EXISTENCE AND GLOBAL ATTRACTIVITY OF PERIODIC SOLUTION OF A MODEL IN POPULATION DYNAMICS

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Abstract

We establish sufficient conditions for the existence and global attractivity of the nonnegative periodic solution of an integro-differential equation which can be taken as a generalization of a model in describing the dynamics of Nicholson's blowflies. In particular, when the coefficients of the equation are constants, the result obtained reveals the threshold property of the equation.

Key words. Global attractivity, existence, periodic solution, population dynamics

1. Introduction

This article investigates the existence and global attractivity of the nonnegative periodic solution of the integro-differential equation

\[ \frac{dN(t)}{dt} = -\gamma(t)N(t) + \alpha(t) \int_{0}^{\infty} K(s)N(t-s)e^{-\beta(t)N(t-s)} ds, \quad t \geq 0, \]  

(1.1)

where \( \alpha(t), \beta(t) \) and \( \gamma(t) \) are positive continuous periodic functions on \([0, +\infty)\) with a positive period \( \omega \); \( K(s) : [0, \infty) \rightarrow [0, \infty) \) is assumed to be piecewise continuous, nonincreasing eventually and normalized such that

\[ \int_{0}^{\infty} K(s) ds = 1. \]  

(1.2)

The equation (1.1) is a generalization of the delay equation

\[ \frac{dN(t)}{dt} = -\gamma N(t) + \alpha N(t-\tau)e^{-\beta N(t-\tau)}, \quad t \geq 0, \]  

(1.3)

which was used by Gurney et al\(^2\) in describing the dynamics of Nicholson's blowflies. Here \( N(t) \) denotes the size of the population at time \( t \); \( \alpha \) is the maximum per capita daily egg production rate; \( 1/\beta \) is the size at which the population reproduces at its maximum rate; \( \gamma \)

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is the adult death rate per capita daily and $\tau$ is the generation time. Equations (1.1) and (1.3) are both models of population dynamics with delays in production, and the periodicity of $\alpha(t), \beta(t), \gamma(t)$ is based on the consideration of the periodic environment (e.g. seasonal effects of weather, mating habits etc.). If one chooses

$$K(s) = \delta(s - \tau), \quad \alpha(t) \equiv \alpha, \quad \beta(t) \equiv \beta, \quad \gamma(t) \equiv \gamma,$$

where $\delta(\cdot)$ is Dirac Delta function, $\alpha, \beta, \gamma$ are positive constants, then (1.1) will simplify to (1.3).

2. Estimates of solutions of (1.1)

In what follows, we always use the following expressions:

$$\alpha_0 = \min_{t \in [0, w]} \{\alpha(t)\}, \quad \alpha^0 = \max_{t \in [0, w]} \{\alpha(t)\};$$

$$\beta_0 = \min_{t \in [0, w]} \{\beta(t)\}, \quad \beta^0 = \max_{t \in [0, w]} \{\beta(t)\};$$

$$\gamma_0 = \min_{t \in [0, w]} \{\gamma(t)\}, \quad \gamma^0 = \max_{t \in [0, w]} \{\gamma(t)\}.$$

Note from the positivity of $\alpha(t), \beta(t)$ and $\gamma(t)$ that $\alpha_0 > 0, \beta_0 > 0, \gamma_0 > 0$. Together with (1.1), we shall consider a continuous initial function $\varphi$ so that

$$N(s) = \varphi(s) \geq 0, \quad s \in (-\infty, 0], \quad \varphi(0) > 0. \quad (2.1)$$

One can show that solutions of (1.1) and (2.1) remain positive and exist for $t \geq 0$, but we omit it.

We introduce the following Lemma 2.1 without proof.

