GLOBAL POPULATION DYNAMICS OF A SINGLE SPECIES STRUCTURED WITH DISTINCTIVE TIME-VARYING MATURATION AND SELF-LIMITATION DELAYS

CHUANGXIA HUANG AND LIHONG HUANG

School of Mathematics and Statistics
Hunan Provincial Key Laboratory of Mathematical Modeling and Analysis in Engineering
Changsha University of Science and Technology, Changsha, 410114, China

JIANHONG WU*  
Laboratory for Industrial and Applied Mathematics, Department of Mathematics and Statistics
York University, Toronto, M3J 1P3, Canada

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ABSTRACT. We consider the classical Nicholson’s blowflies model incorporating two distinctive time-varying delays. One of the delays corresponds to the length of the individual’s life cycle, and another corresponds to the specific physiological stage when self-limitation feedback takes place. Unlike the classical formulation of Nicholson’s blowflies equation where self-regulation appears due to the competition of the productive adults for resources, the self-limitation of our considered model can occur at any developmental stage of an individual during the entire life cycle. We aim to find sharp conditions for the global asymptotic stability of a positive equilibrium. This is a significant challenge even when both delays are held at constant values. Here, we develop an approach to obtain a sharp and explicit criterion in an important situation where the two delays are asymptotically apart. Our approach can be also applied to the non-autonomous Mackey-Glass equation to provide a partial solution to an open problem about the global dynamics.

1. Introduction. Several important classes of infinite dimensional dynamical systems arising from biological and medical sciences are special cases of the following general scalar delay differential equation

\[ x'(t) = \sum_{k=1}^{m} F_k(t, x(t - \tau_1(t)), \ldots, x(t - \tau_l(t))) - G(t, x(t)), \quad (1) \]

where \( G \) is a continuous function of time variable \( t \in \mathbb{R} \) and the state variable \( x \in [0, +\infty) \), that describes the instantaneous mortality rate; and each \( F_k(t, y_1, \ldots, y_l) \) with \( 1 \leq k \leq m \) (\( m \) and \( l \) being given positive integers) is a continuous function of \( t \) and the variable \((y_1, \ldots, y_l) \in [0, +\infty) \times \cdots \times [0, +\infty) \), that describes the

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* Corresponding author: Jianhong Wu.
feedback controls depending on the values of the stable variable with respective delays $\tau_1(t), \cdots, \tau_l(t)$ \cite{1, 2, 3, 4}. Well-known examples include the generalized Nicholson’s blowflies equation from population dynamics

$$x'(t) = \sum_{k=1}^{m} a_k(t)x(t - h_k(t))e^{-\lambda_k x(t-g_k(t))} - b(t)x(t);$$

(2)

and the generalized Mackey-Glass equation from physiological control

$$x'(t) = \sum_{k=1}^{m} a_k(t)x(t - h_k(t)) - \left(b(t) - \frac{c(t)}{1 + x^n(t)}\right)x(t)$$

(3)

with appropriate time lag as continuous and nonnegative functions $h_k(t)$ and $g_k(t)$. These classical examples and their variations have been extensively studied in terms of the existence of biologically meaningful and experimentally observable solutions (stable positive equilibria and/or periodic solutions, for example), persistence/permanence, nonlinear oscillations, and global attractivity of the aforementioned biologically meaningful and experimentally observable solutions (see, for example, \cite{2, 3, 4, 24, 15} and references therein). In particular, Bereznysky and Braverman showed that two or more distinctive delays appearing in the same nonlinear feedback function $F_k$ (even when $k = 1$) can lead to chaotic oscillations, and that the involvement of two distinctive delays can produce sustainable oscillations which can not take place when the two delays are identical \cite{1}. Results on explicit and sharp sufficient conditions on the global attractivity of biologically important solutions are very scarce, with one exception \cite{1} where the global stability of the following delayed Mackey-Glass equation,

$$x'(t) = \beta(t) \left[ ax(t - h(t)) \right. - \left. x(t) \right], \quad a > 1, \nu > 0,$$

(4)

was established under some additional technical conditions on the delay terms. The approach developed is not generic enough to cover other similar delayed systems such as the following

$$x'(t) = \beta(t)\left[ Px(t - h(t))e^{-ax(t-g(t))} - \delta x(t) \right], \quad t \geq t_0,$$

(5)

where $a, \delta, P \in (0, +\infty)$ and $t_0 \in \mathbb{R}$ are all constants, $\beta, g, h : [t_0, +\infty) \rightarrow (0, +\infty)$ are continuous functions with $P > \delta$ and

$$0 < \beta^- = \inf_{t \in [t_0, +\infty)} \beta(t) \leq \sup_{t \in [t_0, +\infty)} \beta(t) = \beta^+ < +\infty.$$

The global attractivity of the positive equilibrium was posed as an open problem (Open Problem in \cite{1}).

