau - \int_0^1 b(\tau) \sin(y\tau)\, d\tau \int_0^1 \cos(y\tau)\, d\tau}{\int_0^1 \sin(y\tau)\, d\tau}. \tag{3.6}$$

Conversely, suppose $y \neq 2n\pi$ satisfies (3.5) then, defining γ by (3.4), we obtain a solution $(0, y, \gamma)$ of (3.1). We conclude that we can find all solutions of (3.1) with $x = 0$ and $y \neq 0$ by finding all solutions of (3.5).

In order to facilitate the formulation of our results we introduce some notation. The Fourier coefficients b_n of b are defined by

$$b_n = 2\int_0^1 b(\tau)\sin(2\pi n\tau)\,d\tau. \tag{3.7}$$

The intervals $I_n^{\pm}$ are defined as follows

$$\begin{aligned} I_n &= ((2n-1)\pi,\ (2n+1)\pi), \\ I_n^+ &= (2n\pi,\ (2n+1)\pi), \\ I_n^- &= ((2n-1)\pi,\ 2n\pi). \end{aligned} \tag{3.8}$$

Our first result gives information about the zeros of K.

Lemma. *If $b_n = 0$ then K has no zero in I_n. If, on the contrary, $b_n \neq 0$ then K has precisely one simple zero in I_n, say y_n. If $b_n > 0$ then $y_n \in I_n^-$ and $K'(y_n) > 0$, whereas if $b_n < 0$ then $y_n \in I_n^+$ and $K'(y_n) < 0$.*

Proof. Using well-known trigonometric identities we rewrite (3.6) as

$$K(y) = -1 - \frac{\int_0^1 b(\tau)\sin((\tau - \frac{1}{2})y)\,d\tau}{\sin(\frac{1}{2}y)}. \tag{3.9}$$

We observe that $K(y) = K(-y)$, $b_{-n} = -b_n$, $I_{-n}^+ = -I_n^-$ and $I_{-n}^- = -I_n^+$. So we restrict our attention to nonnegative n.

In $I_n \backslash \{2n\pi\}$ the equation $K(y) = 0$ is equivalent to

$$y = m(y), \tag{3.10}$$

where by definition

$$m(y) = 2n\pi + (-1)^{n+1}\, 2\arcsin\left\{\int_0^1 b(\tau)\sin((\tau - \tfrac{1}{2})y)\,d\tau\right\}. \tag{3.11}$$

Clearly $m((2n-1)\pi) > (2n-1)\pi$ and $m((2n+1)\pi) < (2n+1)\pi$. Moreover,

$$\begin{aligned} |m'(y)|^2 &= 4\frac{\{\int_0^1 (\tau - \frac{1}{2})b(\tau)\cos((\tau - \frac{1}{2})y)\,d\tau\}^2}{1 - \{\int_0^1 b(\tau)\sin((\tau - \frac{1}{2})y)\,d\tau\}^2} \\ &\leqslant 4\frac{\int_0^1 (\tau - \frac{1}{2})^2 b(\tau)\,d\tau \int_0^1 b(\tau)\cos^2((\tau - \frac{1}{2})y)\,d\tau}{1 - \int_0^1 b(\tau)\,d\tau \int_0^1 b(\tau)\sin^2((\tau - \frac{1}{2})y)\,d\tau} \\ &= 4\int_0^1 (\tau - \tfrac{1}{2})^2 b(\tau)\,d\tau \\ &< 1. \end{aligned}$$

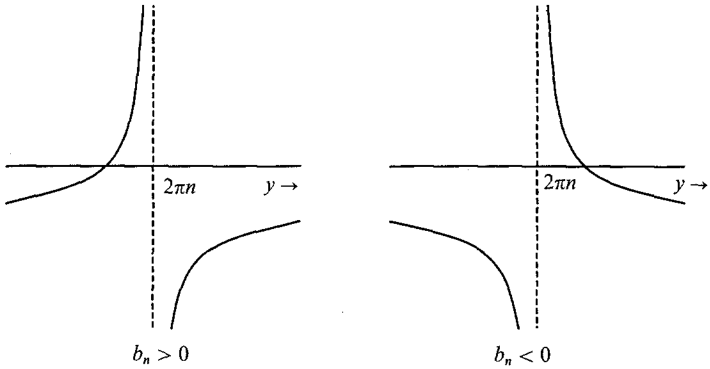

Fig. 2. The graph of K on the interval I_n

(Here we use the Cauchy-Schwarz inequality with respect to the measure $b(\tau)\,d\tau$ in both numerator and denominator, the fact that $\int_0^1 b(\tau)\,d\tau = 1$ and the inequality $(\tau - \frac{1}{2})^2 < \frac{1}{4}$ for $\tau \in (0, 1)$.) So we are in a position to apply the contraction mapping theorem and to conclude that m has a unique fixed point in I_n. Since

$$m(2n\pi) = 2n\pi - 2\arcsin(\tfrac{1}{2}b_n),$$

the fixed point lies in I_n^- if $b_n > 0$ and in I_n^+ if $b_n < 0$, whereas it equals $2n\pi$ if $b_n = 0$.

