ON THE OSCILLATION AND ASYMPTOTIC BEHAVIOR
OF $\dot{N}(t) = N(t)[a + bN(t-\tau) - cN^2(t-\tau)]$

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Abstract. We obtained sufficient conditions for all positive solutions of the equation in the title to oscillate about the positive equilibrium N^*. We also found sufficient conditions for the global attractivity of N^*.

1. Introduction. The scalar autonomous ordinary differential equation

$$\dot{N}(t) = rN(t)\left[1 - \frac{N(t)}{K}\right], \qquad r, K \in (0, \infty) \tag{1.1}$$

commonly known as the logistic equation is most frequently employed in modelling the dynamics of population of single species with $N(t)$ denoting the density (or biomass) of the population at time t. The per-capita growth rate in (1.1) is a linear function of the density N and this growth rate decreases as a linear function of the density. Equation (1.1) has occupied a position of central significance in formulating several multispecies models of interacting populations, especially Lotka-Volterra systems. An alternative to (1.1) has been proposed in the form

$$\dot{N}(t) = rN(t)\left[1 - \left(\frac{N(t)}{K}\right)^{\theta}\right], \qquad r, K, \theta \in (0, \infty) \tag{1.2}$$

by Gilpin and Ayala [4] in order to incorporate the effects of nonlinearity in the per-capita growth rates. While the per-capita growth rate in (1.2) is not linear (when $\theta \neq 1$), positive solutions of (1.2) converge monotonically to K as $t \to \infty$.

The logistic models (1.1) and (1.2) are based on the assumption that the density has a negative effect on the per-capita growth rate. However several species often cooperate among themselves in their search for food and to escape from predators. For instance some predators form hunting groups (packs, prides, etc.) to enable them to capture larger prey; fish and birds often form schools and flocks as a defense against predators; some parasitic insects aggregate so that they can overcome the defense mechanism of a host. A number of social species such as ants, termites, bees, humans, etc., have developed complex cooperative behavior involving division of labor, altruism, etc. Cooperative processes such as the above have a positive feedback

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influence since they provide individuals a greater chance to survive and reproduce as density increases. Moreover in sexual populations cooperation among individuals is necessary for mating, nest building, rearing the young, etc. Aggregation and associated cooperative and social characteristics among members of a species had been extensively studied in animal populations by Allee [1, 2] who had demonstrated what is now known as "Allee effect" in which reproduction rates of individuals decrease when density drops below a certain critical density; in other words, when the density is small, an increase in density enhances an individual's contribution to the average growth rate, an aspect which is not contained in the logistic models (1.1) and (1.2). The model (1.3) which is proposed below amply illustrates the viewpoint that an individual's reproductive potential attains a peak (maximum) at an intermediate level of density rather than at the minimum density as in (1.1) and (1.2). When the densities are not small, the positive feedback effects of aggregation and cooperation are dominated by density-dependent stabilizing negative feedback effects due to intraspecific competition due to excessive crowding and the ensuing shortage of resources; in other words intraspecific mutualism dominates at low densities and intraspecific competition dominates at higher densities (for details we refer to Watt [8]).

The purpose of this article is to propose a model of a single-species population exhibiting the Allee effect in which the per-capita growth rate is a quadratic function of the density and is subject to time delays. In particular we study the oscillatory and asymptotic behavior of the positive solutions of

$$\dot{N}(t) = N(t)[a + bN(t - \tau) - cN^2(t - \tau)] \qquad (1.3)$$

where $a, c \in (0, \infty)$, $b \in \mathbb{R}$ and $\tau \in [0, \infty)$. Let us briefly consider (1.3) with $\tau = 0$. If $a > 0$, $b < 0$, and $c = 0$, then (1.3) simplifies to one of type (1.1) and if $\tau = 0$ and $b = 0$, then (1.3) is of the type (1.2) with $\theta = 2$. Beyond the foregoing relevance of (1.3) in modelling the dynamics of a single-species population, one can interpret (1.3) as a single-species model with a quadratic per-capita growth rate and such a per-capita growth rate is a "first order" nonlinear approximation of more general types of plausible nonlinear growth rates with single humps.