In the formulation for the blowflies equation, $x(t)$ represents the population size, $\delta \beta(t)$ denotes the adult death rate, $1/a$ represents the size at which the population reproduces at its maximum rate, and $\beta(t)Px(t - h(t))e^{-ax(t-g(t))}$ is the birth rate function depending on delays $h(t)$ and $g(t)$, where $g(t)$ represents the developmental or maturation time whereas $h(t)$ represents the lag when the competition of individuals at the corresponding stage has impact on the survival and/or reproduction of the individual during this stage or in subsequent stages. When $h(t) = g(t)$, we have this self-limitation occur at the reproduction stage.

We remark here that the appearance of $\beta$ as a factor in front of the term $[Px(t - h(t))e^{-ax(t-g(t))} - \delta x(t)]$ is quite natural if we derive this delay differential equation using a structured population model. Namely, if we use $u(t, s)$ to denote the density
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of the population with respect to the age-variable \( s \), and if an individual starts to reproduce after it reaches the age \( h \), then

\[
x(t) = \int_h^{+\infty} u(t, s) \, ds.
\]

If the population dynamics is governed by

\[
\left( \frac{\partial}{\partial t} + \frac{\partial}{\partial s} \right) u(t, s) = -\mu(s)u(t, s), \quad s \geq 0
\]

subject to the boundary condition

\[
u(t, 0) = R(x(t)),
\]

and if the death rate \( \mu(s) \) for \( s \geq h \) is a constant (\( \mu(s) = \delta > 0 \) for \( s \geq h \)), then differentiating \( x(t) = \int_h^{+\infty} u(t, s) \, ds \) gives \( \dot{x}(t) = -\delta x(t) + u(t, h) \) and then integration along the characteristics for the evolution equation of the immature populations yields

\[
x'(t) = -\delta x(t) + \rho R(x(t - h)),
\]

with \( \rho \) for the survival probability of the immature individuals during the maturation process. Appropriate choices of the function \( R \) then give the Nicholson’s blowflies equation and the Mackey-Glass equation. If \( h(t) \) is time-dependent, then differentiating \( x(t) = \int_h^{+\infty} u(t, s) \, ds \) yields

\[
x'(t) = \beta(t) \left[ -\delta x(t) + \rho R(x(t - h(t))) \right],
\]

with \( \beta(t) = 1 - h'(t) \).

Note that the non-autonomous equation derived in this way keeps the positive equilibrium unchanged. Note also that in the original form of the Nicholson’s blowflies equation, the delay \( g \) is the same as \( h \) so the reduction of the reproduction is induced by the crowding of the matured population. In other applications, the self-limitation of the species growth may occur in different stages during the life-cycle, for example, in the entire life cycle (that involves egg, larvae, nymph and adult stages) of ticks for a wide range of tick-borne diseases such as Lyme disease, the self-limitation may due to the crowding effect of nymph ticks feeding on the same host and the higher tick loads the larger the host grooming rate and the smaller the tick attaching success [23]. In this case, the self-limitation term in the aforementioned generalized Nicholson’s blowflies equation appears in the format of \( \exp(-ax(t - g(t))) \) with \( g(t) \) strictly less than the maturation delay \( h(t) \).