Lemma 2.1. Assume that $N(t)$ is any positive solution of (1.1) with the initial function $\varphi$ such that

$$0 < \varphi(s) \leq \frac{\alpha^0}{\gamma_0 \beta_0 e} \triangleq n^0, \quad s \in (-\infty, 0].$$

Then $N(t)$ satisfies

$$0 < N(t) \leq n^0 \quad \text{for } t \in R.$$

For convenience, we introduce a function $h(x)$ as follows:

$$h(x) = xe^{-bx^2}, \quad x \geq 0.$$
Lemma 2.2. Assume that $N(t)$ is any positive solution of (1.1) and $\frac{\alpha}{\gamma} > 1$. Then there exists a $T > 0$ such that

$$N(t) \geq N_0 = \frac{1}{\alpha} \ln \frac{\alpha_0}{\gamma}$$

for $t \geq T$, (2.4)

where $a > 1$ is a constant satisfying (2.2) and (2.3).

Proof. Let $N(t)$ be any positive solution of (1.1). If (2.4) is not true, then there are two possibilities:

1. there is a $T_1 > 0$ so that $N(t) < N_0$ for $t \geq T_1$;
2. $N(t)$ oscillates about $N_0$.

We want to show that both (1) and (2) lead to contradictions, thus (2.4) is true.

Suppose that the first alternative holds. Consider a function

$$g(x) = \alpha_0 + \alpha_0 \exp(-\alpha x), \quad x > 0.$$ 

It is not difficult to see that

$$g(A) = 0 \quad \text{and} \quad g(x) > 0 \quad \text{for} \quad x \in (0, A).$$

Since $N(t) \in (0, N_0) \subset (0, A)$ for $t \geq T_1$, we have

$$g(N_0) = -\gamma^0 + \alpha_0 \exp(-\gamma^0 N_0) > 0.$$ 

Thus one can choose a $\delta > 0$ such that

$$0 < \eta \Delta \int_0^\sigma K(s) \, ds \leq 1, \quad -\gamma^0 + \alpha_0 \eta \exp(-\gamma^0 N_0) > 0.$$ 

By using the positivity of $N(t)$, we derive from (1.1) that

$$\frac{dN(t)}{dt} \geq -\gamma^0 N(t) + \alpha_0 \int_0^\infty K(s) N(t-s) \exp\{-\gamma^0 N(t-s)\} \, ds$$

$$\geq -\gamma^0 N(t) + \alpha_0 \int_0^\infty K(s) N(t-s) \exp\{-\gamma^0 N(t-s)\} \, ds.$$ 

There are three sub-possibilities:

1. $N(t)$ is decreasing eventually;
2. there is a sequence $\{t_n\}$ such that $t_n > 0$, $t_n \to \infty$ as $n \to \infty$ and $N(t_n)$ ($n = 1, 2, \cdots$) are local minimums;
3. $N(t)$ is increasing eventually.

Due to the property (ii) of $h(x)$, (2.7) and (2.8), it is easy to show that (a) is impossible.

Now we discuss case (b). Let $B = \lim \inf_{t \to \infty} N(t) \geq 0$. If $B = 0$, from the definition of lower limit and the positivity of $N(t)$, one can find a subsequence $\{t_{n_k}\}$ of $\{t_n\}$ such that

$$N(t_{n_k}) = \min\{N(t) \mid 0 \leq t \leq t_{n_k}\}$$

and $\lim_{k \to \infty} N(t_{n_k}) = 0$. Choosing some $t_{n_m} \in \{t_{n_k}\}$ so that $t_{n_m} > T_1 + \sigma$, then we have

$$N(t_{n_m}) = \min\{N(t) \mid t_{n_m} - \sigma \leq t \leq t_{n_m}\}.$$
We derive from (2.8), (2.10), (2.7) and the monotonicity of $h(x)$ that

\[
0 = \frac{d}{dt} N(t_{nm}) \geq N(t_{nm}) \left[ -\gamma^0 + \alpha_0 \eta \exp \{-\beta^0 N(t_{nm})\} \right] \\
\geq N(t_{nm}) \left[ -\gamma^0 + \alpha_0 \eta \exp \{-\beta^0 N_0\} \right] > 0,
\]

which is impossible. Thus we obtain

\[
B = \liminf_{t \to \infty} N(t) = \liminf_{n \to \infty} N(t_n) > 0, \tag{2.11}
\]

