## STABILITY ANALYSIS FOR A VECTOR DISEASE MODEL

## KENNETH L. COOKE\*

1. Introduction. In this note, we shall analyze the scalar delay-differential equation

(1) 
$$y'(t) = by(t - T)[1 - y(t)] - cy(t)$$

where b, c, and T are positive constants. This equation represents the proportion of infectious persons in a very simple deterministic model for the spread of a communicable disease carried by a vector. The assumptions of the model are explained in § 2.

Despite its simplicity, the nonlinear equation (1) has apparently not been investigated heretofore, except in the case c=0. For c=0, it is equivalent to the equation of Hutchinson for single species population growth and has been studied by a number of authors. However, their assumptions generally seem to exclude the case b>0 of interest to us. See § 7 for further discussion of this.

In § 3, we begin our mathematical analysis by proving that the region  $0 \le y \le 1$  is invariant for (1). That is, if  $\phi$  is a continuous initial function satisfying  $0 \le \phi(\theta) \le 1$  for  $-T \le \theta \le 0$ , then the solution satisfies  $0 \le y(t) \le 1$ . See Lemma 1. We then conduct a linear stability analysis of equilibrium solutions and prove the following theorem.

Theorem 1. Let P denote the class of all nonnegative solutions y(t) of (1) on  $0 \le t < \infty$ . Assume that b > 0,  $c \ge 0$ . Then y = 0 is (locally) asymptotically stable within this class provided c > b. The solution y = 1 - (c/b) is (locally) asymptotically stable within the class P if c < b.

In Sections 4–7, we carry out a global stability analysis, using Liapunov functionals, obtaining the following results.

Theorem 2. If  $c \ge b > 0$ , the solution y = 0 is asymptotically stable and the set  $\{\phi \in C : 0 \le \phi(\theta) \le 1 \text{ for } -T \le \theta \le 0\}$  is a region of attraction. If  $0 \le c < b$ , the solution y = 1 - (c/b) is asymptotically stable and the set  $\{\phi \in c : 0 < \phi(\theta) \le 1 \text{ for } -T \le \theta \le 0\}$  is a region of attraction.

The biological interpretation of these results is that there is a thresh-

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old at b=c, in the following sense. If  $b \le c$ , then the proportion y(t) of infectious individuals tends to zero as t becomes large, and the disease dies out. If b>c, the proportion y(t) tends to an endemic level y=1-(c/b) as t becomes large. Since c represents the recovery rate and b represents a contact rate, this is a very reasonable conclusion. We note that non-constant periodic solutions cannot exist within the region  $0 \le y \le 1$ .

In § 8, several possible extensions of this work are mentioned. No attempt has been made to fit actual data to the model. This is because our principal interest is in determining the general qualitative features of solutions of various functional equations arising from biological models, with the hope that this will show the consequences of the sundry assumptions in these models.

- 2. The Model. The assumptions of this model are as follows.
- (A) The infection is transmitted to man by a vector, such as a mosquito. That is, susceptible persons receive the infection from infectious vectors, and susceptible vectors receive the infection from infectious persons.
- (B) The infection in humans confers negligible immunity and does not result in death or isolation.
- (C) The human population in the community under consideration is fixed. Births, deaths, and migration are ignored.
- (D) When a susceptible vector is infected by a person, there is a fixed time T during which the infectious agent develops in the vector. At the end of this time, the vector can infect a susceptible human.
- (E) There is homogeneous mixing of the human and vector populations.
  - (F) Infected humans have a recovery rate c.

These assumptions apply as a very rough approximation to a disease such as malaria.

Let y(t) denote the proportion of humans in the community who are infectious at time t and let S(t) denote the proportion who are susceptible. Then y(t) + S(t) = 1, by assumption (B). Let z(t) denote the number of infectious vectors in the community at time t. For the sake of simplicity, assume that

(G) The vector population is very large and z(t) is simply proportional to y(t-T).

As usual, interpret assumption (E) to mean that the number of new infections per unit time is a multiple of S(t)z(t). Then, by assumptions (F) and (G) we have

$$y'(t) = bS(t)y(t - T) - cy(t)$$

and

(1) 
$$y'(t) = by(t - T)[1 - y(t)] - cy(t).$$

Here b > 0 and  $c \ge 0$ .

3. Linearized Stability Analysis. We wish to determine the nature of all solutions of (1) within the biologically meaningful range  $0 \le y \le 1$ . We first give a simple lemma on invariance of this region.