Though non-autonomous Nicholson’s blowflies model incorporating a single time-varying delay has been extensively studied in the literature (see [7, 10, 22, 20, 19, 5], to name a few), the global behaviors of solutions for the non-autonomous Nicholson’s blowflies model incorporating multiple time lags have been recognized to be challenging and less have been achieved. A recent study reported in [8], the authors employed the classical method of decomposing and embedding to establish some criteria on the global attraction of a positive equilibrium for the autonomous model with two constant delays

\[
x'(t) = -\delta x(t) + \delta F(x(t - \sigma), x(t - \tau)),
\]

with \( \delta, \sigma, \tau \in [0, +\infty) \) and \( \sigma \leq \tau \), while the work by [9] established the permanence for the non-autonomous equation with two constant delays

\[
x'(t) = \alpha(t)H(x(t - \sigma), x(t - \tau)) - \beta(t)f(x(t)).
\]

To our best knowledge, there is no available result on the global attractivity of (5), so the open problem by Berezansky and Braverman remains unsolved.
2. Preliminary results. Denote $\tau = \max\{\tau_1, \tau_2\}$ and $r = \min\{r_1, r_2\}$, where

\[
\tau_1 = \sup_{t \in [t_0, +\infty)} h(t), \tau_2 = \sup_{t \in [t_0, +\infty)} g(t), r_1 = \inf_{t \in [t_0, +\infty)} h(t), r_2 = \inf_{t \in [t_0, +\infty)} g(t).
\]

In the sequel, it is always assumed that $r > 0$.

The Banach space of continuous functions from $[-\tau, 0]$ to $\mathbb{R}$ equipped with the supremum norm $|| \cdot ||$ denoted by $C([\tau, 0], \mathbb{R})$, and

\[
C_+ = \{ \varphi \in C | \varphi(\theta) \geq 0 \text{ for } \theta \in [-\tau, 0] \}.
\]

For $t_0 \in \mathbb{R}$ and $\sigma > 0$, if $x$ is a continuous function from $[t_0 - \tau, t_0 + \sigma)$ into $\mathbb{R}$, then for $t_0 \leq t < t_0 + \sigma$, we define $x_t \in C$ by $x_t(\theta) = x(t + \theta)$ for $\theta \in [-\tau, 0]$.

With the biological applications in mind, we consider (5) with the initial condition

\[
x_{t_0} = \varphi \in C_+ \text{ and } \varphi(0) > 0.
\]

By the standard theory in functional differential equations, this initial value problem has a unique solution on $[t_0 - \tau, +\infty)$, denoted by $x_t(t_0, \varphi)$ or $x(t; t_0, \varphi)$.

**Lemma 2.1.** $x(t; t_0, \varphi) > 0$ for all $t \in [t_0, +\infty)$.

**Proof.** The proof is straight forward, using the variation-of-constants formula to the equation on subsequent intervals $[t_0, t_0 + r], [t_0 + r, t_0 + 2r], [t_0 + 2r, t_0 + 3r], \cdots.$

**Lemma 2.2.** Suppose

\[
\delta - P^2 \beta^+ \limsup_{t \to +\infty} |h(t) - g(t)| > 0.
\]

Then the solution $x(t) = x(t; t_0, \varphi)$ is bounded above.

**Proof.** By way of contradiction, suppose that $x(t)$ is not bounded above. For $t \geq t_0$, define $M(t) = \max\{\xi \in [t_0 - \tau, t] : x(\xi) = \max_{t_0 - \tau \leq s \leq t} x(s)\}$. Then $\lim_{t \to +\infty} M(t) = +\infty$. Let $T^* \geq t_0$ be such that $M(t) \geq t_0 + \tau$ for $t \geq T^*$. Since $\delta - P^2 \beta^+ \limsup_{t \to +\infty} |h(t) - g(t)| > 0$, we choose $\varepsilon > 0$ small enough so that

\[
\delta - P^2 \beta^+ (\varepsilon + \limsup_{t \to +\infty} |h(t) - g(t)|) > 0.
\]

For this $\varepsilon$, there exists $T^{**} \geq T^*$ such that

\[
|h(t) - g(t)| < \limsup_{t \to +\infty} |h(t) - g(t)| + \varepsilon \quad \text{for } t \geq T^{**}.
\]
Note that for \( t \geq t_0 \), according to (5), we have \( |x'(t)| \leq P\beta^+ x(M(t)) \) as \( P > \delta \). This, combined with (5) and the fact that \( \sup_{w \geq 0} we^{-w} = \frac{1}{t} \), gives us

\[
0 \leq x'(M(t)) = \beta(M(t)) \left[ -\delta x(M(t)) + P x(M(t) - h(M(t))) e^{-ax(M(t) - g(M(t)))} \right]
\]