In Sec. 2, we discuss the oscillations of all positive solutions of (1.3) about its positive equilibrium; also, we establish that all nonoscillatory positive solutions of (1.3) converge to the equilibrium as $t \to \infty$. In Sec. 3, we consider the asymptotic behavior of all oscillatory solutions and obtain sufficient conditions for the global attractivity of the positive equilibrium of (1.3). As special cases, our results will contain several results known for the usual delay-logistic equation

$$\dot{N}(t) = rN(t) \left(1 - \frac{N(t - \tau)}{K} \right), \qquad r, K, \tau \in (0, \infty) \qquad (1.4)$$

and we comment on this aspect in Sec. 4 below.

For a discussion concerning the importance of delays in the logistic equation see Hutchinson [6].

In the sequel we will consider only those solutions of (1.3) which correspond to initial functions of the form

$$N(t) = \varphi(t), \qquad -\tau \leq t \leq 0 \quad \text{with } \varphi \in C[[-\tau, 0], \mathbb{R}^+] \text{ and } \varphi(0) > 0. \qquad (1.5)$$

Clearly (1.3) and (1.5) have a unique solution which exists and is positive for all $t \geq 0$.

As is customary, a solution $N(t)$ of Eq. (1.3) is said to *oscillate* about N^* if the function $N(t) - N^*$ has arbitrarily large zeros.

2. Oscillations about the positive equilibrium. Consider the delay-differential equation (1.3) with

$$a, c \in (0, \infty), \qquad b \in \mathbb{R} \quad \text{and} \quad \tau \in [0, \infty). \tag{2.1}$$

Then Eq. (1.3) has a positive equilibrium N^* given by

$$N^* = \frac{b + \sqrt{b^2 + 4ac}}{2c}. \tag{2.2}$$

Set

$$N(t) = N^* e^{x(t)}.$$

Then

$$\dot{x}(t) - bN^*[e^{x(t-\tau)} - 1] + c(N^*)^2[e^{2x(t-\tau)} - 1] = 0 \tag{2.3}$$

and $N(t)$ oscillates about N^* if and only if $x(t)$ oscillates about zero.

The first lemma deals with the nonoscillatory solutions of Eq. (2.3).

LEMMA 2.1. Assume that condition (2.1) holds. Then every nonoscillatory solution of Eq. (2.3) tends to zero as $t \to \infty$.

Proof. Set

$$F(u) = cu^2 - bu - a$$

and observe that

$$F(u) > 0 \quad \text{for } u > N^* \tag{2.4}$$

and

$$F(u) < 0 \quad \text{for } 0 < u < N^*. \tag{2.5}$$

In view of (2.4) and (2.5), (2.3) yields that, eventually,

$$\dot{x}(t) < 0 \quad \text{if } x(t) > 0$$

and

$$\dot{x}(t) > 0 \quad \text{if } x(t) < 0.$$

It follows that every nonoscillatory solution of Eq. (2.3) tends to a finite limit ℓ as $t \to \infty$. Then, from (2.3) we find that

$$\lim_{t \to \infty}[\dot{x}(t)] = cN^{*2}[e^{2\ell} - 1] + bN^*[e^\ell - 1]$$
$$= F(N^* e^\ell).$$

Hence, ℓ must be zero, or else, in view of (2.4) and (2.5), $F(N^* e^\ell) \neq 0$ which implies that $|\ell| = \infty$. This contradiction completes the proof of the lemma.

THEOREM 2.1. Assume that condition (2.1) holds and

$$(2cN^* - b)N^*\tau > 1/e. \tag{2.6}$$

Then every positive solution of Eq. (1.3) oscillates about the positive equilibrium N^*.