From (3.9) and the properties of b we deduce that

$$K((2n \pm 1)\pi) = -1 \mp (-1)^n \int_0^1 b(\tau)\sin((\tau - \tfrac{1}{2})(2n \pm 1)\pi)\,d\tau < 0$$

and, as $y \rightarrow 2n\pi$,

$$K(y) = -1 - \frac{b_n}{y - 2n\pi} + \int_0^1 (1 - 2\tau)b(\tau)\cos(2n\pi\tau)\,d\tau + o(1).$$

This implies that $K'(y_n) > 0$ if $b_n > 0$ and $K'(y_n) < 0$ if $b_n < 0$ (note that $K'(y_n) \neq 0$ since $m'(y_n) \neq 1$). Finally, if $b_n = 0$ then

$$K(2n\pi) = -1 + \int_0^1 (1 - 2\tau)b(\tau)\cos(2n\pi\tau)\,d\tau < 0. \quad \square$$

We are now ready to state the main result.

Theorem. *As γ increases from one to infinity, exactly as many pairs of conjugated roots of the characteristic equation* (2.5) *pass the imaginary axis as there are $n \in \mathbb{N}$ for which $b_n > 0$. They cross from left to right with a positive velocity, one in the interval I_n^- and the other in I_{-n}^+. Moreover, they are simple.*

Proof. For symmetry reasons we can restrict our attention to the upper half plane. As noted before, any crossing of the positive imaginary axis must take place in I_n for some $n \in \mathbb{N}$. According to the Lemma, a root of (2.5) lies, for some value of γ, in I_n if and only if $b_n \neq 0$. The first equation of (3.1) implies that

$$(1-\gamma)\frac{\sin(y)}{y} = 1 - \int_0^1 b(\tau)\cos(y\tau)\,d\tau > 0,$$

and consequently the corresponding value of γ will be greater than one if and only if $y \in I_n^-$, which in turn, by the Lemma, will be the case if and only if $b_n > 0$.

In order to obtain some more information about the crossing we want to solve (3.1) by the implicit function theorem for x and y as a function of γ, starting from such a point on the imaginary axis. We observe that

$$\frac{\partial f_{1,2}}{\partial x, y}(0, y, \gamma) = \begin{pmatrix} c & d \\ -d & c \end{pmatrix},$$

with

$$c = -\int_0^1 \tau b(\tau)\cos(y\tau)\,d\tau - (1-\gamma)\int_0^1 \tau\cos(y\tau)\,d\tau,$$

$$d = -\int_0^1 \tau b(\tau)\sin(y\tau)\,d\tau - (1-\gamma)\int_0^1 \tau\sin(y\tau)\,d\tau.$$

Since

$$K'(y) = d - c\frac{\sin(y)}{\cos(y)-1} \neq 0,$$

it cannot happen that both c and d are zero. So the roots are simple and we can solve indeed for x and y as a function of γ. Along this curve we have

$$\frac{\partial x, y}{\partial \gamma} = -\left(\frac{\partial f_{1,2}}{\partial x, y}\right)^{-1}\frac{\partial f_{1,2}}{\partial \gamma}$$

$$= \frac{-1}{c^2+d^2}\begin{pmatrix} c & -d \\ d & c \end{pmatrix}\begin{pmatrix} -\dfrac{\sin(y)}{y} \\ \dfrac{1-\cos(y)}{y} \end{pmatrix}$$

and thus

$$\frac{\partial x}{\partial \gamma} = \frac{1}{c^2+d^2}\,\frac{1-\cos(y)}{y}\left(d - c\frac{\sin(y)}{\cos(y)-1)}\right)$$

$$= \frac{1}{c^2+d^2}\,\frac{1-\cos(y)}{y}K'(y) > 0. \quad \square$$

We remark that a similar result relates the zeros of K corresponding to $b_n < 0$ to pairs of roots of (2.5) which cross the imaginary axis from right to left when γ increases from minus infinity to one.

4. A Description of Trajectories of Roots in the Complex Plane

In this section we shall give a description in words of the typical features that appear from a computer study of the roots of (2.5) in the case where the kernel is a block function on $[\alpha, \beta]$ with $0 \leqslant \alpha < \beta < 1$ (see Montijn [18]).

