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ANALYSIS OF NONLINEAR INTEGRO-DIFFERENTIAL EQUATIONS ARISING IN AGE-DEPENDENT EPIDEMIC MODELS

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1. INTRODUCTION

BASICALLY, there are two modes for directly transmitting an infectious disease within a single population: vertical transmission and horizontal transmission. Vertical transmission is defined as the direct transfer of infection from a parent organism to its offsprings. Horizontal transmission is any transfer of infection except that which is vertically transmitted. For example AIDS is both vertically and horizontally transmitted while malaria is horizontally transmitted.

Vertically transmitted diseases have seldom been considered in mathematical models of epidemics. Examples of previous such models are found in Anderson and May [1]. Cooke and Busenberg [7], Busenberg and Cooke [3], Busenberg, Cooke and Pozio [4], Fine [10] and Re'gniere [17].

Likewise age-dependent diseases has been presented by Cooke and Busenberg [7] and Dietz [8]. Age-dependence introduces a coupling of age-structure and vertical transmission which can produce novel dynamic behavior.

In this paper, a system of nonlinear integro-differential equations which model an age-dependent epidemic of a disease with vertical transmission is investigated. This model treats the simple $S \to I$ type of epidemic in this new setting. Existence and uniqueness are proved under suitable hypotheses and the asymptotic behavior of the system is determined. A renewal theorem is used to study the behavior of the model equations in various pertinent parameter ranges. A numerical method for integrating this system of equations is developed and is used to obtain approximations of its solutions for some special cases which illustrate the results obtained via analytical means. Moreover, numerical integrations of the equations are used to study some phenomena that were not treated analytically.

2. A MODEL OF A VERTICALLY TRANSMITTED DISEASE

Consider an age-structured population of variable size exposed to a disease which is both horizontally and vertically transmitted with the following assumptions on the model.

(a) Let $s(a, t)$ and $i(a, t)$, respectively, denote the age-density for susceptibles and infectives of age a at time t. Then

$$\int_{a_1}^{a_2} s(a, t)\,\mathrm{d}a = \text{total number of susceptibles at time } t \text{ of ages between } a_1 \text{ and } a_2.$$

$$\int_{a_1}^{a_2} i(a, t)\,\mathrm{d}a = \text{total number of infectives at time } t \text{ of ages between } a_1 \text{ and } a_2.$$

We assume that the total population consists only of susceptibles and infectives.

(b) Assume that the rate of horizontal transmission occurs according to the following mass action law:

$$ks(a,t)\int_0^\infty i(a,t)\,\mathrm{d}a = ks(a,t)I(t).$$

k is a constant, which combines a multitude of environmental, social and epidemiological factors that play a role in transmitting the disease. The expression $k\int_0^\infty i(a,t)\,\mathrm{d}a$ is often called the "force of infection."

(c) The death rate $\mu(a)$ is the same for susceptibles and infectives, and we assume that $\mu(a)$ is nonnegative, bounded and eventually nondecreasing.

(d) The birth rate $\beta(a)$ is nonnegative, bounded and has compact support $[0, S]$ and has finite total variation over $(0,\infty)$.

(e) Assume that the birth is modelled by

$$s(0,t) = \int_0^\infty \beta(a)[s(a,t) + (1-q)i(a,t)]\,\mathrm{d}a,\ t \geqslant 0$$

$$i(0,t) = q\int_0^\infty \beta(a)i(a,t)\,\mathrm{d}a,\ q \in [0,1],\ t \geqslant 0.$$

This assumption incorporates the vertical transmission since it says that a fraction $(1-q)$ of offspring from infected parents are susceptible and a fraction q are infective. We also assume that the birth rate for all parents of the same age is the same, and the population is asexual.

(f) We assume that the initial age distributions are given by

$$s(a,0) = s_0(a),\ i(a,0) = i_0(a),\ a \in (0,\infty).$$

The above assumptions lead to the following equations

$$\left.\begin{aligned}
&\frac{\partial s(a,t)}{\partial a} + \frac{\partial s(a,t)}{\partial t} + \mu(a)s(a,t) = -ks(a,t)\int_0^\infty i(a,t)\,\mathrm{d}a \qquad \text{for } a>0,\ t>0\\
&\frac{\partial i(a,t)}{\partial a} + \frac{\partial i(a,t)}{\partial t} + \mu(a)i(a,t) = ks(a,t)\int_0^\infty i(a,t)\,\mathrm{d}a \qquad \text{for } a>0,\ t>0\\
&s(0,t) = \int_0^\infty \beta(a)[s(a,t) + (1-q)i(a,t)]\,\mathrm{d}a, \quad t \geqslant 0\\
&i(0,t) = q\int_0^\infty \beta(a)i(a,t)\,\mathrm{d}a, \quad t \geqslant 0\\
&s(a,t),\ i(a,t) \to 0 \quad \text{as } t \to \infty.
\end{aligned}\right\} \tag{2.1}$$

Concerning assumption (b) we note that recently Liu, Levin and Iwasa [14] generalized this type of transmission for an SIR model to take the following form kI^pS^q where $p, q > 0$. However, their model does not consider age dependence.

The above model is an SI model as far as the horizontal transmission is concerned. However, the age dependence introduces an effective removed class (removed via death) and a return of the susceptibles as well as the infectives via birth and vertical transmission.

3. FORMAL REDUCTION OF THE MODEL

In this section, we will develop the transformation of problem (2.1) which allows us to analyze this model. We follow the method of Busenberg and Iannelli [5, 6] and introduce the age-profile $w(a, t)$ given by

$$w(a,t) = i(a,t)/I(t), I(t) = \int_0^\infty i(a,t)\,\mathrm{d}a. \tag{3.1}$$

First, note that if the problem has a regular solution and if we set $P(a, t) = s(a, t) + i(a, t)$, then $p(a, t)$ satisfies the following McKendrick–VonFoerster equation

$$\left.\begin{aligned} &\frac{\partial p(a,t)}{\partial a} + \frac{\partial p(a,t)}{\partial t} + \mu(a)p(a,t) = 0, \qquad a>0, t>0 \\ &p(0,t) = \int_0^\infty \beta(a)p(a,t)\,\mathrm{d}a, \qquad t \geqslant 0 \\ &p(a,0) = p_0(a), p(a,t) \to 0 \quad \text{as} \quad a \to +\infty \qquad \text{for } t \geqslant 0. \end{aligned}\right\} \tag{3.2}$$

Let $P(t) = \int_0^\infty p(a, t)\,\mathrm{d}a$ = total population at time t. Then problem (2.1) can be rewritten in the following equivalent form, provided that $w(a, t) = i(a, t)/I(t)$ is defined and

$$\left.\begin{aligned} &\frac{\partial}{\partial t}\int_0^\infty i(a,t)\,\mathrm{d}a = \int_0^\infty \frac{\partial i(a,t)}{\partial t}\,\mathrm{d}a\text{:} \\ &\frac{\partial w(a,t)}{\partial a} + \frac{\partial w(a,t)}{\partial t} + \mu(a)w(a,t) = kp(a,t) \\ &+\left\{-kP(t) + \int_0^\infty [\mu(a) - q\beta(a)]w(a,t)\,\mathrm{d}a\right\} w(a) \qquad a>0, t>0 \\ &w(0,t) \overset{\text{def}}{=} B(t) = q\int_0^\infty \beta(a)w(a,t)\,\mathrm{d}a \qquad t \geqslant 0 \\ &\int_0^\infty w(a,t)\,\mathrm{d}a = 1 \qquad a>0, t\geqslant 0 \\ &w(a,0) = w_0(a), w(a,t) \to 0 \quad \text{as} \quad a \to +\infty, \end{aligned}\right\} \tag{3.3}$$

and $I(t)$ satisfies

$$\left.\begin{aligned} &\frac{\mathrm{d}I(t)}{\mathrm{d}t} + I(t)\int_0^\infty [\mu(a) - q\beta(a)]w(a,t)\,\mathrm{d}a = k[P(t) - I(t)]I(t) \\ &I(0) = I_0. \end{aligned}\right\} \tag{3.4}$$

We note that, in this formulation of the model, one can first solve for $p(a, t)$ using the classical linear theory of the VonForster–McKendrick equation (see [2, 11, 16, 19]); then solve (3.3) to obtain $w(a, t)$. Once this is done, equation (3.4) can be analyzed to obtain the behavior of $I(t)$ and hence $i(a, t) = w(a, t)I(t)$ and $s(a, t) = p(a, t) - i(a, t)$. The only one of the three problems that poses difficulties is problem (3.3), which is a nonlinear age-dependent equation. Also equation (3.2) involves only one independent variable $p(a, t)$, while (3.3) involves both

$w(a,t)$, and $p(a,t)$ and, hence is not separable in the sense of Busenberg and Iannelli [6]. But, since $p(a,t)$ satisfies the classical McKendrick–VonFoerster linear equation (3.2), it is essentially known; and we call (3.3) "almost separable," in keeping with the notation of [6].