and (1) implies that $B \leq N_0$. Noting that

\[
-\gamma^0 B + \alpha_0 \eta B \exp \{-\beta^0 B\} \geq B \left( -\gamma^0 + \alpha_0 \eta \exp \{-\beta^0 N_0\} \right) > 0, \tag{2.12}
\]

this, together with the continuity of $x(-\gamma^0 + \alpha_0 \eta \exp \{-\beta^0 x\})$, means that we can find a small $\varepsilon_0 > 0$ such that $B - \varepsilon_0 > 0$ and

\[
-\gamma^0 (B + \varepsilon_0) + \alpha_0 \eta (B - \varepsilon_0) \exp \{-\beta^0 (B - \varepsilon_0)\} > 0. \tag{2.13}
\]

For such an $\varepsilon_0 > 0$ we know from the definition of lower limit and (2.11) that there exist a $T_3 > T_1 + \sigma$ and a subsequence $\{t_{nm}\}$ of $\{t_n\}$ such that

\[
N(t) > B - \varepsilon_0 \quad \text{for } t \geq T_3 \quad \text{and} \quad N(t_{nm}) < B + \varepsilon_0 \quad \text{for } k = 1, 2, \ldots. \tag{2.14}
\]

Note that $B - \varepsilon_0 < N(t) \leq N_0 < \frac{1}{\beta^0}$, $t \geq T_3$, and $h(x)$ is increasing in $(0, \frac{1}{\beta^0})$. We derive from (2.8), (2.13) and (2.14) that

\[
0 = \frac{d}{dt} N(t_{nm}) \geq -\gamma^0 N(t_{nm}) + \alpha_0 \int_0^\sigma K(s) N(t_{nk} - s) \exp \{-\beta^0 N(t_{nk} - s)\} ds \\
\geq -\gamma^0 (B + \varepsilon_0) + \alpha_0 \eta (B - \varepsilon_0) \exp \{-\beta^0 (B - \varepsilon_0)\} > 0 \tag{2.15}
\]

if $t_{nk} > T_3 + \sigma$. This is a contradiction. Thus case (b) is impossible.

Finally, for case (c) we suppose that there is a $T_4 > 0$ such that $N(t)$ is increasing for $t \geq T_4$. From (1) we have that $\lim_{t \to \infty} N(t)$ exists and

\[
0 < C \overset{\Delta}{=} \lim_{t \to \infty} N(t) \leq N_0. \tag{2.16}
\]

By a derivation procedure similar to that in (2.13) we have $C - \varepsilon_1 > 0$ and

\[
-\gamma^0 C + \alpha_0 \eta (C - \varepsilon_1) \exp \{-\beta^0 (C - \varepsilon_1)\} > 0 \tag{2.17}
\]

for some small $\varepsilon_1 > 0$. For such an $\varepsilon_1 > 0$, there exists a $T_5 \geq T_4$ such that

\[
C - \varepsilon_1 < N(t) \leq C \leq N_0 < \frac{1}{\beta^0} \quad \text{for } t \geq T_5. \tag{2.18}
\]

Thus we get

\[
\frac{dN(t)}{dt} \geq -\gamma^0 N(t) + \alpha_0 \int_0^\sigma K(s) N(t - s) \exp \{-\beta^0 N(t - s)\} ds \\
\geq -\gamma^0 C + \alpha_0 \eta (C - \varepsilon_1) \exp \{-\beta^0 (C - \varepsilon_1)\} > 0, \tag{2.19}
\]
for $t \geq T_5 + \sigma$ from (2.8), (2.17), (2.18) and the monotonicity of $h(x)$. (2.19) implies that 
\[ \lim_{t \to \infty} N(t) = +\infty, \] 
which contradicts (1). Thus case (c) is false.

In summary, we conclude from the above discussion that case (1) is impossible.