\[
\leq \beta(M(t)) \left[ -\delta x(M(t)) + P x(M(t) - g(M(t))) e^{-ax(M(t) - g(M(t)))} \right] + \beta(M(t)) P \frac{\left| x(M(t) - h(M(t))) - x(M(t) - g(M(t))) \right| e^{-ax(M(t) - g(M(t)))}}{ae}
\]

\[
\leq -\beta(M(t)) \left[ \delta - P^2 \beta^+ \sup_{t\in[T^*,+\infty]} |h(t) - g(t)| \right] x(M(t)) + \frac{P \beta(M(t))}{ae}
\]

and hence

\[
0 < x(M(t)) < \frac{P}{\delta - P^2 \beta^+ \left( \sup_{t\to+\infty} |h(t) - g(t)| + \varepsilon \right)} \] for \( M(t) \geq T^* \),

which contradicts the assumption of unboundedness. This finishes the proof. \( \square \)

3. Global attractivity of the positive equilibrium. In what follows, we assume \( P > \delta \). Clearly, (5) has two equilibria 0 and \( N^* = \frac{1}{a} \ln \frac{P}{\delta} (> 0) \). In this section, we study the global attractivity of \( N^* \) by starting with the asymptotical behavior of solutions which are not oscillatory about \( N^* \).

Lemma 3.1. If \( x(t; t_0, \varphi) - N^* \) is eventually non-positive, then \( \lim_{t\to+\infty} x(t; t_0, \varphi) = N^* \).

Proof. For simplicity, denote \( x(t; t_0, \varphi) \) by \( x(t) \). We claim that \( \liminf_{t\to+\infty} x(t) = l > 0 \). Otherwise \( l = 0 \). Choose \( T \geq t_0 + \tau \) such that

\[
x(t) - N^* \leq 0 \quad \text{for all } t \geq T.
\]

For each \( t \geq T \), define

\[
m(t) = \min\{\xi \in [T, t] : x(\xi) = \min_{T \leq s \leq t} x(s)\}.
\]

It follows from \( l = 0 \) and \( x([t_0 + r_1, +\infty)) \subset (0, +\infty) \) that

\[
\lim_{t\to+\infty} m(t) = +\infty, \quad \lim_{t\to+\infty} x(m(t)) = 0,
\]

and

\[
x(m(t) - h(m(t))) > x(m(t)) > 0 \quad \text{for any } m(t) > T + 2\tau.
\]
From the definition of $m(t)$, for $t \geq T + 2\tau$, we get

\[
0 \geq x'(m(t))
= \beta(m(t))[-\delta x(m(t)) + P x(m(t) - h(m(t)))e^{-ax(m(t)) - g(m(t))}]
\geq \beta(m(t))[x(m(t))(-\delta + Pe^{-aN^*})]
= 0,
\]
a contradiction. This completes the proof.

Now we show $\limsup_{t \to +\infty} x(t) = N^*$ by using the fluctuation lemma [17, Lemma A.1]. By the fluctuation lemma, one can find a sequence $\{t_k\}_{k \geq 1}$, such that

\[
t_k \to +\infty, \quad x(t_k) \to l, \quad x'(t_k) \to 0 \quad \text{as} \quad k \to +\infty.
\]
Moreover, from the boundedness of $\{\beta(t_k]\}_{k \geq 1}$, without loss of generality, we can assume that $\lim_{k \to +\infty} \beta(t_k)$ exists and $\lim_{k \to +\infty} \beta(t_k) \geq \beta^- > 0$. Thus

\[
0 = \lim_{k \to +\infty} x'(t_k)
= \lim_{k \to +\infty} \beta(t_k) \lim_{k \to +\infty} [-\delta x(t_k) + P x(t_k - h(t_k)))e^{-ax(t_k - g(t_k))}]
= \lim_{k \to +\infty} \left[\left[-\delta + Pe^{-a \limsup_{t \to +\infty} x(t)}\right] \lim_{k \to +\infty} \beta(t_k)\right].
\]

This implies that $\limsup_{t \to +\infty} x(t) \geq N^*$. As $\limsup_{t \to +\infty} x(t) \leq N^*$, we get $\limsup_{t \to +\infty} x(t) = N^*$.