Let p^* be the unique real number which satisfies

$$\int_0^\infty \beta(a)\pi(a)\, e^{-p^* a}\, da = 1, \pi(a) = e^{-\int_0^a \mu(s)ds}. \tag{3.5}$$

Then $p(a,t)$ has the following asymptotic behavior

$$p(a,t) = \begin{cases} p_0(a-t)\pi(a)/\pi(a-t), & a > t \\ [c + \theta(t-a)]\, e^{p^*(t-a)}\pi(a), & a < t \end{cases} \tag{3.6}$$

where $\theta(t)$ is a function satisfying

$$\theta(t) \to 0 \quad \text{(exponentially) as } t \to \infty, \tag{3.7}$$

and c is a constant.

Now, let $q \in (0,1)$ and let p_q^* be the unique real number which satisfies

$$1 = q\int_0^\infty \beta(a)\, e^{-p_q^* a}\pi(a)\, da, \pi(a) = e^{-\int_0^a \mu(s)ds} \tag{3.8}$$

then it is easily seen that p^* and p_q^* are related as follows.

LEMMA 1.1. Let p^*, p_q^* be given by (3.5) and (3.8) respectively. Then $p_q^* < p^*$.

p^* is the unique solution of the characteristic equation for the linear problem $P(a,t)$ and p_q^* is the unique solution of the characteristic equation for the nonlinear problem $(w(a,t))$.

In order to treat problem (3.3) we define the following new variable

$$Q(a,t) = w(a,t)\, e^{-\int_0^t A(s)ds}$$

where $A(s)$ is given by

$$A(s) = -kP(s) + \int_0^\infty [\mu(a) - q\beta(a)]w(a,t)\, da.$$

Then problem (3.3) can be written in the following form

$$\left.\begin{aligned}
&\frac{\partial Q(a,t)}{\partial a} + \frac{\partial Q(a,t)}{\partial t} + \mu(a)Q(a,t) = F(a,t), \qquad a > 0, t > 0 \\
&Q(0,t) = q\int_0^\infty \beta(a)Q(a,t)\, da \overset{\text{def}}{=} B_q(t), \qquad t \geqslant 0 \\
&\int_0^\infty Q(a,t)\, da = e^{-\int_0^t A(s)ds} \\
&Q(a,0) = w(a,0) \overset{\text{def}}{=} w_0(a), \\
&\lim_{t\to\infty} Q(a,t) = 0 \\
&F(a,t) = kp(a,t)\, e^{-\int_0^t A(s)ds}.
\end{aligned}\right\} \tag{3.9}$$

By integrating along charcteristics we find that $Q(a, t)$ satisfies

$$Q(a,t) = \begin{cases} w_0(a-t)\pi(a)/\pi(a-t) + \pi(a)\int_0^t F(a-t+h', h')/\pi(a-t+h')\,dh', & a > t \\ B_q(t-a)\pi(a) + \pi(a)\int_0^a F(h', t-a+h')/\pi(h')\,dh', & a < t \end{cases} \tag{3.10}$$

and $B_q(t)$ satisfies the following Volterra integral equation

$$B_q(t) = q\int_0^t B_q(t-a)\beta(a)\pi(a)\,da + G(t) \tag{3.11}$$

where $G(t)$ is given by

$$G(t) = q\left\{\int_0^t \beta(a)\pi(a)\left[\int_0^a F(h', t-a+h')/\pi(h')\,dh'\right]da + \int_t^\infty \beta(a)w_0(a-t)\pi(a)/\pi(a-t)\,da \right.$$
$$\left. + \int_t^\infty \beta(a)\pi(a)\left[\int_0^t F(a-t+h', h')\,dh'\right]da\right\}.$$

Since $\beta(a)$ has a compact support $[0, S]$, then $G(t)$ has a Laplace transform, likewise the kernel and hence (3.11) has one and only one nonnegative solution $B_q(t)$ which is bounded in every finite interval, see [11]. Moreover, $B_q(t)$ has a Laplace transform. We base our analysis of the model on the renewal equation (3.11). In the next section we outline the proof of existence and uniqueness of solution. Such proofs for similar equations have been established by Busenberg and Iannelli [5], Webb [19–21] and Elderkin [9]. Then in Section 5 we study in detail the asymptotic behavior of these solutions in various parameter ranges.

4. EXISTENCE AND UNIQUENESS

To consider problem (3.3), let $C[0, t_0]$ denote the Banach space of continuous functions on $[0, t_0]$, $L^1(0, \infty)$ denote the Banach space of equivalence classes of Lebesque integrable functions. Let

$$E = \left\{ w(a,t) : w(\cdot, t) \in L^1([0,\infty); C[0,t_0]),\ a \in [0,\infty),\ t \in [0,t_0] \right.$$
$$\left. |||w(a,t)||| = \sup_{t\in[0,t_0]} \|w(a,t)\|_{L^1} \right\}.$$

We note that E is a Banach space.

THEOREM 1. Suppose that $\beta(a)$ and $\mu(a)$ are nonnegative, bounded and continuous functions, $\beta(a)$ has compact support, $\mu(a)$ is eventually nondecreasing. Suppose also that $w_0(a)$ and $p_0(a)$ are continuous and integrable functions on $[0, \infty)$. Then there exists one and only one solution for the integrated form of problem (3.3) in E.

Proof. Define a map T by $T: E \to E$, and for $w(a,t) \in E$, Tw is given by

$$Tw(a,t) = e^{\int_0^t A(s)\,ds} \begin{cases} w_0(a)\pi(a)/\pi(a-t) + [k\pi(a)p_0(a-t)/\pi(a-t)] \int_0^t e^{\int_0^{h'} A(s)\,ds}\, dh', & a > t \\ B_q(t-a)\pi(a) + kp(a,t-a) \int_0^a e^{-\int_0^{t-a+h'} A(s)\,ds}\, dh', & a < t. \end{cases} \tag{4.1}$$

Notice that, since $w_0(a)$, $p_0(a)$ and $B_q(t)$ are continuous and integrable, T maps E into E. Let w_1, w_2 be elements of E. Let

$$K_1 = \sup_{t\in[0,\infty)} \int_t^\infty w_0(a)\pi(a)/\pi(a-t)\, da$$

$$K_2 = \sup_{t\in[0,t_0]} k\int_t^\infty \pi(a)\, e^{p^*(t-a)}[c + \theta(t-a)]\, da$$

$$K_4 = \sup_{t\in[0,\infty)} k\int_t^\infty p_0(a-t)\pi(a)/\pi(a-t)\, da$$

$$K_5 = \sup_{t\in[0,\infty)} |\mu(t) - q\beta(t)|$$

$$K_6 = |||w_1(a,t)||| + |||w_2(a,t)|||.$$

$A(t)$ satisfies

$$A(t) = -kP(t) + \int_0^\infty \{\mu(a) - q\beta(a)\}w(a,t)\, da \le K_5 \int_0^\infty w(a,t)\, da = K_5.$$

Then

$$|||Tw_1 - Tw_2||| \le K_5\, e^{K_5 t}|||w_1 - w_2|||t \begin{cases} K_1\left\{1 + K_5|||w_1 - w_2|||\frac{t}{2!} + K_5^2|||w_1 - w_2|||^2\frac{t^2}{3!} + \dots\right\} \\ + K_4\left\{t/2 + K_5|||w_1 - w_2|||\frac{t^2}{3!} + \dots\right\} \\ + K_2\left\{1 + K_5|||w_1 - w_2|||\frac{t}{2!} + K_5^2|||w_1 - w_2|||^2\frac{t^2}{3!} + \dots\right\} \\ + K_3\left\{t + K_5|||w_1 - w_2|||\frac{t^2}{2!} + K_5^2|||w_1 - w_2|||^2\frac{t^2}{3!} + \dots\right\}. \end{cases}$$

Let

$$\bar{K}_1 = 2\max\{K_1, K_2\}$$
$$\bar{K}_3 = 2\max\{K_4, K_3\}.$$

Then

$$|||Tw_1 - Tw_2||| \le K_5\, e^{k_5 t}t|||w_1 - w_2|||\{\bar{K}_1\, e^{K_5K_6t} + \bar{K}_3 t\, e^{K_5K_6t}\}.$$

If we set $M_1 = K_5\bar{K}_1$, $M_2 = K_5\bar{K}_3$, $M_3 = K_5K_6$ then

$$|||Tw_1 - Tw_2||| \leqslant [M_1 + M_2t]\,e^{M_3 t}t|||w_1 - w_2|||.$$

Now, choose t_0 such that $t \in [0, t_0]$ implies that $[M_1 + M_2t]\,e^{M_3 t}t < 1$, so T is a contraction.