LEMMA 1. Let  $\phi$  be a continuous function on [-T,0] into R satisfying  $0 \le \phi(\theta) \le 1$  for  $-T \le \theta \le 0$ . If  $y:[-T,\alpha) \to R$  is a solution of (1) for  $0 < t < \alpha$  satisfying the initial condition

$$y(\theta) = \phi(\theta), \quad -T \le \theta \le 0$$

then

$$(2) 0 \le y(t) \le 1, \quad 0 \le t < \alpha.$$

Moreover, if  $0 < \phi(\theta) \le 1$  then  $0 < y(t) \le 1$ . If  $0 < \phi(\theta) < 1$  and c > 0, then 0 < y(t) < 1.

PROOF. First suppose that  $0 \le \phi(\theta) \le 1$ . Then from (1)

(3) 
$$\frac{d}{dt}[y(t)e^{ct}] = be^{ct}y(t-T)[1-y(t)].$$

Now suppose that y(t) does not satisfy (2). By continuity of y(t), there is a largest number  $\beta$ ,  $0 \le \beta < \alpha$ , such that  $0 \le y(t) \le 1$  for  $0 \le t \le \beta$ , and either

- (i)  $y(\beta) = 0$  and y(t) < 0 on  $(\beta, \beta + \epsilon)$  for some  $\epsilon > 0$ , or
- (ii)  $y(\beta) = 1$  and y(t) > 1 on  $(\beta, \beta + \epsilon)$  for some  $\epsilon > 0$ .

Consider (i). From (3) (assuming, as we may, that  $\epsilon < T$ ) we see that  $y(t)e^{ct}$  is non-decreasing on  $(\beta, \beta + \epsilon)$ , which is a contradiction. Next, consider (ii). Then from (1) we get  $y'(t) \le -cy(t) \le -c$  for  $\beta \le t \le \beta + \epsilon$ . Hence y(t) is non-increasing on  $(\beta, \beta + \epsilon)$ , which is a contradiction. This proves that y satisfies (2).

Next, suppose that  $0 < \phi(\theta) \le 1$ . From the above, we know that y satisfies (2), and we wish to show that y(t) remains strictly positive. If not, let  $t_1$  be the first point where  $y(t_1) = 0$ . Then  $y'(t_1) \le 0$ . However, from (3) we have  $y'(t_1) > 0$ , a contradiction.

Finally, if  $0 < \phi(\theta) < 1$  and c > 0, y(t) must remain strictly less than one. If not, let  $t_1$  be the first point where  $y(t_1) = 1$ . Then (1) implies  $y'(t_1) = -c < 0$ , a contradiction.

Our next result concerns local stability of equilibrium solutions.

Clearly y=0 is an equilibrium point for all b, c, T. The only other equilibrium point is y=1-(c/b), which is within the allowable range if b>0 and  $0 \le c \le b$ .

Theorem 1. Let P denote the class of all nonnegative solutions y(t) of (1) on  $0 \le t < \infty$ . Assume that b > 0,  $c \ge 0$ . Then y = 0 is (locally) asymptotically stable within the class P provided c > b. The solution y = 1 - (c/b) is (locally) asymptotically stable within the class P if c < b.

Proof. We begin by considering the linearization of (1) near y=0, which is the equation

$$(4) u'(t) = bu(t-T) - cu(t).$$

The associated characteristic equation is

$$\lambda = be^{-T\lambda} - c.$$

Let  $z = T\lambda$ . Then

$$(6) Tb - Tce^z - ze^z = 0.$$

We now apply the following well-known theorem of Hayes [3].

Theorem. A necessary and sufficient condition in order that every root of the equation

$$pe^z + q - ze^z = 0$$

have negative real part is that

- (a) p < 1, and
- (b)  $p < -q < (a_1^2 + p^2)^{1/2}$ where  $a_1$  is the root of  $a = p \pmod{a}$  such that

where  $a_1$  is the root of  $a=p\,(\tan a)$  such that  $0 < a < \pi$ . (If p=0, take  $a_1=\pi/2$ .)