To complete the proof, we only need to prove $\liminf_{t \to +\infty} x(t) \geq N^*$. For any $\varepsilon \in (0, l)$, we can choose $\bar{T} > T$ such that $x(t) > l - \varepsilon$ for all $t \geq \bar{T}$. Then, for $t \geq \bar{T} + \tau$, one has

\[
\left(x(t)e^{\int_0^t \delta \beta(v)dv}\right)' = e^{\int_0^t \delta \beta(v)dv} P \beta(t)x(t - h(t))e^{-ax(t - g(t))}
\geq e^{\int_0^t \delta \beta(v)dv} P \beta(t)[l - \varepsilon]e^{-aN^*}.
\]  

(7)

Let $k_0$ be a positive integer such that $k_0 \tau_1 \geq \bar{T} + \tau$. For any positive integer $k \geq k_0$, select $s_k$, $S_k \in [k \tau_1, (k + 1) \tau_1]$ such that

\[
x(S_k) = \max_{t \in [k \tau_1, (k + 1) \tau_1]} x(t) \quad \text{and} \quad x(s_k) = \min_{t \in [k \tau_1, (k + 1) \tau_1]} x(t).
\]

We show that $\{x(s_k)\}_{k \geq k_0}$ is nondecreasing. If this is not true, then there is a positive integer $n_0 \geq k_0$ such that $x(s_{n_0}) > x(s_{n_0 + 1})$. One can easily see that $s_{n_0 + 1} \in ((n_0 + 1) \tau_1, (n_0 + 2) \tau_1]$. Let $s^* = \inf_{\omega \in [(n_0 + 1) \tau_1, (n_0 + 2) \tau_1]} x(\omega) = x(s_{n_0 + 1})$. Then

\[
x'(s^*) \leq 0 \quad \text{and} \quad x(s^*) < x(t) \quad \text{for all} \quad t \in [n_0 \tau_1, s^*).
\]

This, together with (5), gives us

\[
0 \geq x'(s^*) = \beta(s^*)[Px(s^*) - h(s^*))e^{-ax(s^*) - g(s^*)} - \delta x(s^*)]
\geq \beta(s^*)[x(s^*)](Pe^{-aN^*} - \delta)]
= 0,
\]
a contradiction. This proves the required monotonicity of $\{x(s_k)\}_{k \geq k_0}$. With this monotonicity, we know

\[
\lim_{k \to +\infty} x(s_k) = l.
\]  

(8)
Now we choose a subsequence \( \{ k_j \} \) of \( \{ k \} \) such that
\[
\lim_{j \to +\infty} x(S_{k_j}) = \limsup_{t \to +\infty} x(t) = N^*. \tag{9}
\]
As \( \{ \int_{s_{k+1}}^{S_{k}} \beta(v)dv \} \) is bounded, without loss of generality, we assume that
\[
\lim_{j \to +\infty} \int_{S_{k_j}}^{S_{k_j}+1} \beta(v)dv = \tau^* \in [-2\tau_1\beta^+, 0]. \tag{10}
\]
Integrating (7) on \([S_{k_j}, s_{k_j+1}]\), we get
\[
x(s_{k_j+1})e^{\int_{s_{k_j}}^{s_{k_j}+1} \beta(v)dv} \geq x(S_{k_j})e^{\int_{t_0}^{t_{S_{k_j}}} \beta(v)dv} + P[l - \varepsilon] e^{-aN^*} \int_{S_{k_j}}^{S_{k_j}+1} e^{\int_{t_0}^{t_{S_{k_j}}+1} \beta(v)dv} \delta \beta(t)dt
\]
\[
= x(S_{k_j})e^{\int_{t_0}^{t_{S_{k_j}}} \beta(v)dv} + [l - \varepsilon] P e^{-aN^*} \left( e^{\int_{t_0}^{t_{S_{k_j}+1}} \beta(v)dv} - e^{\int_{t_0}^{t_{S_{k_j}}} \beta(v)dv} \right)
\]
\[
= x(S_{k_j})e^{\int_{t_0}^{t_{S_{k_j}}} \beta(v)dv} + [l - \varepsilon] \left( e^{\int_{t_0}^{t_{S_{k_j}+1}} \beta(v)dv} - e^{\int_{t_0}^{t_{S_{k_j}}} \beta(v)dv} \right)
\]
and hence
\[
x(s_{k_j+1}) \geq x(S_{k_j})e^{\int_{t_0}^{t_{S_{k_j}+1}} \delta \beta(v)dv} + [l - \varepsilon] \left[ 1 - e^{\int_{t_0}^{t_{S_{k_j}+1}} \delta \beta(v)dv} \right]. \tag{11}
\]
With the help of (8)–(10), letting \( j \to +\infty \) in (11) leads to
\[
l \geq N^* e^{\delta \tau^*} + (l - \varepsilon)[1 - e^{\delta \tau^*}].
\]
As \( \varepsilon \) is arbitrary, we get \( l \geq N^* \). This completes the proof. \( \square \)