Now, we discuss the continuation of the solution. So far we have a unique solution in $[0, \infty) \times [0, t_0]$ where $t_0 > 0$ and t_0 satisfies

$$[M_1 + M_2t_0]\,e^{M_3 t_0}t_0 < 1.$$

We start the solution at $t = t_0$ and take $w(a, t_0) = w_{t_0}(a)$ as the initial age distribution. Then, since K_1, K_2, K_3, K_4, and K_5 are chosen to be independent of the initial age distribution $w_0(a)$, if we put $\bar{t} = t - t_0$ for $t \in [t_0, 2t_0]$, we see that we get the following estimate:

$$|||Tw_1 - Tw_2||| \leqslant [M_1 + M_2\bar{t}]\,e^{M_3 \bar{t}}\bar{t}|||w_1 - w_2||| \qquad \text{for } t \in [t_0, 2t_0].$$

But $[M_1 + M_2t]\,e^{M_3 t}t < 1$ for $t \in [0, t_0]$ implies that

$$[M_1 + M_2\bar{t}]\,e^{M_3 \bar{t}}\bar{t} = [M_1 + M_2(t - t_0)]\,e^{M_3(t-t_0)}(t - t_0) < 1 \quad \text{for } t \in [t_0, 2t_0]$$

and hence, we have a unique solution in $[0, \infty) \times [0, 2t_0]$. In this way the solution can be extended similarly to $[0, \infty) \times [0, \infty)$ in the unique fashion. The continuity of $w(a, t)$ follows from that of w_0 and p_0 by noting that if $w \in E$, then the right-hand side of (4.1) is continuous and hence, so is $w = Tw$.

5. THE LIMITING BEHAVIOR

In this section we study the asymptotic behavior of $w(a, t)$ and $I(t)$ in the three different cases, namely $p^* < 0$, $p^* = 0$ and $p^* > 0$. In all the results in this section we assume that $q \in (0, 1)$ and w_0 and p_0 are continuous integrable functions.

THEOREM 2. Suppose the following hold:

(1) $p^* < 0$;

(2) $\beta(a)$ and $\mu(a)$ are nonnegative, bounded and continuous functions, $\beta(a)$ with support $[0, S]$, for some $S > 0$, $\mu(a)$ is eventually nondecresing and $\beta(a)$ has finite total variation over $[0, S]$;

(3) $\int_0^\infty e^{-(p_q^* + p^*)a}\pi(a)\,da < +\infty$;

(4) $p^* - p_q^* + kM_1 + M_2 < 0$;

where

$$M_1 = \sup_{t \in [0,\infty]} p(t)$$

$$M_2 = \sup_{a \in [0,\infty]} [q\beta(a) - \mu(a)].$$

Then the nonnegative and unique solution $w(a, t)$ satisfies

$$\lim_{t\to\infty} w(a, t) = w_\infty(a) \stackrel{\text{def}}{=} e^{-p_q^* a}\pi(a) \Big/ \int_0^\infty e^{-p_q^* a}a\pi(a)\,da.$$

Provided that the support of $\beta(a)$ intersects the support of $w_0(a)$.

Proof. Conditions (2) and (4) imply that equation (3.11) has the following asymptotic behavior (See [2, 11])

$$B_q(t) = [b + \theta(t)]\, e^{p_q^* t}, \qquad b \geqslant 0. \tag{5.1}$$

Then (3.6), (3.10) and (5.1) imply that $w(a, t)$ satisfies

$$w(a, t) = e^{\int_0^t A(s)\,ds}$$
$$\times \begin{cases} w_0(a)\pi(a)/\pi(a-t) + kp_0(a-t)\pi(a)/\pi(a-t)\displaystyle\int_0^t e^{-\int_0^{h'} A(s)\,ds}\, dh' & a<t \\ [b+\theta(t-a)]\, e^{p_q^*(t-a)}\pi(a) + k\pi(a)\, e^{p^*(t-a)}[c+\theta(t-a)]\displaystyle\int_0^a e^{-\int_0^{t-a+h'} A(s)\,ds}\, dh', & -a<5. \end{cases} \tag{5.2}$$

Then $\int_0^\infty w(a, t)\, da = 1$ implies that

$$\begin{aligned} 1 &= e^{\int_0^t [A(s)+p_q^*]\,ds}\int_0^t [b + \theta(t-a)]\, e^{-p_q^* a}\pi(a)\, da \\ &+ k\, e^{\int_0^t [A(s)+p_q^*]\,ds}\int_0^t [c + \theta(t-a)]\, e^{-p^* a}\pi(a)\left\{\int_0^a e^{\int_0^{t-a+h'} A(s)\,ds}\, dh'\right\} da \\ &+ e^{\int_0^t [A(s)+p_q^*]\,ds}\left\{e^{-p_q^* t}\int_t^\infty w_0(a-t)\pi(a)/\pi(a-t)\, da\right\} \\ &+ e^{\int_0^t [A(s)\,ds}\int_t^\infty p_0(a-t)\pi(a)/\pi(a-t)\left\{\int_0^t e^{-\int_0^{h'} [A(s)\,ds}\, dh'\right\} da. \end{aligned} \tag{5.3}$$

Assumptions (1) and (3) imply that $\int_0^\infty e^{-p_q^* a}\pi(a)\, da < +\infty$, and hence by considering equation (5.3), $\exists M > 0$ such that $e^{\int_0^t [A(s)+p_q^*]\,ds} < M\ \forall t \in [0, \infty)$. Accordingly $e^{\int_0^t [A(s)+p_q^*]\,ds}\int_0^t \theta(t-a)e^{-p_q^* a}\pi(a)\,d\,a \to 0$ as $t \to +\infty$ by the dominated convergence theorem.

Also

$$e^{\int_0^t [A(s)+p_q^*]\,ds}\left\{e^{-p_q^* t}\int_t^\infty w_0(a-t)\pi(a)/\pi(a-t)\, da\right\} \leqslant M\, e^{-p_q^* t}\int_t^\infty \frac{w_0(a-t)\pi(a)\, da}{\pi(a-t)}$$

$$= M\, e^{-p_q^* t}\int_0^\infty w_0(a)\pi(a+t)/\pi(a)\, d(a),$$

since $\int_0^\infty e^{-p_q^* a}\pi(a)\, da < +\infty$, $-p_q^* - \mu^* < 0$, where $\mu^* = sup_{a \in [0,\infty)}\, \mu(a)$ (note that this exists by assumption (2)). This implies that $e^{-p_q^* t}\pi(a)$ is monotone decreasing if a is sufficiently large, hence, for such an a, $e^{-p_q^*(a+t)}\pi(a+t) < e^{-p^* a}\pi(a)$. Then we have the following:

$$M\, e^{-p_q^* t}\int_0^\infty w_0(a)\pi(a+t)/\pi(a)\, da = M\int_0^\infty [w_0(a)/e^{-p_q^* a}\pi(a)]\, e^{-p_q^*(t+a)}\, da.$$

We now apply the dominated convergence theorem to get that

$$M \int_0^\infty [w_0(a)/e^{-p_q^* a}\pi(a)]\, e^{-p_q^*(t+a)}\, da \to 0 \quad \text{as } t \to \infty$$

that is,

$$e^{\int_0^t [A(s)+p_q^*]ds} \left\{ e^{-p_q^* t} \int_t^\infty w_0(a-t)\pi(a)/\pi(a-t)\, da \right\} \to 0 \quad \text{as } t \to +\infty.$$

Now, we estimate the following term

$$k\, e^{\int_0^t [A(s)+p^*]ds} \int_0^t [c+\theta(t-a)]\, e^{-p^* a}\pi(a) \left\{ \int_0^a e^{\int_0^{t-a+h'} [A(s)ds} dh' \right\} da$$

$$= k\, e^{p^* t} \int_0^t [c+\theta(t-a)]\, e^{-(p^*+p_q^*)a}\pi(a) \left\{ \int_0^a e^{\int_{t-a+h'} [A(s)+p_q^*]ds} e^{p_q^* h'}\, dh'\, da \right\}$$

$$\leqslant e^{p^* t}\{kM \int_0^t [c+\theta(t-a)]\, e^{-(p^*+p_q^*)a}\pi(a) \left\{ \int_0^a e^{p_q h'}\, dh' \right\} da\} \to 0$$

by assumptions (1) and (3).