Applying this to (6) with p=-Tc,  $v\ Tb$ , we observe that (a) certainly holds since  $Tc \ge 0$ , and (b) reduces to c > b. Assume that c > b. Then the zero solution of (4) is uniformly asymptotically stable. Moreover, (1) is a nonlinear perturbation of (4) that may be written, in the notation of functional differential equations, in the form

$$y'(t) = L(y_t) + f(y_t)$$

where L and f are the functions

$$L(\phi) = b\phi(-T) - c\phi(0),$$

$$f(\phi) = -b\phi(-T)\phi(0).$$

Let  $\|\phi\|$  denote the usual supremum norm. Then for any  $\epsilon > 0$ ,

$$|f(\phi)| \le \epsilon ||\phi||$$
, for  $t \in R$ ,  $||\phi|| \le \epsilon/b$ .

Using Hale [2], Theorem 18.3),we may conclude that the zero solution of (1) is also uniformly asymptotically stable. Thus, if y(t) is any solution of (1) with y in class P and  $\|\phi\|$  sufficiently small, then y(t) remains within the class P (by Lemma 1) and y(t) tends to zero as  $t \to \infty$ .

If b > c > 0, then the result of Hayes shows that the zero solution of (4) is unstable. We therefore consider the other equilibrium point, y = 1 - (c/b).

To examine (1) around this point, we set

(7) 
$$y(t) = \left(1 - \frac{c}{b}\right) (1 + v(t))$$

and find the equation

(8) 
$$v'(t) = cv(t-T) - bv(t) - (b-c)v(t)v(t-T).$$

Note that the region  $0 \le y \le 1$  corresponds to the region  $-1 \le v \le c/(b-c)$ . The latter therefore has invariance properties for solutions v(t) of (8) which are like those in Lemma 1.

The linearization of (8) near v = 0 is

(9) 
$$u'(t) = cu(t - T) - bu(t).$$

This equation has the same form as (4), but with b and c interchanged. Therefore by the previous discussion (theorem of Hayes), u=0 is uniformly asymptotically stable for (9) if c < b and unstable if c > b. Since the nonlinearity in (8) is again quadratic, the previous argument also shows that v=0 is uniformly asymptotically stable for (8) relative to solutions v in the specified region. Translating this result back to y(t), we find that if c < b, then y=1-(c/b) is uniformly asymptotically stable within the class P. Note that if c > b, the point y=1-(c/b) becomes unstable for the linearized equation. This completes the proof of Theorem 1.

In the following sections, we shall obtain global stability results for the cases b < c and b > c, as well as for the case b = c where there is an "exchange of stabilities".

4. Liapunov Stability Analysis for c > b > 0. We shall now establish asymptotic stability of y = 0 for (1) when c > b by using a Liapunov functional. Let C = C([-T, 0], R) and for  $\phi$  in C define

(10) 
$$V(\phi) = \frac{1}{2c} \phi(0)^2 + \frac{1}{2} \int_{-T}^{0} \phi(\theta)^2 d\theta.$$

For the sake of convenience, write (1) in the form

$$(11) y'(t) = f(y_t).$$

It is easy to see that f as a map from C to R is continuous and takes closed bounded sets into bounded sets. Now for  $\phi$  in C, let  $y_t$  denote the solution with initial condition  $\phi$ . Then the derivative of V is

$$\begin{split} \dot{V}(\phi) &= \lim\sup_{t\to 0+} \, \frac{1}{t} \left[ V(y_t) - V(\phi) \right] \\ &= \lim\sup_{t\to 0+} \, \left\{ \, \frac{1}{2c} \, \frac{y_t(0)^2 - \phi(0)^2}{t} \right. \\ &+ \left. \frac{1}{2} \, \, \int_{-T}^0 \, \frac{y_t(\theta)^2 - \phi(\theta)^2}{t} \, d\theta \, \, \right\}. \end{split}$$

The first term on the right is

$$\lim_{t \to 0+} \frac{1}{2c} \frac{y(t)^2 - y(0)^2}{t} = \frac{1}{c} y(0)y'(0)$$
$$= \frac{1}{c} \phi(0)f(\phi)$$

and the second is

$$\begin{split} & \lim_{t \to 0+} \; \frac{1}{2} \; \int_{-T}^{0} \frac{y(t+\theta)^{2} - \phi(\theta)^{2}}{t} \, d\theta \\ & = \; \int_{-T}^{0} \; \phi(\theta) \phi'(\theta) \, d\theta = \; \frac{1}{2} \left[ \phi(0)^{2} - \phi(-T)^{2} \right]. \end{split}$$