Proof. It suffices to show that every solution of Eq. (2.3) oscillates about zero. Assume, for the sake of contradiction, that Eq. (2.3) has a nonoscillatory solution $x(t)$. Then, in view of Lemma 1

$$\lim_{t \to \infty} x(t) = 0.$$

We rewrite Eq. (2.3) in the form

$$\dot{x}(t) + \left[2c(N^*)^2 \frac{c^{2x(t-\tau)} - 1}{2x(t-\tau)} - bN^* \frac{e^{x(t-\tau)} - 1}{x(t-\tau)}\right] x(t-\tau) = 0$$

or

$$\dot{x}(t) + P(t)x(t-\tau) = 0 \tag{2.7}$$

where

$$\lim_{t \to \infty} P(t) = (2cN^* - b)N^* > 0.$$

Hence

$$\liminf_{t \to \infty} \int_{t-\tau}^{t} P(s)\,ds = (2cN^* - b)N^*\tau > \frac{1}{e}$$

and by Ladas [7] every solution of (2.7) oscillates. This is a contradiction and the proof is complete.

3. Global attractivity. In this section we derive sufficient conditions for all positive solutions of Eq. (1.3) to converge to the positive equilibrium N^* as $t \to \infty$.

The transformation

$$N(t) = N^*[1 + y(t)] \tag{3.1}$$

reduces Eq. (1.3) to

$$\dot{y}(t) = -A(t)y(t-\tau), \qquad t \geq 0 \tag{3.2}$$

where A (which depends on y) is given by

$$A(t) = [(2cN^* - b)N^* + c(N^*)^2 y(t-\tau)][1 + y(t)]. \tag{3.3}$$

As $N(t) > 0$, (3.1) implies that

$$y(t) > -1 \tag{3.4}$$

and from (3.3) we see that

$$A(t) \geq (cN^* - b)N^*[1 + y(t)] > 0. \tag{3.5}$$

It follows from (3.1) that

$$\lim_{t \to \infty} N(t) = N^* \quad \text{if and only if} \quad \lim_{t \to \infty} y(t) = 0.$$

First we will show that under the condition

$$cN^* - b > 0 \tag{3.6}$$

every nonoscillatory solution of Eq. (3.2) tends to zero as $t \to \infty$.

LEMMA 3.1. Assume that (2.1) and (3.6) hold. Then every nonoscillatory solution of Eq. (3.2) tends to zero as $t \to \infty$.

Proof. Assume that $y(t)$ is a nonoscillatory solution of Eq. (3.2). We will assume that $y(t)$ is eventually positive. The case where $y(t)$ is eventually negative [because of (3.4) and (3.5)] is similar and will be omitted. From Eq. (3.2) and because of (3.5) we see that eventually,

$$\dot{y}(t) < 0$$

and so

$$L \equiv \lim_{t \to \infty} y(t)$$

exists and is nonnegative. If $L > 0$ then

$$\lim_{t \to \infty} [\dot{y}(t)] = -[(2cN^* - b)N^* + c(N^*)L]L < 0$$

which implies that $y(t)$ is eventually negative. This is a contradiction and the proof is complete.

Next, we will show that under the condition (3.6) the oscillatory solutions of Eq. (3.2) have certain global lower and upper bounds. For simplicity we set

$$L = 2cN^* - b$$

and

$$M = [LN^* + c(N^*)^2(e^{LN^*\tau} - 1)](e^{LN^*\tau} - 1).$$

LEMMA 3.2. Assume that condition (2.1) holds and

$$cN^* - b > 0. \tag{3.7}$$

Let $y(t)$ be an oscillatory solution of Eq. (3.2). Then there exists a $T = T(y) > 0$ such that

$$e^{-M\tau} \le 1 + y(t) \le e^{LN^*\tau} \quad \text{for } t \ge T. \tag{3.8}$$