Finally, we estimate the following term

$$e^{\int_0^t A(s)ds} \int_t^\infty [p_0(a-t)\pi(a)/\pi(a-t)] \left\{ \int_0^t e^{\int_0^{h'} A(s)ds}\, dh' \right\} da$$

$$= \int_t^\infty p_0(a-t)\pi(a)/\pi(a-t) \int_0^t e^{\int_{h'}^t [A(s)+p_q^*]ds}\, e^{p^*{}_q h'}\, dh'\, da$$

$$\leqslant M\, e^{-p^*{}_q t} \int_t^\infty p_0(a-t)\pi(a)/\pi(a-t) \left\{ \int_0^t e^{p_{h'}^*}\, dh' \right\} da$$

$$= M\, e^{-p_q^* t} \int_0^\infty p_0(a)\pi(a+t)/\pi(a) \left\{ \int_0^t e^{p_q^* h'}\, dh' \right\} da$$

$$= M \int_0^\infty [p_0(a)/e^{-p_q^* a}\pi(a)]\pi(a+t)\, e^{-p_q^*(a+t)} \frac{[e^{p^*{}_q t}-1]}{p_q^*}\, da \to 0$$

by the dominated convergence theorem.

Therefore,

$$b\, e^{\int_0^t [A(s)+p_q^*]ds} \to 1 \Big/ \int_0^\infty e^{-p_q^* a}\pi(a)\, da \qquad \text{as } t \to +\infty.$$

And hence (5.2) implies that

$$\lim_{t\to\infty} w(a,t) = e^{-p_q^* a}\pi(a) \Big/ \int_0^\infty e^{-p_q^* a}\pi(a)\, da.$$

In the following theorem we shall determine the asymptotic behavior of $w(a, t)$ when $p^* = 0$, that is, under the assumption that the total population reaches a steady state. This is an important special case since many researchers to simplify their model equations, start by assuming such a situation, for example Gripenberg [12] and Hethcote [13].

THEOREM 3. Suppose that the following hold:

(1) $p^* = 0$;
(2) assumption (2) of theorem 2;
(3) assumption (3) of theorem 2;
(4) assumption (4) of theorem 2;
(5) $k < [-p_q^*/c]/[\int_0^\infty e^{-p_q^* a}\pi(a)\,da - \int_0^\infty \pi(a)\,da]$ where $c = \dfrac{P_\infty}{\int_0^\infty \pi(a)\,da}$ and $P_\infty = \lim_{t\to\infty} P(t)$.

Then

$$\lim_{t\to\infty} w(a,t) = w_\infty(a)\left\{1 + \frac{kc}{(-p_q^*)}\left[e^{-p_q^* a}\int_0^\infty \pi(a)\,da - \int_0^\infty e^{-p_q^* a}\pi(a)\,da\right]\right\}$$

where $w_\infty(a) = e^{-p_q^* a}\pi(a)/\int_0^\infty e^{-p_q^* a}\pi(a)\,da$.

Proof. Relation (5.2) and the calculation in theorem 2 implies that

$$1 - b\,e^{\int_0^t [A(s)+p_q^*]ds}\int_0^t e^{-p_q^* a}\pi(a)\,da$$
$$+ kc\,e^{\int_0^t [A(s)+p_q^*]ds}\int_0^t \pi(a)\,e^{-p_q^* a}\int_0^a e^{\int_0^t [A(s)+p_q^*]ds}\,e^{p_q^* h'}\,dh'\,da.$$

Since $w(a,t)$ exists, is unique, and satisfies $\int_0^\infty w(a,t)\,da = 1$, then

$$0 < e^{\int_0^t [A(s)+p_q^*]ds} < +\infty \text{ for each } t \text{ and } \lim_{t\to\infty} e^{\int_0^t [A(s)+p_q^*]ds} \text{ exists.}$$

Let $\phi(t) = e^{\int_0^t [A(s)+p_q^*]ds}$. Then $\phi(t)$ satisfies

$$\phi_\infty = \lim_{t\to\infty}\phi(t) = b\int_0^\infty e^{-p_q^* a}\pi(a)\,da$$
$$+ kc\int_0^\infty \pi(a)\,e^{-p_q^* a}\left\{\int_0^a \lim_{t\to\infty}\phi(t-a+h')\,e^{p_q^* h'}\,dh'\right\}da$$

or

$$\phi_\infty = b\int_0^\infty e^{-p_q^* a}\pi(a)\,da\bigg/\left\{1 + \frac{kc}{(-p_q^*)}\left[\int_0^\infty e^{-p_q^* a}\pi(a)\,da\right]\right\}$$

provided that $k < e^{-p^*}q/c/[\int_0^\infty e^{-p_q^* a}\pi(a)\,da - \int_0^\infty \pi(a)\,da]$.

Then using (5.2) we find that

$$\lim_{t\to\infty} w(a,t) = w_\infty(a)\left\{1 + \frac{kc}{(-p_q^*)}\left[\int_0^\infty \pi(a)\,da - e^{p_q^* a}\int_0^\infty e^{-p_q^* a}\pi(a)\,da\right]\right\}.$$

Now, we treat the case when $p^* > 0$, i.e. the total population is increasing exponentially, our result here agrees with that of Busenberg, Cooke and Pozio [4] for a model of a vertically transmitted disease with no age-dependence.

THEOREM 4. Suppose that the following hold:

(1) $p^* > 0$;
(2) assumption (2) of theorem 2;
(3) assumption (3) of theorem 2.

Then

$$\lim_{t\to\infty} I(t)/p(t) = 1.$$

Proof. Assumptions (2) and (3) provide existence and uniqueness for $w(a, t)$ and hence $I(t)$ satisfies

$$I(t) = \frac{I(0)\,e^{\int_0^t A(s)\,ds}}{1 + kI(0)\displaystyle\int_0^t e^{\int_0^s A(s')\,ds'}\,ds},$$

where $A(t)$ is given by

$$A(t) = -kP(t) + \int_0^\infty [\mu(a) - q\beta(a)]w(a, t)\,da.$$

Note that $P(t) \sim [c \int_0^\infty e^{-p^*a}\pi(a)\,da]\,e^{p^*t}$ as $t \to +\infty$.

Since

$$\int_0^\infty \{\mu(a) - q\beta(a)\}w(a, t)\,da \leq \sup_{a\in[0,\infty)} \{\mu(a) - q\beta(a)\} \int_0^\infty w(a, t)\,da$$
$$= \sup_{a\in[0,\infty]} \{\mu(a) - q\beta(a)\},$$

if we set $f(t) = e^{-\int_0^\infty A(s)\,ds}$ then $f(t) \to +\infty$ as $t \to +\infty$. Hence

$$\lim_{t\to\infty} I(t) = \lim_{t\to\infty} \frac{I(0)f(t)[-A(t)]}{kI(0)f(t)} \quad \text{i.e.} \lim_{t\to\infty} I(t) = \lim_{t\to\infty}\left[-\frac{A(t)}{k}\right].$$

Therefore, given $\varepsilon > 0$ there exists $T \in R$ such that

$$\left|I(t) + \frac{A(t)}{k}\right| < \varepsilon \text{ for } t > T.$$

But,

$$-\frac{A(t)}{k} = P(t) - \frac{1}{k}\int_0^\infty \{\mu(a) - q\beta(a)\}w(a, t)\,da.$$

Then

$$-\frac{A(t)}{kP(t)} = 1 - \frac{1}{kP(t)}\int_0^\infty \{\mu(a) - q\beta(a)\}w(a, t)\,da.$$

Therefore, for $t > T$, since $P(t) \to +\infty$ as $t \to +\infty$

$$\left| \frac{A(t)}{kP(t)} + 1 \right| < \varepsilon$$

which implies that $\lim_{t\to\infty} \frac{I(t)}{P(t)} = 1$.

6. APPLICATION

In this section we apply theorems 1–4 to completely analyze our model. Needless to say, we are assuming the hypotheses of these theorems each time we apply them.