If γ increases beyond one, one real root moves into the l.h.p. and at the same time one real root originates at minus infinity and starts to move in the positive direction. If γ is further increased, these roots collaps, take off into the complex plane and move back to the imaginary axis. Whether they cross or not depends on the value of b_1. As γ tends to infinity they tend to $\pm 2\pi i$.

Similarly, other couples move towards the imaginary axis. Whether they cross or not depends on the sign of some b_n. If they cross, they make an excursion into the r.h.p., but inevitably they turn back and move towards the imaginary axis again. The Theorem implies that roots cannot cross from right to left. As γ tends to infinity *all* roots settle down asymptotically at some integer multiple of $2\pi i$.

Using the implicit function theorem with γ^{-1} as a variable one can deduce that *all* the points $\pm 2n\pi i$, $n \in \mathbb{N}$, occur as limits of roots as $\gamma \to +\infty$. Detailed elaboration shows that $\pm 2n\pi i$ will be approached from the r.h.p. if $b_n > 0$ and from the l.h.p. if $b_n < 0$. It is suggested by the Theorem and the numerical results that, in the case $b_n = 0$, the approach is from the l.h.p..

5. Interpretation and Discussion of the Results

The Theorem implies that $\bar{x}_2$ retains its stability if and only if $b_n \leqslant 0$ for all $n \in \mathbb{N}$ (which is the case if, for instance, b is symmetric about $\frac{1}{2}$).

If $b_n > 0$ for some $n \in \mathbb{N}$ we are in a position to apply a Hopf bifurcation theorem. Unfortunately, it is not clear to us whether roots can pass the imaginary axis simultaneously and "in resonance" (i.e., some being integer multiples of others). We think this will "generically" (with respect to the kernel b) not happen, but we do not know how to prove it. However, we do know that at most finitely many roots can pass simultaneously (equation (2.5) involves analytic functions and we can apply the Riemann-Lebesgue lemma). So there is always a largest one which then, according to the Theorem, satisfies all the assumptions of the usual Hopf bifurcation theorem. In particular, under mild assumptions on b, a variant of Gripenberg's theorem [8] is directly applicable ("variant" because one of the kernels is the characteristic function of [0, 1] which is not absolutely continuous as he requires; however, his proof can easily be adapted to cover this situation as well). We conclude that at least one periodic solution bifurcates if at least one $b_n > 0$ and that countably many periodic solutions bifurcate if countably many $b_n > 0$ (note that all $b_n > 0$ if, for instance, b is decreasing).

The period T of the bifurcating periodic solution corresponding to some $b_n > 0$ will, at least initially, satisfy the inequality

$$\frac{1}{n} < T < \frac{1}{n - \frac{1}{2}}.$$

So the period will in general be less than one with only one possible exception.

Only the first bifurcating periodic solution can possibly be stable for parameter values near to the bifurcation value. Gripenberg [8] gives a formula to determine the stability character, at least in a (formal) linearized sense. Numerical evaluation of his formula for various choices of the kernel b proves that both stability and instability are possible. However, it seems that the situation in which the first bifurcating periodic solution is stable occurs more frequently.

Our result shows that the endemic state may or may not remain stable when the population size increases. In terms of the original variables we have

$$b_n = \frac{\displaystyle\int_0^{\tau_1} A(\tau)\sin\left(\frac{2\pi n\tau}{\tau_2}\right)d\tau}{\displaystyle\int_0^{\tau_1} A(\tau)\,d\tau}.$$

Since $A(\tau) \geqslant 0$ and $\sin(\tau) \geqslant 0$ for $0 \leqslant \tau \leqslant \pi$, it follows directly that $b_1, \ldots, b_k > 0$ if

$$\frac{\tau_1}{\tau_2} < \frac{1}{2k}.$$

So, if $\tau_2 \geqslant 2\tau_1$, the endemic state will loose its stability, irrespective any other property of the infectivity function A. This corollary clearly shows that one can always destabilize the endemic state by both lengthening the immunity period and increasing the population size. Similar conclusions have been drawn by Hethcote et al. [12] and Stech and Williams [19] for related but somewhat different models.

Let us make an attempt to explain the results. In the endemic state each infective replaces itself by passing on the disease to exactly one susceptible. If, by some disturbance (which does not influence the total population size), there are less infectives, then automatically there are more susceptibles and consequently the number of contaminations by one infective will increase above one. Conversely, if there are more infectives then there are less susceptibles and the number of contaminations by one infective will decrease below one. This is the basic feedback mechanism which brings about the stability of the endemic state $1 - \gamma^{-1}$ in the ordinary differential equation model

$$\dot{y} = \gamma y(1 - y) - y.$$

In this case the stability of the endemic state increases with γ in the sense that the characteristic exponent is given by $1 - \gamma$.