Next, suppose $N(t)$ oscillates about $N_0$. Then there exists a sequence $\{t_n\}$, $t_n > 0$, \[ \lim_{t \to \infty} t_n = +\infty \] 
such that $N(t_n) \leq N_0$ ($n = 1, 2, \cdots$) are local minimums. Furthermore, we have
\[ E \triangleq \lim_{t \to \infty} \inf N(t) = \lim_{n \to \infty} \inf N(t_n) \leq N_0. \]
On the other hand, we can show by an argument similar to that in Lemma 2.1 that there is a $T_9 > 0$ such that 
\[ N(t) \leq n^0 \quad \text{for} \quad t \geq T_9, \]
which together with (2.2), (2.3) and the properties (ii), (iv) of $h(x)$ can lead to a conclusion that
\[ h(N(t - s)) > h(N(t)) \quad (2.20) \]
if there is some $t$ satisfying $t \geq T_9 + \sigma$ and 
\[ N(t) = \min \{ N(s) \mid t - \sigma < s < t \} \quad \text{and} \quad N(t) \leq N_0. \]

Now we can show from (2.8) and (2.20) that $E > 0$ by an argument similar to that in situation (1)-(b) which shows that $B > 0$, but we omit the details.

Replacing $B, T_3$ by $E, T_7$ ($T_7 \geq T_9$) from (2.11) to (2.15) respectively, we obtain a contradiction which says that case (2) is impossible. Thus we complete the proof.

3. Existence of Nonnegative Periodic Solution of (1.1)

The following lemma changes the existence problem of periodic solution of (1.1) into the same problem of another equation with finite delay.

**Lemma 3.1.** Any $\omega$-periodic solution $P(t)$ of (1.1) is also an $\omega$-periodic solution of the following equation
\[ \frac{dN(t)}{dt} = -\gamma(t)N(t) + \alpha(t) \int_0^\omega H(s)N(t - s)e^{-\beta(t)g(t-s)}\,ds, \quad t \geq 0, \quad (3.1) \]
where $H(s) = \sum_{r=0}^\infty K(s + r\omega), s \in [0, \omega]$, and vice versa.

**Lemma 3.2.** There exists an $\omega$-periodic solution $P(t)$ of (3.1) such that $0 \leq P(t) \leq n^0$ for $t \geq 0$.

A proof of a lemma similar to Lemma 3.1 can be found in [5]. The proof of Lemma 3.2 is completed by showing that solutions of (3.1) are uniformly bounded and uniformly ultimately bounded (for instance see [3, p.120]), and by using Theorem 37.1 in [4].

**Lemma 3.3.** Assume that $\frac{\omega}{\sigma} > 1$. Then there exists a positive $\omega$-periodic solution $P^*(t)$ of (3.1) such that $N_0 \leq P^*(t) \leq n^0$ for $t \geq 0$.

**Proof.** We have from (3.1) that
\[ \frac{dN(t)}{dt} \geq -\gamma^0N(t) + \alpha_0 \int_0^\omega H(s)N(t - s)e^{-\beta^0g(t-s)}\,ds. \quad (3.2) \]
In proving Lemma 2.2, by replacing $\eta, \sigma, K(s)$ by $1, \omega, H(s)$ respectively, we can obtain that there is a $T \geq 0$ such that all positive solutions of (3.1) satisfy
\[ N(t) \geq N_0 \quad \text{for} \quad t \geq T. \quad (3.3) \]
On the other hand, one can show that
\[ N_0 \leq N(t) \leq n^0 \quad \text{for } t \geq 0 \quad (3.4) \]
if the initial function \( \psi(s) \) satisfies
\[ N_0 \leq \psi(s) \leq n^0 \quad \text{for } s \in [-\omega, 0]. \quad (3.5) \]
That is to say, \( I_1 = [N_0, n^0] \) is an invariant set of equation (3.1). Now we derive from (3.3) and (3.4) that all of the positive solutions of (3.1) are uniformly ultimately bounded with a lower bound \( N_0 \). Combining this with the conclusion of Lemma 3.2, we know that (3.1) must have a positive periodic solution \( P^*(t) \) lying in \( I_1 = [N_0, n^0] \). The proof is complete.