(a) *The case of a decreasing population* ($p^* < 0$)
By theorem 2 we know that for $q \in (0, 1)$

$$\lim_{t\to\infty} w(a, t) \overset{\text{def}}{=} w_\infty(a)\, \mathrm{e}^{-p_q^* a} \pi(a) \Big/ \int_0^\infty \mathrm{e}^{-p_q^* a} \pi(a)\, \mathrm{d}a.$$

Since $p^* < 0$ then $P(t) \to 0$ and therefore $I(t) \to 0$ as $t \to \infty$. In fact since $w(a, t) = i(a, t)/I(t)$ this implies that

$$\lim_{t\to\infty} i(a, t) = \frac{\mathrm{e}^{-p_q^* a} \pi(\mathrm{a})}{\int_0^\infty \mathrm{e}^{-p_q^* a} \pi(a)\, \mathrm{d}a} \lim_{t\to\infty} I(t),$$

since $A(t)$ is given by

$$A(t) = -kP(t) + \int_0^\infty [\mu(a) - q\beta(a)] w(a, t)\, \mathrm{d}a.$$

So

$$\lim_{t\to\infty} A(t) = \int_0^\infty [\mu(a) - q\beta(a)] \lim_{t\to\infty} w(a, t)\, \mathrm{d}a = -p_q^*.$$

By (3.4) $I(t)$ is given by

$$I(t) = \frac{I(0)\, \mathrm{e}^{\int_0^t A(s)\,\mathrm{d}s}}{1 + kI(0) \int_0^t \mathrm{e}^{\int_0^s A(s')\,\mathrm{d}s'}\, \mathrm{d}s}$$

and, therefore,

$$I(t) \leq K\, \mathrm{e}^{-p_q^* t} \text{ for some constant } K.$$

This implies that

$$i(a, t) \leq \frac{K\, \mathrm{e}^{-p_q^*(t-a)} \pi(a)}{\int_0^\infty \mathrm{e}^{-p_q^* a} \pi(a)\, \mathrm{d}a} \to 0.$$

Moreover since $s(a, t) = p(a, t) - i(a, t) \sim [c + \theta(t - a)]\, e^{p^*(t-a)}\pi(a) - \lim_{t\to\infty} i(a, t)$ as $t \to \infty$ by (3.6). Then

$$\lim_{t\to\infty}\frac{i(a,t)}{s(a,t)} \sim \lim_{t\to\infty}\frac{i(a,t)}{c\, e^{p^*(t-a)}\pi(a) - i(a,t)} = \frac{1}{\lim_{t\to\infty}\left(\dfrac{(e^{p^*(t-a)}\pi(a))}{i(a,t)}\right) - 1}$$

$$\leq \lim_{t\to\infty}\frac{1}{\left[\dfrac{c}{k}\displaystyle\int_0^\infty e^{-p_q^* a}\pi(a)\,da\right] e^{(t-a)(p^* - p_0^*)} - 1} \to 0$$

by lemma 1. That is

$$\lim_{t\to\infty}\frac{i(a,t)}{s(a,t)} = 0,$$

also $\lim_{t\to\infty} i(a, t) = \lim_{t\to\infty} s(a, t) = 0$.

(b) *The case $p^* = 0$ (steady state population)*
In this case $w(a, t)$ satisfies

$$\lim_{t\to\infty} w(a,t) = w_\infty(a)\left\{1 + \left(\frac{kc}{p_q^*}\right)\left[\int_0^\infty \pi(a)\,da - e^{p_q^* a}\int_0^\infty e^{-p_q^* a}\pi(a)\,da\right]\right\}.$$

Notice that $A(t)$ satisfies

$$\lim_{t\to\infty} A(t) = kP_\infty/p_q^* - p_q^*,\ P_\infty = \lim_{t\to\infty} P(t) = c\int_0^\infty \pi(a)\,da$$

so, if $kP_\infty/p_q^* > p_q^*$ then $i(a, t) \to 0$ and $s(a, t) \to c\pi(a)$, but if

$$kP/p_q^* < p_q^* \text{ then } \lim_{t\to\infty} I(t) = p_q^*/k - P_\infty/p_q^* > 0.$$

Hence

$$\lim_{t\to\infty} i(a,t) = w_\infty(a)[p_q^*/k - p_\infty/p_q^*]\left\{1 + \frac{kc}{(-p_q^*)}\left[\int_0^\infty \pi(a)da - e^{p_q^* a}\int_0^\infty e^{-p_q^* a}\pi(a)\,da\right]\right\}$$

and

$$\lim_{t\to\infty} s(a,t) = c\pi(a) - \lim_{t\to\infty} i(a,t)$$

$$= c\pi(a) - w_\infty(a)\left[p_q^*/k - \frac{P_\infty}{p_q^*}\right]\left\{1 + \frac{kc}{(-p_q^*)}\left[\int_0^\infty \pi(a)\,da - e^{p_q^* a}\int_0^\infty e^{-p_q^* a}\pi\,da\right]\right\}.$$

If $P_\infty/p_q^* = p_q^*/k$ then $i(a, t) \to 0$ as $t \to \infty$ and $s(a, t) \to c\pi(a)$ as $t \to \infty$.

(c) *The case $p > 0$ (an increasing population)*
By theorem 4 we know that $\lim_{t\to\infty} I(t) = +\infty$. Also we know that $\lim_{t\to\infty} I(t)/P(t) = 1$. This situation seems to be unrealistic from the modelling point of view, since this result

implies that, in an exponentially growing population (i.e. $p^* > 0$) the total number of infectives, in the limit, equals the total population. This situation can perhaps be rectified by putting a bound on the total population, for example, by assuming a logistic growth regulation mechanism.

In the following we will discuss the special cases $q = 0$ and $q = 1$. We note that if $q = 0$ then we do not have a renewal theorem so, one has to analyze this special case separately.

(d) *Case* $p^* < 0$, $q = 0$

In this case $A(t)$ satisfies

$$A(t) = -kP(t) + \int_0^\infty \mu(a)w(a, t)\,da.$$

We note that if we set

$$\mu_* = \inf_{a\in[0,\infty)} \mu(a),\ \mu^* = \sup_{a\in[0,\infty)} \mu(a). \tag{6.1}$$

Then $i(a, t) \leq K\,e^{(p^*-\mu_*)t}\,e^{p^*a}$ for t sufficiently large. Then

$$\lim_{t\to\infty}\frac{i(a,t)}{s(a,t)} = \lim_{t\to\infty}\frac{i(a,t)}{c\pi(a)\,e^{p^*(t-a)} - i(a,t)} \leq \lim_{t\to\infty}\frac{1}{((c\pi(a)\,e^{p^*(t-a)})/(K\,e^{(p^*-\mu_*)t}\,e^{-p^*a})) - 1} \to 0$$

as $t \to \infty$. That is

$$\lim_{t\to\infty}\frac{i(a,t)}{s(a,t)} = 0.$$

(e) *Case* $p^* = 0$, $p = 0$

In this case if $\mu_* - kP_\infty > 0$ then

$$I(t) = \frac{I(0)\,e^{-\int_0^t A(s)\,ds}}{1 + kI(0)\displaystyle\int_0^\infty e^{-\int_0^s A(s')\,ds'}\,ds} \to 0 \qquad \text{as } t \to +\infty.$$

If $\mu^* - kP_\infty < 0$ then $I(t) \to P_\infty - \lim t\to\infty \int_0^\infty \mu(a)w(a,t)\,da \geq P_\infty - \mu^* > 0$.

We notice that although we do not know whether $w(a, t)$ has a limit as $t \to +\infty$ or not, we know that $I(t)$ has a lower bound.

(*f*) *The case* $p^* > 0$, $q = 0$ (*an increasing population with no vertical transmission*)

In this case theorem 4 implies that

$$\lim_{t\to\infty} I(t)/P(t) = 1 \qquad \lim_{t\to\infty} I(t) = +\infty.$$

(*g*) *Case* $q = 1$

Finally, we will turn to a very special case, namely $q = 1$. In this case $p_q^* = p^*$. One can see that theorem 2 is applicable, and hence,

$$\lim_{t\to\infty} w(a,t) = e^{-p^*a}\pi(a) \Big/ \int_0^\infty e^{-p^*a}\pi(a)\,da,$$

then

$$\lim_{t\to\infty} \frac{s(a,t)}{i(a,t)} \to \text{constant.}$$

This is different from the result we had when $q < 1$ where

$$\lim_{t\to\infty} \frac{i(a,t)}{s(a,t)} = 0.$$

Also note if $p^* = 0$ and $q = 1$ then theorem 3 implies that

$$\lim_{t\to\infty} w(a,t) = \pi(a) \Big/ \int_0^\infty \pi(a)\, \mathrm{d}a$$

which is much simpler than that which we get if $q < 1$ and $p^* = 0$.

7. NUMERICAL METHODS

In this section we develop a numerical solution for problem (1.1) by using the equivalent set of problems (3.2), (3.3) and (3.4). Our method is a generalization of the method developed for the McKendrick–Von Foerster equation by Lopez and Trigiante [15].