In the case of equation (1.6) = (2.2) the feedback mechanism is influenced by time delays. For instance, if a disturbance increases the number of immune but non-infectuous individuals and decreases the number of infectives as well as the number of susceptibles then there will be, at first, only very few new cases of contamination. Some time later this may lead to a situation with very many susceptibles (over compensation) etc. Thus a strong but time delayed feedback mechanism may lead to instability and to oscillations. Whether or not this actually happens depends on the details of the mechanism as described by the kernel b. In particular we found that the Fourier coefficients b_n are the critical parameters and that a long immunity period leads to destabilization.

The fact that all roots approach the imaginary axis as $\gamma \to +\infty$ indicates that, although the endemic state may indeed retain its stability, nevertheless the stability becomes marginal. It seems possible that the domain of attraction shrinks and that equation (2.2) has lots of periodic solutions for large values of γ even when $b_n \leqslant 0$ for all n. In that case they do not bifurcate from $\bar{x}_2$, but they may originate from "free" bifurcations. Moreover, by analogy with the well-known difference equation $x_{n+1} = \gamma(1 - x_n)x_n$, we are led to conjecture that (2.2) exhibits chaotic behaviour for large values of γ. In spite of the simplicity of the model, the qualitative behaviour of solutions is possibly fairly complicated. These remarks are speculations and many questions remain. We hope to be able to say more about equation (2.2) at a later time.

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References

1. Busenberg, S., Cooke, K. L.: The effect of integral conditions in certain equations modelling epidemics and population growth. J. Math. Biol. **10**, 13–32 (1980)
2. Cushing, J. M.: Nontrivial periodic solutions of some Volterra integral equations. In: Volterra equations, S.-O. Londen, O. J. Staffans (eds.), Vol. 737, pp. 50–66, Lecture notes in mathematics. Berlin-Heidelberg-New York: Springer 1979
3. Cushing, J. M.: Bifurcation of periodic solutions of nonlinear equations in age-structured population dynamics. To appear in the Proceedings of the International Conference on Nonlinear Phenomena in Mathematical Sciences, Arlington, 1980
4. Cushing, J. M., Simmes, S. D.: Bifurcation of asymptotically periodic solutions of Volterra integral equations. J. Int. Eq. **2**, 339–361 (1980)
5. Diekmann, O.: Volterra integral equations and semigroups of operators. Math. Centre Report TW 197, 1980
6. Diekmann, O., Van Gils, S. A.: A variation of constants formula for nonlinear Volterra integral equations of convolution type. In: Nonlinear Differential Equations: Invariance, Stability and Bifurcation. P. de Mottoni, L. Salvadori (eds.), pp. 133–143, Academic Press, 1981
7. Diekmann, O., Van Gils, S. A.: Invariant manifolds for Volterra integral equations of convolution type. (Preprint) Math. Centre Report TW 219, 1981
8. Gripenberg, G.: Periodic solutions of an epidemic model. J. Math. Biol. **10**, 271–280 (1980)
9. Hale, J. K.: Behavior near constant solutions of functional differential equations. J. Diff. Eq. **15**, 278–294 (1974)
10. Hale, J. K.: Nonlinear oscillations in equations with delays. In: F. Hoppensteadt (ed.), Nonlinear oscillations in biology. Providence: AMS 1979
11. Hale, J. K., De Oliveira, J. C. F.: Hopf bifurcation for functional equations. J. Math. Anal. Appl. **74**, 41–59 (1980)
12. Hethcote, H. W., Stech, H. W., Van den Driessche, P.: Nonlinear oscillations in epidemic models. SIAM J. Applied Math. **40**, 1–9 (1981)
13. Hethcote, H. W., Stech, H. W., Van den Driessche, P.: Stability analysis for models of diseases without immunity. J. Math. Biol. **13**, 185–198 (1981)
14. Hethcote, H. W., Tudor, D. W.: Integral equations describing endemic infectious diseases. J. Math. Biol. **9**, 37–48 (1980)
15. Hoppensteadt, F.: Mathematical theories of populations: Demographics, genetics, and epidemics. Philadelphia: SIAM 1975
16. Lauwerier, H. A.: Mathematische modellen voor epidemische processen, unpublished manuscript (in Dutch)
17. Lauwerier, H. A.: Mathematical models of epidemics. Math. Centre Tract 138, 1981
18. Montijn, R.: Een karakteristieke vergelijking uit de mathematische epidemiologie. Math. Centre Report TN 94, 1980 (in Dutch)
19. Stech, H. W., Williams, M.: Stability in a class of cyclic epidemic models with delay. J. Math. Biol. **11**, 95–103 (1981)

20. Turyn, L.: Functional difference equations and an epidemic model. To appear in the Proceedings of the International Conference on Nonlinear Phenomena in Mathematical Sciences, Arlington, 1980

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