Now we can state the following theorems from Lemma 3.1-3.3.

**Theorem 3.4.** There exists a nonnegative \( \omega \)-periodic solution \( P(t) \) of equation (1.1) such that \( 0 \leq P(t) \leq n^0 \) for \( t \geq 0 \).

**Theorem 3.5.** Assume that \( \alpha_0/\gamma_0 > 1 \). Then there exists a positive \( \omega \)-periodic solution \( P^*(t) \) of (1.1) such that \( N_0 \leq P^*(t) \leq n^0 \) for \( t \geq 0 \).

4. Global Attractivity

In this section we investigate the global attractivity of the periodic solution \( P(t) \) or \( P^*(t) \).

**Theorem 4.1.** Assume that
\[ \int_0^\infty sK(s) \, ds < \infty \quad (4.1) \]
and \( \gamma_0 > \alpha_0 \). Then all positive solutions \( N(t) \) of (1.1) satisfy
\[ \lim_{t \to \infty} N(t) = 0. \quad (4.2) \]

**Proof.** Suppose that \( N(t) \) is any positive solution of (1.1). Define a Lyapunov functional \( V(t) = V(N(t)) \) as follows:
\[ V(t) = |N(t)| + \int_0^\infty K(s) \left[ \int_{t-s}^t \alpha(u+s) |N(u)| \exp \{-\beta(u+s)N(u)\} \, du \right] \, ds. \quad (4.3) \]
Calculating the upper right derivative of \( V \) along the positive solutions of (1.1), we can obtain the conclusion of the theorem, but we omit the details.

**Remark.** Under the assumption of Theorem 4.1 we know that \( N(t) \equiv 0 \) is the only periodic solution of (1.1), i.e., (1.1) has no any positive periodic solution.

**Theorem 4.2.** Assume that (4.1) holds and
\[ \gamma_0 < \alpha_0 \leq \alpha^0 < \frac{\gamma_0}{F}, \quad (4.4) \]
where \( F = \max\{e^{-2}, 1 - \beta_0 N_0\} \). Then there exists a unique positive periodic solution \( P^*(t) \) of (1.1) such that any positive solution \( N(t) \) of (1.1) satisfies
\[ \lim_{t \to \infty} [N(t) - P^*(t)] = 0. \]
Proof. Let 

$$Y(t) = N(t) - P^*(t), \quad t \in \mathbb{R}.$$ 

It is found from (1.1) that $Y(t)$ satisfies

$$\frac{dY(t)}{dt} = -\gamma(t)Y(t) + \alpha(t) \int_0^\infty K(s) \left[ N(t - s) \exp \left\{ -\beta(t)N(t - s) \right\} - P^*(t - s) \exp \left\{ -\beta(t)P^*(t - s) \right\} \right] ds, \quad t \geq 0.$$ 

Consider a Lyapunov functional $V(t) = V(Y)(t)$ as follows:

$$V(t) = |Y(t)| + \int_0^\infty K(s) \left( \int_{t-s}^t \alpha(u) \left[ N(u) \exp \left\{ -\beta(u + s)N(u) \right\} - P^*(u) \exp \left\{ -\beta(u + s)P^*(u) \right\} \right] du \right) ds.$$ 

We obtain

$$D^+V(t) \leq -\gamma(t)|Y(t)| + \int_0^\infty K(s) \alpha(t + s) \left| N(t) \exp \left\{ -\beta(t + s)N(t) \right\} - P^*(t) \exp \left\{ -\beta(t + s)P^*(t) \right\} \right| ds$$

$$= -\gamma(t)|Y(t)| + \int_0^\infty K(s) \alpha(t + s) \left| \exp \left\{ -\theta(t, s) \right\} \left( 1 - \theta(t, s) \right) \right| \beta(t + s) Y(t) ds,$$

where $\theta(t, s)$ lies between $\beta(t + s)P^*(t)$ and $\beta(t + s)N(t)$. We have from the conclusion of Lemma 2.2 that

$$N(t) > N_0 \quad \text{for} \quad t \geq T,$$

where $T > 0$ is as in Lemma 2.2. Thus

$$\theta(t, s) > \beta_0 N_0 \quad \text{for} \quad t \geq T, \quad s \geq 0. \quad (4.6)$$