Using the definition of f, we obtain

$$\dot{V}(\phi) = \frac{1}{c} \phi(0)[b\phi(-T) - b\phi(-T)\phi(0) - c\phi(0)]$$

$$+ \frac{1}{2} [\phi(0)^2 - \phi(-T)^2]$$

$$= -\frac{1}{2} [\phi(0)^2 - \frac{2b}{c} \phi(0)\phi(-T)$$

$$+ \phi(-T)^2] - \frac{b}{c} \phi(0)^2\phi(-T).$$

We now define

$$G = \{ \phi \in C : 0 \le \phi(\theta) \le 1 \text{ for } -T \le \theta \le 0 \}.$$

It is clear that V is continuous on  $\overline{G} = G$ . Also, the quadratic form  $x^2 - 2bc^{-1}xy + y^2$  is positive definite since 0 < b < c. Therefore for  $\phi$  in G we have

$$\dot{V}(\phi) \le -\frac{b}{c} \phi(0)^2 \phi(-T) \le 0.$$

Thus, V is a Liapunov function on G relative to the given equation. Further, let

$$E = \{ \phi \in \overline{G} : \dot{V}(\phi) = 0 \}.$$

From (12) it is clear that

$$E = \{ \phi \in \overline{G} : \phi(0) = \phi(-T) = 0 \}.$$

Let M denote the largest subset of E that is invariant under the equation (1). Now if  $\phi(0) = \phi(-T) = 0$  then the corresponding solution y of (1) satisfies y(t) = 0 for  $t \ge 0$ . Consequently, M consists of the identically zero function only.

Now let  $\phi \in G$  and let y be the corresponding solution of (1). By Lemma 1, y remains in G for all  $t \ge 0$ . Also, the positive trajectory

$$\gamma^+(\phi) = \{y_t : 0 \le t < \infty\}$$

is compact in C. For, this family is uniformly bounded, and equicontinuous since

$$|y'(t)| \le b|y(t-T)|[1+|y(t)|] + c|y(t)| \le 2b + c.$$

It follows from Theorem 4.7, Chapter 3, in La Salle [7] that  $y_t$  tends to M as  $t \to \infty$ . That is,  $y(t) \to 0$  as  $t \to \infty$ . This proves that 0 is asymptotically stable for (1), and G is a region of attraction.

5. Liapunov Stability Analysis for 0 < c < b. When c < b, we study the equation in the form (8), which for convenience we can write as  $v'(t) = g(v_t)$  where

(13) 
$$g(\phi) = c\phi(-T) - b\phi(0) - (b - c)\phi(0)\phi(-T).$$

Define

$$V(\phi) = \frac{1}{2b} \phi(0)^2 + \frac{k}{2} \int_{-T}^{0} \phi(\theta)^2 d\theta.$$

The constant k will be chosen later. Then

$$\dot{V}(\phi) = \frac{1}{b} \phi(0)g(\phi) + \frac{k}{2} [\phi(0)^2 - \phi(-T)^2].$$

Using (13), and defining d = c/b, we get

$$\dot{V}(\phi) = \left( \begin{array}{c} \frac{k}{2} - 1 \end{array} \right) \phi(0)^2 + d\phi(0)\phi(-T)$$

$$- \frac{k}{2} \phi(-T)^2 + (d-1)\phi(0)^2 \phi(-T).$$

Define

$$G = \left\{ \phi \in C : -1 < \phi(\theta) \le \frac{c}{b-c} \text{ for } -T \le \theta \le 0 \right\}.$$

For  $\phi$  in G, we have

$$(d-1)\phi(0)^2\phi(-T) \le (1-d)\phi(0)^2$$

and hence

$$\dot{V}(\phi) \le \left(\frac{k}{2} - d\right) \phi(0)^2 + d\phi(0)\phi(-T) - \frac{k}{2}\phi(-T)^2.$$

Choosing k = d, we obtain

$$\dot{V}(\phi) \le -\frac{d}{2} [\phi(0) - \phi(-T)]^2 \le 0.$$

Since V is continuous on G, and  $\dot{V}(\phi) \leq 0$  on G, V is a Liapunov function on G. Let

$$E = \{ \phi \in \overline{G} : \dot{V}(\phi) = 0 \}.$$

If  $\phi$  is in E, and d > 0, then it is necessary that  $\phi(0) = \phi(-T)$ . Then

$$\dot{V}(\phi) = (d-1)\phi(0)^2[1+\phi(0)].$$

Therefore  $\phi(0)=0$  or  $\phi(0)=-1$ . Hence E contains  $\phi$  for which  $\phi(0)=\phi(-T)=0$  and  $\phi$  for which  $\phi(0)=\phi(-T)=-1$ . We find that M, the largest invariant set in E, consists of the functions  $\phi(\theta)\equiv -1$  and  $\phi(\theta)\equiv 0$ .