We consider the following discretization for the age interval $[0, \tau]$ where τ represents an upper bound for the age of an individual. $\{a_i/a_i = i\Delta a,\ i = 0, 1, 2, \ldots \nu\}$, where $\Delta a = \tau/\nu + 1$ and ν is a positive integer. Let us denote by $w_i(t)$ the approximation of $w(a, t)$ when $a = a_i$ and time equals t. Using a backward difference scheme and assuming that $\beta(0) = 0$ and $\int_0^\infty \mu(a)\,\mathrm{d}a = \infty$ we obtain the following:

$$\dot{w}(t) = \frac{1}{\Delta a}\{-(-1+\mu_i \Delta a)w_i + w_{i-1}\} + k\mathbf{P}_i(t) \tag{7.1}$$

$$+ \left\{-kP(t) + \sum_{i=0}^{\nu} [\mu_i - q\beta_i]w_i(t)\right\} w_i(t).$$

Let

$$\mathbf{w}(t) = \begin{pmatrix} w_1(t) \\ w_\nu(t) \end{pmatrix}, \qquad \mathbf{P}(t) = \begin{pmatrix} P_1(t) \\ P_\nu(t) \end{pmatrix}$$

$$\gamma(t)(\mathbf{w}) = \left\{ -kP(t) + \sum_{i=0}^{\nu} \alpha_i[\mu_i - q\beta_i]w_i(t)\right\}$$

where $\alpha_0, \alpha_1, \ldots, \alpha_\nu$ are the quadrature weights.

Then $w(t)$ satisfies

$$\begin{aligned} \mathbf{w}(t) &= A\mathbf{w}(t) + \gamma(t)(\mathbf{w}) + k\mathbf{P}(t) + F(\mathbf{w}(t)) \\ \mathbf{w}(0) &= (w_0(a_1), \ldots, w_0(a_\nu))^t \end{aligned} \tag{7.2}$$

where $(\ )^t$ denotes the transpose, and

$$F(\mathbf{w}(t)) = \frac{1}{\Delta a}\left(\sum_{i=1}^{\nu} q\alpha_i\beta_i w_i(t), 0, \dots, 0\right)^t$$

$$A = \frac{1}{\Delta a}\begin{bmatrix} -\lambda_1 & & 0 \\ 1 & -\lambda_2 & \\ 0 & & 1^{-\lambda}\nu \end{bmatrix} \begin{array}{l} \lambda_i = 1 + \Delta a\mu(a_i) \\ \text{for } i = 1, 2, \dots, \nu. \end{array}$$

Next, we apply the linearized implicit scheme to obtain

$$\mathbf{w}^{n+1} = [I - \Delta t A]^{-1}\{\mathbf{w}^n + \Delta t F(\mathbf{w}^n) + k\Delta t\mathbf{P}(t) + \Delta t\gamma(t)(\mathbf{w}^n)\mathbf{w}^n - k\Delta t\mathbf{P}(t)\mathbf{w}^n\} \tag{7.3}$$

$$\mathbf{w}^0 = \mathbf{w}(0) = (w_0(a_1), \dots, w_0(a_\nu))^t$$

where $\mathbf{w}^n$ is defined by

$$\mathbf{w}^n = \mathbf{w}(n\Delta t) \qquad n = 0, 1, 2, \dots$$

Now, we first solve for $p(a, t)$ (see [15]) and then for $w(a, t)$ which satisfies (7.3), and finally, we solve the ordinary differential equation for $I(t)$. Once we have $p(a, t)$, $w(a, t)$ and $I(t)$ we can determine $i(a, t)$, $s(a, t)$, $S(t)$ and $P(t)$, since

$$w(a, t) = \frac{i(a, t)}{I(t)}$$

implies that

$$i(a, t) = w(a, t)\, I(t)$$

and

$$p(a, t) = s(a, t) + i(a, t)$$

implies that

$$s(a, t) = p(a, t) - i(a, t)$$

and

$$P(t) = \int_0^\tau p(a, t)\, \mathrm{d}s$$

$$S(t) = \int_0^\tau s(a, t)\, \mathrm{d}a$$

hence,

$$S(t) = P(t) - I(t).$$

In order to carry out the computation in (7.3) we define the initial age-distributions for $p(a, t)$ and $w(a, t)$ which are described in Fig. 1. The mortality rate $\mu(a)$ is described in Fig. 2.

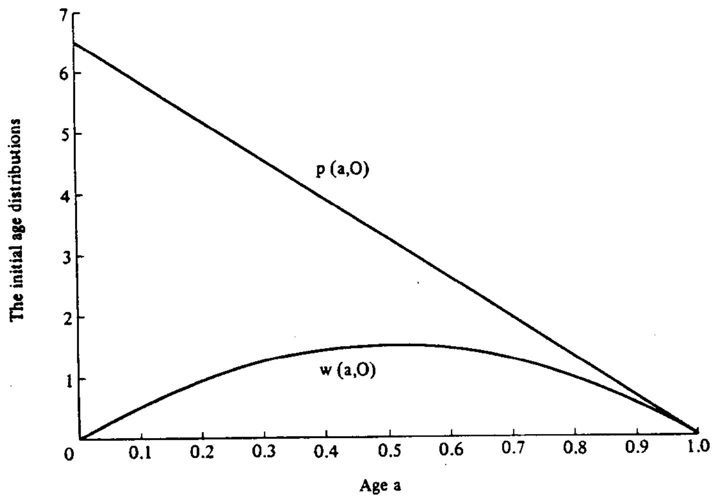

FIG. 1.

In the following examples we fix the initial age-distributions, the mortality rate, and set $k = 0.5$, $\nu = 9$, $q = 0.6$, $\Delta t = \Delta a = 0.1$ and $\tau = 1$. We let $\beta(a)$ take the form

$$\beta(a) = \begin{cases} 0, & 0 \leqslant a < m \\ \alpha(a - m)\,e^{-\gamma(a-m)}, & m \leqslant a < 1 \end{cases}$$

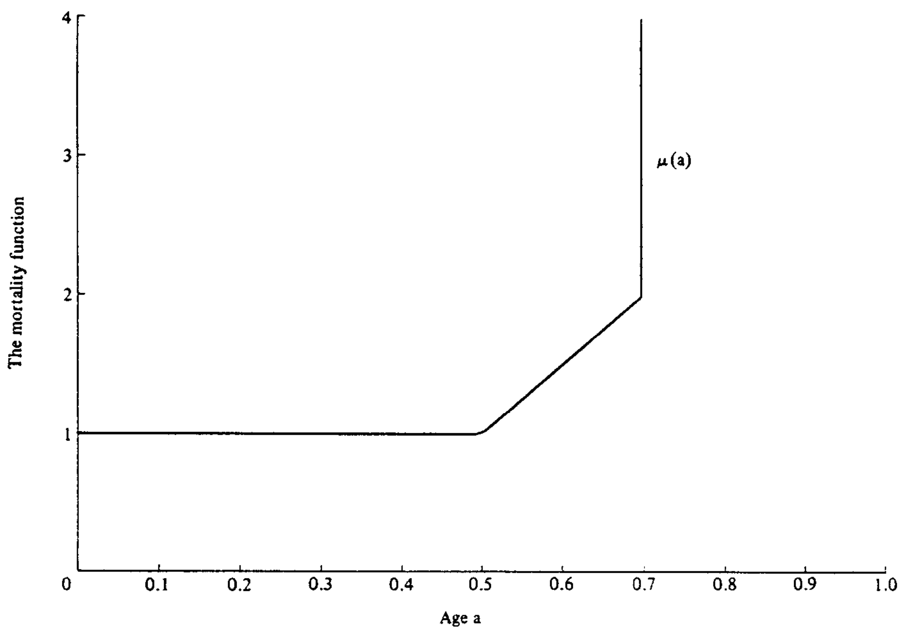

FIG. 2.

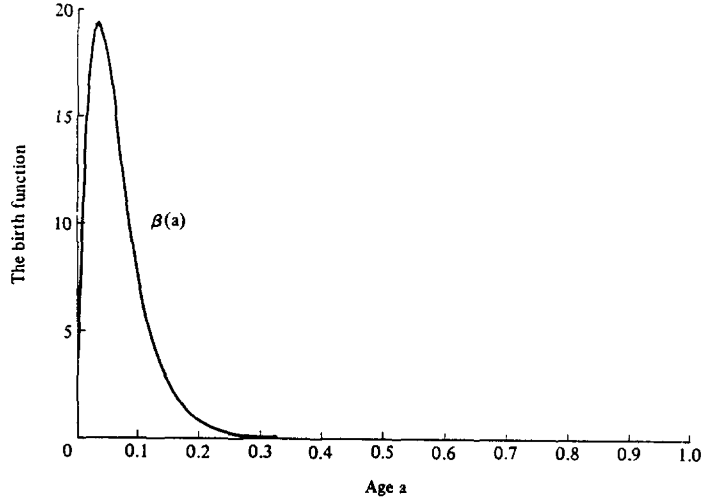

FIG. 3.

where α, γ, m are nonnegative real numbers, γ is taken to be equal to 30, $m = 0, 0.3, 0.5, 0.7$ and for each value of m, α is found so that the linear problem attains its steady state for the corresponding $\beta(a)$, i.e. $p^* = 0$. The parameter m has been called the maturation period by Busenberg and Iannelli [6] and this form of $\beta(a)$ the "shifted fecundity rate." Note that increasing the maturation period m corresponds to delaying the fertility window by m age units. We now numerically study the effects of changing the maturation period.