Proof. Let $2\tau \le t_1 < t_2 < \cdots$ be a sequence of zeros of $y(t)$ with $\lim_{n \to \infty} t_n = \infty$. Our strategy is to show that (3.8) holds in each interval (t_n, t_{n+1}). Let $\xi_n \in (t_n, t_{n+1})$ be a point where $y(t)$ obtains its maximum or its minimum in (t_n, t_{n+1}). It suffices to show that in either case

$$e^{-M\tau} \le 1 + y(\xi_n) \le e^{LN^*\tau}, \qquad n = 1, 2, \ldots. \tag{3.9}$$

As $\dot{y}(\xi_n) = 0$, it follows from (3.5) and (3.2) that $y(\xi_n - \tau) = 0$. Dividing both sides of (3.2) by $1 + y(t)$ and integrating from $\xi_n - \tau$ to ξ_n we obtain

$$\ln[1 + y(\xi_n)] = -\int_{\xi_n - \tau}^{\xi_n} [LN^* + c(N^*)^2 y(s - \tau)] y(s - \tau) \, ds \tag{3.10}$$

$$\le -\int_{\xi_n - \tau}^{\xi_n} LN^* y(s - \tau) \, ds$$

$$\le \int_{\xi_n - \tau}^{\xi_n} LN^* \, ds$$

$$= LN^* \tau.$$

This shows that

$$1 + y(\xi_n) \le e^{LN^*\tau}, \qquad n = 1, 2, \ldots$$

and so

$$1 + y(t) \le e^{LN^*\tau}, \qquad t \ge T. \tag{3.11}$$

Now returning to (3.10) and using (3.11) and the definition of M we find

$$-\ln[1 + y(\xi_n)] = \int_{\xi_n - \tau}^{\xi_n} [LN^* + c(N^*)^2 y(s - \tau)] y(s - \tau) \, ds$$
$$\le M\tau$$

which implies that

$$e^{-M\tau} \le 1 + y(\xi_n), \qquad n = 1, 2, \ldots.$$

The proof is complete.

An elementary consequence of (3.5) and (3.8) is that

$$A(t) \ge (cN^* - b)N^* e^{-M\tau} \quad \text{for } t \ge T. \tag{3.12}$$

On the other hand, (3.3) and (3.8) imply that

$$A(t) \le \widetilde{M} \quad \text{for } t \ge T \tag{3.13}$$

where

$$\widetilde{M} = [LN^* + c(N^*)^2(e^{LN^*\tau} - 1)]e^{LN^*\tau}. \tag{3.14}$$

The following result provides sufficient conditions for the global attractivity of the positive equilibrium N^* of Eq. (1.3).

THEOREM 3.1. Assume that conditions (2.1) and (3.6) hold and that

$$\widetilde{M}\tau < 1 \tag{3.15}$$

where $\widetilde{M}$ is defined by (3.14). Then all positive solutions of Eq. (1.3) satisfy

$$\lim_{t \to \infty} N(t) = N^*.$$

Proof. In view of (3.1) it suffices to show that for every solution $y(t)$ of (3.2) which satisfies (3.4),

$$\lim_{t \to \infty} y(t) = 0. \tag{3.16}$$

In Lemma 3.1 we proved that (3.16) holds for the nonoscillatory solutions of Eq. (3.2). It remains to show that (3.16) also holds for every oscillatory solution $y(t)$ of Eq. (3.2). To this end, we define the nonnegative function

$$v(y(t)) = \left[y(t) - \int_{t-\tau}^{t} A(s + \tau) y(s) \, ds \right]^2 + \int_{t-\tau}^{t} A(s + 2\tau) \left[\int_{s}^{t} A(u + \tau) y^2(u) \, du \right] ds \tag{3.17}$$

and observe that

$$\frac{d}{dt}[v(y(t))] = 2 \left[y(t) - \int_{t-\tau}^{t} A(s + \tau)y(s)\,ds \right] [-A(t + \tau)y(t)]$$