If  $\phi \in G$ , and v is the corresponding solution of  $v'(t) = g(v_t)$ , it follows from Lemma 1 that v remains in G for all  $t \ge 0$ . The positive trajectory  $\gamma^+(\phi)$  is compact in C. Therefore,  $v_t$  tends to M as  $t \to \infty$ . That

is, either  $v(t) \to 0$  or  $v(t) \to -1$  as  $t \to \infty$ . Equivalently, y(t) tends to 1-(c/b) or to 0 as t tends to  $\infty$ . However, we showed in the proof of Theorem 1 that when b>c, the zero solution is unstable. Consequently, y=1-(c/b) is asymptotically stable and the set (which corresponds to G)

$$\{\phi \in C : 0 < \phi(\theta) \le 1\}$$

is a region of attraction.

6. Stability Analysis for c = b > 0. If c = b > 0, (1) takes the form

(15) 
$$y'(t) = by(t - T) - by(t)y(t - T) - by(t).$$

The only equilibrium point is y = 0. Defining  $V(\phi)$  as in (10), we obtain (12) with b = c, that is,

$$\dot{V}(\phi) = -\frac{1}{2} [\phi(0) - \phi(-T)]^2 - \phi(0)^2 \phi(-T).$$

We again take

$$G = \{ \phi \in C : 0 \le \phi(\theta) \le 1 \text{ for } -T \le \theta \le 0 \}$$

and we have  $\dot{V}(\phi) \leq 0$  for  $\phi$  in G. Defining the set E as before, we find that if  $\phi$  is in E then  $\phi(0) = \phi(-T)$  and  $\phi(0)^2 \phi(-T) = 0$ . Therefore

$$E = \{ \phi \in G : \phi(0) = \phi(-T) = 0 \}$$

and M contains only the zero function. Thus, y = 0 has G as a region of attraction, for (15).

7. The case c = 0, b > 0. If c = 0 then (1) reduces to

(16) 
$$y'(t) = by(t - T)[1 - y(t)].$$

There are two equilibrium solutions, y = 0 and y = 1. The local stability analysis of § 3 shows that y = 0 is unstable for all b > 0. The substitution y = 1 + v yields the equation

(17) 
$$v'(t) = -bv(t)[1 + v(t - T)].$$

The linearization near v=0 is

$$u'(t) = -bu(t)$$

and clearly u = 0 is stable. Therefore y = 1 is stable for (16). It should also be noted that Lemma 1 is still valid for (16). Therefore the region  $-1 \le v \le 0$  is invariant for (17).

Now we choose

$$V(\phi) = \frac{1}{2h} \phi(0)^2 + \frac{1}{2} \int_{-T}^{0} \phi(\theta)^2 d\theta$$

and find for (17)

$$\dot{V}(\phi) = \; - \; rac{1}{2} \; \; \phi(0)^2 \, - \; \phi(0)^2 \phi(-T) \, - rac{1}{2} \; \phi(-T)^2.$$

Let

$$G = \{ \phi \in C : -1 \le \phi(\theta) \le 0 \text{ for } -T \le \theta \le 0 \}.$$

If  $\phi$  is in G, we have  $-\phi(0)^2\phi(-T) \leq |\phi(0)^2\phi(-T)| \leq \phi(0)\phi(-T)$ . Therefore, for  $\phi$  in G,

$$\begin{split} \dot{\mathbf{V}}(\phi) \, & \leq \, - \, \frac{1}{2} \ \ \, \phi(0)^2 \, + \, \phi(0)\phi(-T) \, - \, \quad \frac{1}{2} \, \phi(-T)^2 \\ \\ & = \, - \, \frac{1}{2} \, \left[ \phi(0) - \, \phi(-T) \right]^2 \, \leq \, 0 \, \, . \end{split}$$

Thus V is a Liapunov function on G. If we define E in the usual way, then  $\phi$  in E implies  $\phi(0) = \phi(-T)$  and therefore

$$\dot{V}(\phi) = -\phi(0)^2[1 + \phi(0)] = 0.$$

Hence E consists of  $\phi$  in G for which  $\phi(0) = \phi(-T) = 0$  or  $\phi(0) = \phi(-T) = -1$ , and M consists of the functions  $\phi(\theta) = -1$  and  $\phi(\theta) = 0$ . Arguing as in § 5, we deduce that v(t) tends to 0 or -1 as  $t \to \infty$ , or correspondingly y(t) tends to 1 or 0. Since y = 0 is unstable, we conclude that y = 1 has as region of attraction the set of  $\phi$  satisfying  $0 < \phi(\theta) \le 1$ . By combining the results in Sections 4–7, we find that we have now completed the proof of Theorem 2.