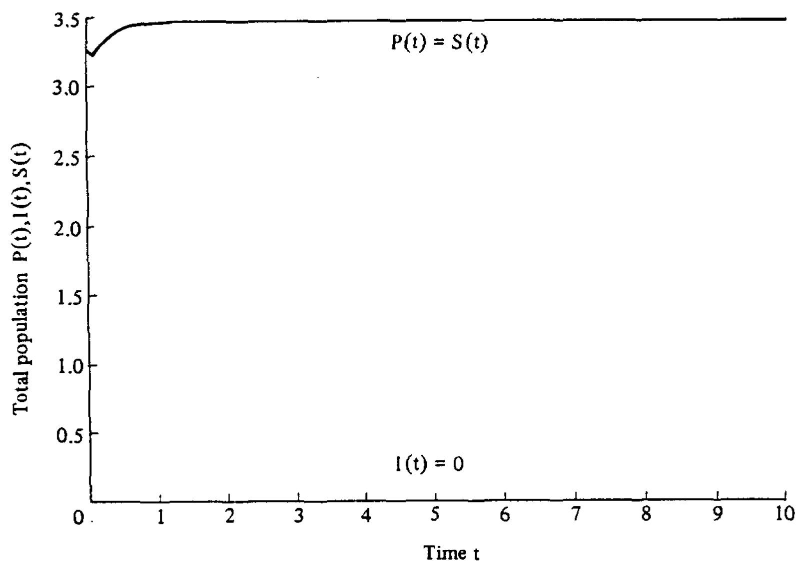

FIG. 4.

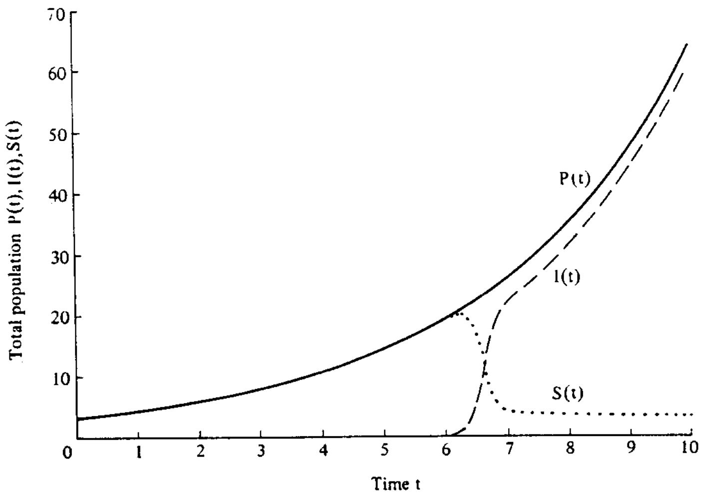

FIG. 5.

Example 1. Let $\beta(a)$ be as described in Fig. 3, i.e. $m = 0$. This $\beta(a)$ is chosen such that $p(a, t)$ is in the steady ($p^* = 0$). In Fig. 4 we see $P(t)$, $I(t)$ and $S(t)$ and notice that $S(t)$ approaches $P(t)$ as $t \to +\infty$, and $I(t)$ approaches zero as $t \to +\infty$.

Now, we multiply $\beta(a)$ by a factor bigger than one and then we are in the case $p^* > 0$. In Fig. 5 we see $P(t)$, $I(t)$ and $S(t)$ and we notice that

$$\lim_{t\to\infty} \frac{P(t)}{I(t)} = 1$$

and this is exactly what theorem 4 asserts in this case.

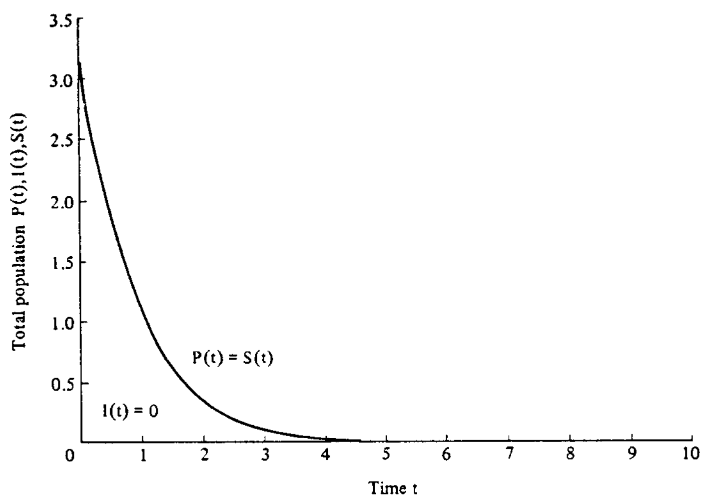

FIG. 6.

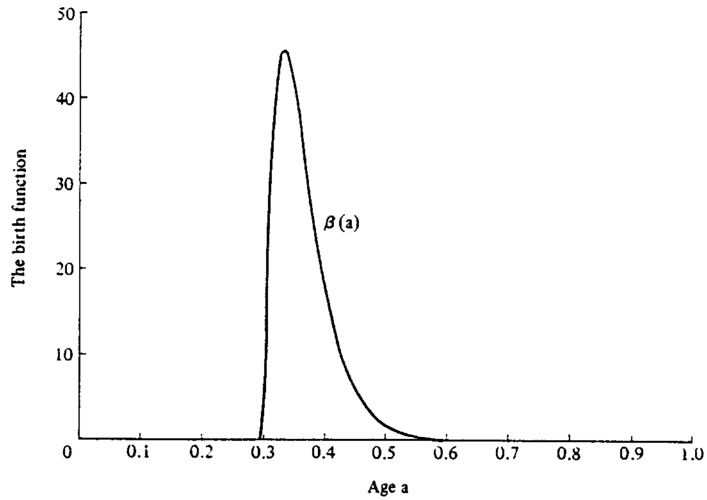

FIG. 7.

Finally, we multiply $\beta(a)$ by a factor smaller than one, and then we are in the case $p^* < 0$. In Fig. 6 we see that $I(t)$ approaches zero faster than $S(t)$.

Example 2. Let $\beta(a)$ be as described in Fig. 7, i.e. $m = 0.3$. This $\beta(a)$ is chosen such that $p(a, t)$ attains its steady state ($p^* = 0$). In Fig. 8 we notice that $S(t)$ approaches $P(t)$as $t \to \infty$ but, slower than in example (1) Fig. 4.

Now, we multiply $\beta(a)$ by a factor bigger than one and then we are in the case $p^* > 0$. In Fig. 9 we notice that

$$\lim_{t \to \infty} \frac{I(t)}{P(t)} = 1$$

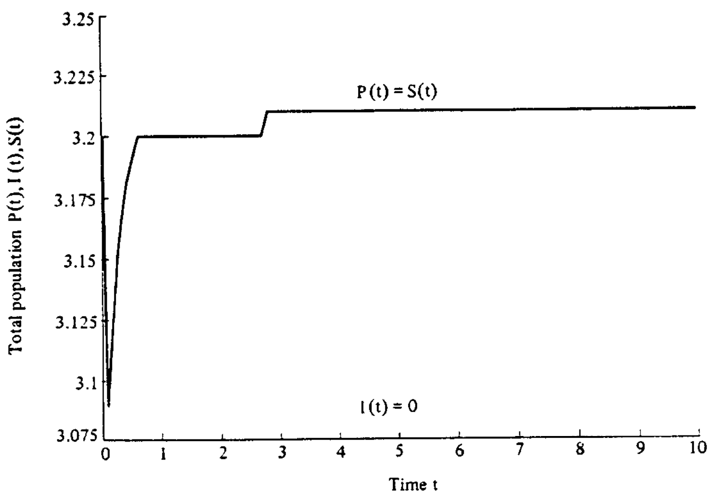

FIG. 8.

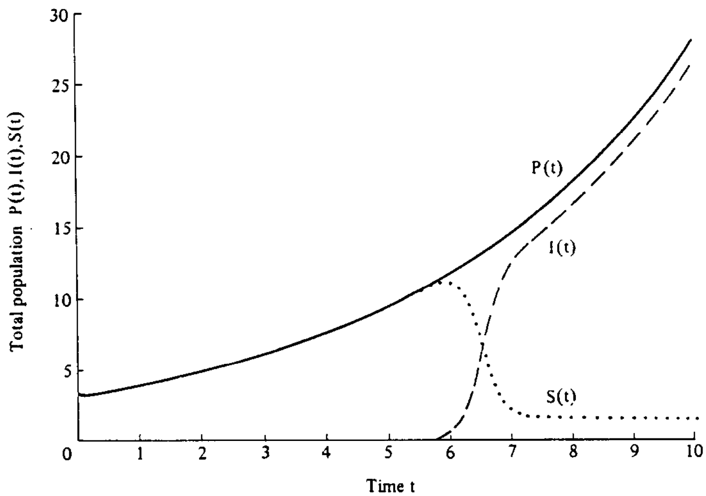

FIG. 9.

which is exactly what theorem 4 asserts in this case.