$$- A(t + \tau) \int_{t-\tau}^{t} A(u + \tau)y^2(u)\,du$$

$$+ \int_{t-\tau}^{t} A(s + 2\tau)A(t + \tau)y^2(t)\,ds$$

$$= -2A(t + \tau)y^2(t) + 2A(t + \tau) \int_{t-\tau}^{t} A(s + \tau)y(s)y(t)\,ds$$

$$- A(t + \tau) \int_{t-\tau}^{t} A(s + \tau)y^2(s)\,ds$$

$$+ A(t + \tau)y^2(t) \int_{t-\tau}^{t} A(s + 2\tau)\,ds. \tag{3.18}$$

Using the inequality

$$2y(t)y(s) \leq y^2(t) + y^2(s),$$

(3.18) yields

$$\frac{d}{dt}[v(y(t))] \leq -A(t + \tau)y^2(t) \left[2 - \int_{t-\tau}^{t} A(s + \tau)\,ds - \int_{t-\tau}^{t} A(s + 2\tau)\,ds \right]$$

which, in view of (3.13) and (3.5), gives

$$\frac{d}{dt}[v(y(t))] \leq -2(1 - \widetilde{M}\tau)A(t + \tau)y^2(t) < 0. \tag{3.19}$$

Integrating both sides of (3.19) we see that

$$v(y(t)) + 2(1 - \widetilde{M}\tau) \int_{T}^{t} A(s + \tau)y^2(s)\,ds \leq v(y(T))$$

where T is as in Lemma 3.2. Hence,

$$A(t + \tau)y^2(t) \in L^1[T, \infty) \tag{3.20}$$

and

$$\left[y(t) - \int_{t-\tau}^{t} A(s + \tau)y(s)\,ds \right]^2 \leq v(y(t)) \leq v(y(T)).$$

From this and (3.13) we find

$$|y(t)| \leq \widetilde{M} \int_{t-\tau}^{t} |y(s)|\,ds + [vy(T))]^{1/2}. \tag{3.21}$$

Set

$$\rho(t) = \max_{-\tau \leq s \leq t} |y(s)|.$$

Then from (3.21) and (3.15),

$$\rho(t) \leq \frac{[v(y(T))]^{1/2}}{1 - \widetilde{M}\tau}$$

which shows that $y(t)$ is bounded. As $A(t)$ is also bounded, it follows from (3.2) that $\dot{y}(t)$ is bounded. Hence $A(t+\tau)y^2(t)$ is uniformly continuous. This and (3.20) imply, by Barbalat's Lemma [3], that

$$\lim_{t\to\infty}[A(t+\tau)y^2(t)] = 0$$

and so by (3.12)

$$\lim_{t\to\infty} y(t) = 0.$$

The proof is complete.

4. Some remarks. The techniques proposed in Secs. 2 and 3 for the derivation of conditions respectively for the oscillation and asymptotic convergence as $t \to \infty$ of positive solutions of (1.3) can be easily modified to obtain the corresponding results for the delay-logistic equation (1.4); this can be done by assuming $a > 0$, $b < 0$, $c = 0$ in (1.3) and deriving the corresponding results. If this is done, it will be found that a sufficient condition for all positive solutions of (1.4) to oscillate about $K > 0$ is that $r\tau e > 1$ and a sufficient condition for all positive solutions of (1.4) to converge to K as $t \to \infty$ is that $r\tau e^{r\tau} < 1$. If the delay τ is sufficiently large, periodic solutions exist and this aspect is discussed by Gopalsamy [5].

It is well known that construction of positive definite Lyapunov functions and functionals for nonlinear equations is usually difficult. In Sec. 3 we have shown a simple way to overcome this difficulty (for a class of equations) by constructing a degenerate or Lyapunov-like functional which is not necessarily positive definite; this does not guarantee boundedness of solutions; but boundedness can be established by exploiting other properties of solutions. We conclude with the note that this technique is not restricted to scalar equations or equations with a single delay; this method can be used for vector matrix systems. A detailed application of this technique for such systems will be considered in a subsequent investigation.

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