Equation (16) is closely related to several equations that have been studied in the literature. For example, Waltman [8, page 52] has mentioned the equation

(18) 
$$S'(t) = -rS(t)[N - S(t - m/\rho_1)].$$

If we define  $T = m/\rho_1$  and

$$S(t) = N[1 - y(t)],$$

this equation reduces to (16) with b = rN.

By a change of time scale in (16), we may assume without loss of generality that T = 1. If we then let y(t) = -x(t) we obtain

(19) 
$$x'(t) = bx(t-1)[1 + x(t)].$$

This equation has been extensively studied by Hutchinson [4], Wright [9], Kakutani and Markus [6], Jones [5], and others. However, almost all this work has concentrated on the case in which b is negative, which is not the case of interest to us here. For  $b < -\pi/2$ , (19) has a periodic solution. Braddock and van den Driessche [1] have studied the equation

(20) 
$$x'(t) = -[\alpha x(t) + \beta x(t-1)][1 + x(t)]$$

which reduces to (19) for  $\alpha = 0$ ,  $\beta = -b$ , but their work is also primarily for the case  $\beta > 0$  (b < 0).

8. Extensions. although the above discussion is definitive for (1) in all cases of physical interest in the model, it might be of mathematical interest to investigate other cases. For example, we can drop the assumption that b and c are positive. In this connection, we note that a modification of the argument of § 4 can be used to show that y=0 is stable when  $0<|b|\leq c$ . In fact, defining  $V(\phi)$  as in (10), and using (12), we get

$$\dot{V}(\phi) = -\frac{1}{2} \left[ \phi(0)^2 + \phi(-T)^2 \right] + bc^{-1}\phi(0)\phi(-T)[1 - \phi(0)].$$

If  $\phi(-T) \ge 0$  and  $0 \le \phi(0) \le 1$  then for negative b we obtain

$$\dot{V}(\phi) \le - \frac{1}{2} [\phi(0)^2 + \phi(-T)^2] \le 0.$$

The argument is completed as before.

Another possible extension is obtained by discarding the restriction to solutions satisfying  $0 \le y \le 1$ . In a number of numerical solutions with c > b > 0 and initial functions such as  $\phi(t) = 2.0$ ,  $\sin 2\pi t$ ,  $\sin 3\pi t$ , we have found that y(t) tends to zero as  $t \to \infty$ . In a few computer runs with 0 < c < b, we have found the results in the following table.

b	c	$\phi(oldsymbol{ heta})$	y(t)
2	1	-1.0	$y \rightarrow -\infty$
4.5	3	$\theta(\theta + \frac{1}{2})(\theta + 1)$	$y \rightarrow 1/3$
6	2	$1 + 2 \sin 2\pi\theta$	$y \rightarrow 2/3$
9	7	$1+2\sin 2\pi\theta$	$y \rightarrow -\infty$
8	4	$4\sin 4\pi  heta$	$y \to -\infty$

A generalization of the model which may permit greater biological

realism or flexibility can be formulated as follows. Instead of assuming that the number of new infectives per unit time is proportional to S(t)z(t), let us assume that it is a function  $g(S(t),\,z(t))$ . Also, assume that z(t)=h(y(t-T)) rather than z(t)=y(t-T). Any biologically desirable assumptions about the nature of the functions  $g(S,\,z)$  and h(y) can be imposed. We now obtain the equation

$$y'(t) = g(1 - y(t), h(y(t - T))) - cy(t).$$

If we let f(S, y) = g(S, h(y)), we may write this in the form

(21) 
$$y'(t) = f(1 - y(t), y(t - T)) - cy(t).$$

It might be of interest to determine conditions on f or on g and h under which results such as those in Lemma 1 or Theorem 1 will remain valid.

In (1), we have assumed that b and c are constants. In real cases, however, there often is a considerable seasonal fluctuation of contact or recovery rates. With Professor S. Busenberg, we have accordingly begun to study an equation of the form (1) having periodic coefficient functions.

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DEPARTMENT OF MATHEMATICS, POMONA COLLEGE, CLAREMONT, CA 91711