Finally, we multiply $\beta(a)$ by a factor smaller than one and then we are in the case $p^* < 0$. In Fig. 10 we see that $I(t)$ approaches zero faster than $S(t)$.

Example 3. Let $\beta(a)$ be as described in Fig. 11, i.e. $m = 0.5$. This $\beta(a)$ is chosen such that $p(a, t)$ attains its steady state, i.e $p^* = 0$. In Fig. 12 we notice that $I(t)$ approaches a nonzero constant value, i.e. an endemic level.

This example illustrates the powerful effect of age dependence in vertically transmitted

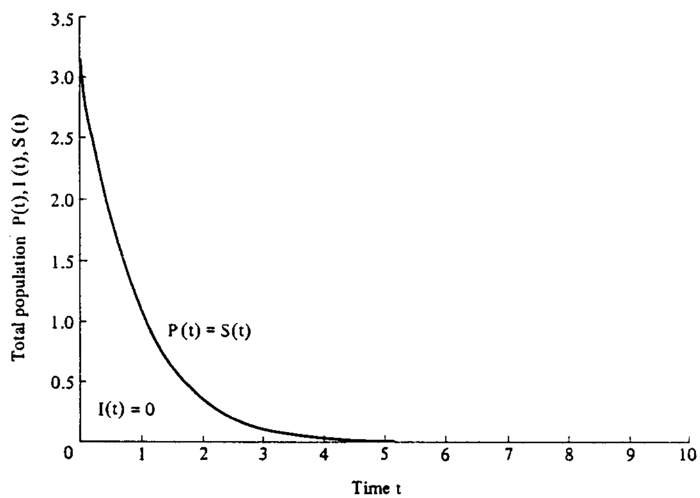

FIG. 10.

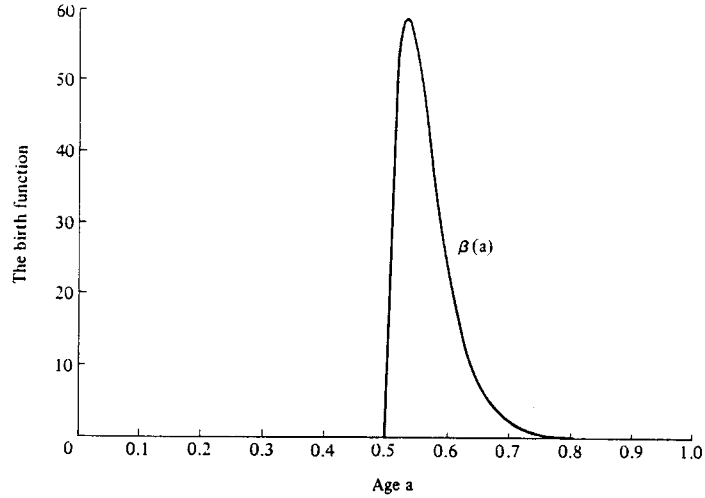

FIG. 11.

diseases. It is not easy to see such effects theoretically, although it is intuitive that, if the population reproductive capacity is concentrated in an older age, then the combined effect of vertical transmission and horizontal transmission is capable of maintaining the disease, because the longer individuals survive, the more likely it is that they get infected via horizontal transmission. If they are able to reproduce at an older age, then it is likely that their offspring will get infected via vertical transmission.

Example 4. Let $\beta(a)$ be as described in Fig. 13, i.e. $m = 0.7$. This $\beta(a)$ is chosen such that $p(a, t)$ attains its steady state, i.e. $p^* = 0$. In Fig. 14 we notice that $I(t)$ approaches a constant which is close to the total population while $S(t)$ approaches a constant which is close to zero.

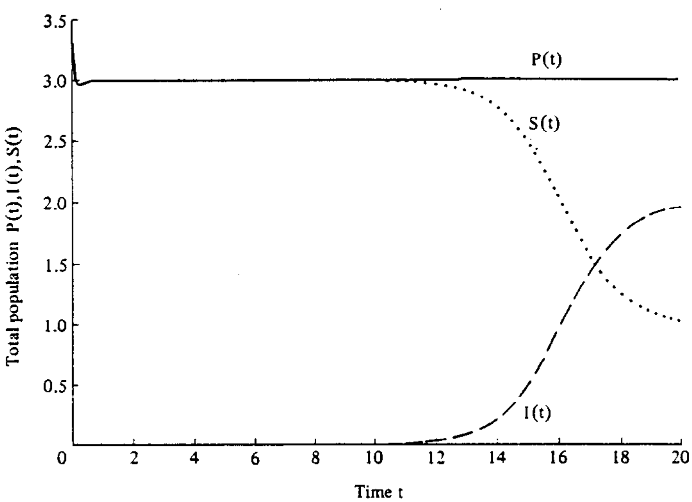

FIG. 12.

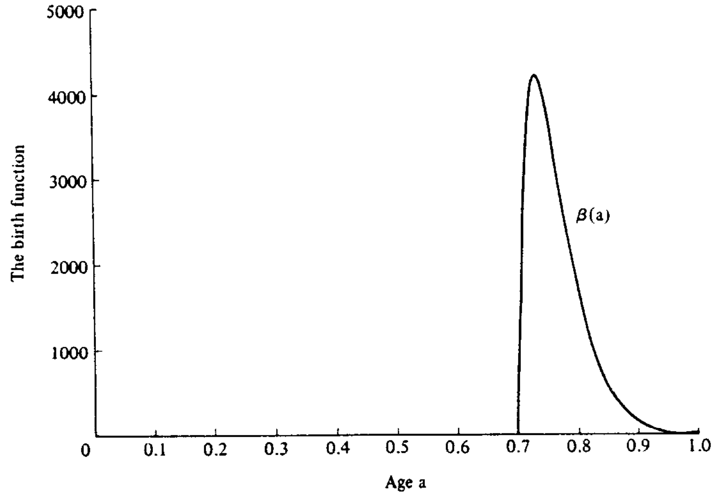

FIG. 13.

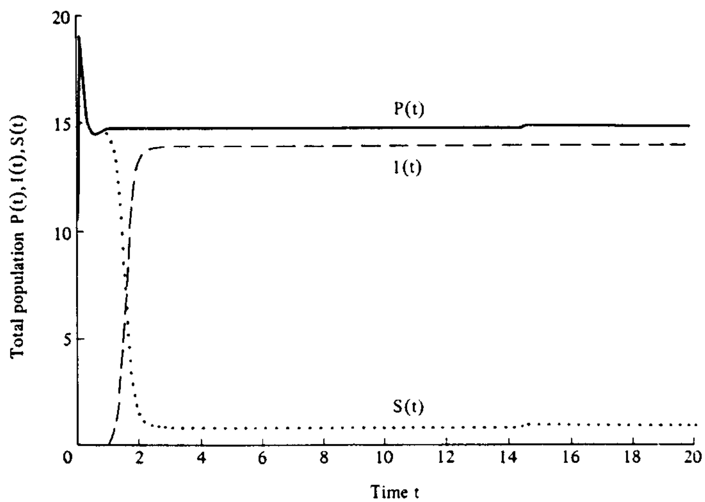

FIG. 14.

Table 1.

$p_q^* < p^* = 0$	$P(t)$	$I(t)$	$S(t)$
$m = 0$	3·45	0·00	3·45
$m = 0.3$	3·2·5	0·00	3·205
$m = 0·5$	3·00	1·90	1·1
$m = 0·7$	15·00	14·00	1·00

This example confirms what has been said in the previous example about the powerful effect of age-dependence in vertically transmitted diseases.

Finally, in Table 1 we summarize the results in the above examples for the case $p^* = 0$. (Note the relationship between $\beta(a)$ and $P(t)$.)

Note that

$$\lim_{t\to\infty} P(t) = P_\infty = c\int_0^\infty \pi(a)\,\mathrm{d}a$$

where c is given by

$$c = \int_0^\infty \beta(a)\pi(a)\left[\int_0^a p_0(t)/\pi(t)\,\mathrm{d}t\right]\mathrm{d}a \bigg/ \int_0^\infty a\beta(a)\pi(a)\,\mathrm{d}a.$$

So, c changes with $\beta(a)$. Moreover, the delay in the maturation period forces α to be an increasing function of m. This happens because when m increases there is an increasing interval where the population is reduced by death before reproduction occurs. So in order that the total population reach steady state, α must increase to compensate for the loss due to death.

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