Define a function $f(x)$ as follows:

$$f(x) = e^{-x}(1 - x), \quad x \geq 0.$$ 

It is known that

(i) $\max_{x \geq 0} \{ f(x) \} = 1$, $\min_{x \geq 0} \{ f(x) \} = -e^2$, $0 \leq f(x) \leq 1 - x$ for $x \in [0, 1]$;

(ii) $f(x)$ is decreasing for $x \in [0, 2]$;

(iii) $f(x)$ is increasing for $x \geq 2$.

Since

$$f(\beta_0 N_0) = \exp\{ -\beta_0 N_0 \}(1 - \beta_0 N_0) \leq 1 - \beta_0 N_0$$

when $\beta_0 N_0 \leq 1$, by using the properties of $f(x)$ we obtain

$$|f(x)| \leq \max\{ e^{-2}, 1 - \beta_0 N_0 \} \Delta F \quad (4.7)$$
when \( x \geq \beta_0 N_0 \). We derive from (4.5)-(4.7) that
\[
D^+ V(t) < -\gamma_0 |Y(t)| + \alpha^0 F|Y(t)| = (-\gamma_0 + \alpha^0 F)|Y(t)| < 0 \quad \text{for } t \geq T.
\]
By a derivation procedure similar to that in the proof of Theorem 4.1, we can obtain
\[
\lim_{t \to \infty} Y(t) = 0.
\]
Thus the proof is complete.

**Corollary 4.3.** Assume that \( \int_0^\infty sK(s) \, ds < \infty \) and \( \alpha(t) \equiv \alpha, \beta(t) \equiv \beta, \gamma(t) \equiv \gamma \), where \( \alpha, \beta \) and \( \gamma \) are positive constants. Then the following conclusions hold.

(i) All positive solutions \( N(t) \) of (1.1) satisfy
\[
\lim_{t \to \infty} N(t) = 0,
\]
when \( \gamma > \alpha \);

(ii) All positive solutions \( N(t) \) of (1.1) satisfy
\[
\lim_{t \to \infty} N(t) = P^*,
\]
when \( \gamma < \alpha < \frac{\gamma_0}{\beta} \), where \( P^* = \frac{1}{\beta} \ln \frac{\alpha}{\gamma} \), \( F = \max \{e^{-\gamma}, 1 - \frac{1}{\alpha} \ln \frac{\alpha}{\gamma} \} \), constant \( \alpha > 1 \) satisfying
\[
\frac{1}{\alpha} \ln \frac{\alpha}{\gamma} < \min \left\{ 1, \frac{\alpha}{\gamma} \right\}, \quad \frac{1}{\alpha} \exp \left\{ 1 + \frac{\alpha}{\gamma} \right\} \ln \frac{\alpha}{\gamma} \leq \left( \frac{\alpha}{\gamma} \right)^{1+1/\alpha}.
\]

It can be seen from Corollary 4.3 that for the case of constant coefficients and infinite delay, the result of this paper reveals the threshold property of the equation: If a certain quantity involving the coefficients is negative, the origin is stable; while when the same quantity becomes positive, a unique globally attractive positive equilibrium appears and persists as long as another expression of the coefficients is negative. It is well known that the system
\[
\frac{dn(t)}{dt} = -\gamma n(t)
\]
is a dissipative system. Hence our result is of significance that a delay induced Hopf type bifurcation to a positive equilibrium is possible and this can be used for devising population control and stabilization strategies.

A more extensive generalization of (1.3) involving continuously distributed delays over an unbounded interval is the equation of the form
\[
\frac{dN(t)}{dt} = -\gamma(t)N(t) + \alpha(t) \int_0^\infty K(s)G(N(t - s), t) \, ds, \quad t \geq 0,
\]
where \( G(x, t) \) denotes a suitable growth rate function, but we do not discuss it in this paper.

References