**Lemma 3.2.** If \( x(t; t_0, \varphi) - N^* \) is eventually non-negative, then \( \lim_{t \to +\infty} x(t; t_0, \varphi) = N^* \).

**Proof.** The proof is a minor modification of that for Lemma 3.1. We first show
\[
\limsup_{t \to +\infty} x(t; t_0, \varphi) < +\infty.
\]
Then use the fluctuation lemma to show \( \liminf_{t \to +\infty} x(t; t_0, \varphi) = N^* \). Finally, with the assistance of this, we show
\[
\limsup_{t \to +\infty} x(t; t_0, \varphi) \leq N^*.
\]
To avoid repetition, we omit the details here.

Next we provide a delay-dependent condition on the asymptotic behavior of all oscillatory solutions about \( N^* \).

**Lemma 3.3.** Suppose
\[
\begin{cases}
(e^{\delta \tau^+} - 1) \ln \left( \frac{P}{\delta} \right) \leq 1, \\
0 < e^{\delta \tau^+} - e^{\delta \tau+1}, \frac{e^{\delta \tau+1} - 1}{\delta} \ln \left( \frac{P}{\delta} \right) \leq 1, \\
\delta - P^2 \beta^+ \limsup_{t \to +\infty} |h(t) - g(t)| > 0.
\end{cases}
\tag{12}
\]
If \( x(t; t_0, \varphi) \) oscillates about \( N^* \), then
\[
\lim_{t \to +\infty} x(t; t_0, \varphi) = N^*.
\]
Proof. As before, denote $x(t; t_0, \varphi)$ by $x(t)$. Let $z(t) = a(x(t) - N^*)$, and

$$\lambda = \liminf_{t \to +\infty} z(t) \quad \text{and} \quad \mu = \limsup_{t \to +\infty} z(t).$$

In view of Lemma 2.2 and the oscillatory property of $z(t)$, we have

$$-\infty < \lambda \leq 0 \leq \mu < +\infty.$$

It suffices to show that $\lambda = \mu = 0$.

As $z(t)$ is oscillatory about 0, we can take a strictly increasing sequence $\{q_n\}_{n \geq 1}$ in $[t_0 + \tau, +\infty)$ increasing to $+\infty$ such that

$$z(q_n) = 0, \quad z((q_n, q_{n+1})) \cap (0, +\infty) \neq \emptyset, \quad z((q_n, q_{n+1})) \cap (-\infty, 0) \neq \emptyset$$

for $n \in \mathbb{N}$. Then, for each $n \in \mathbb{N}$, there exist $t_n, v_n \in (q_n, q_{n+1})$ such that

$$z(t_n) = \max_{t \in [q_n, q_{n+1}]} z(t) > 0, \quad z(v_n) = \min_{t \in [q_n, q_{n+1}]} z(t) < 0, \quad z'(t_n) = z'(v_n) = 0.$$

Obviously, $\lambda = \liminf_{n \to +\infty} z(v_n)$ and $\mu = \limsup_{n \to +\infty} z(t_n)$.

We claim that for $n \in \mathbb{N}$, there exists $T_n \in [t_n - \tau, t_n) \cap (q_n, t_n)$ such that

$$z(T_n) = 0 \quad \text{and} \quad z(t) > 0 \quad \text{for all} \quad t \in (T_n, t_n).$$

In fact, if $t_n - \tau \leq q_n$, this is obvious. Now assume $q_n < t_n - \tau$. If the conclusion does not hold, then $z(t) > 0$ for all $t \in [t_n - \tau, t_n]$. It follows that

$$0 = z'(t_n) = -a \delta \beta(t_n) \left[ N^* + \frac{1}{a} z(t_n) \right] + a \delta \beta(t_n) \left[ \frac{1}{a} z(t_n) \right] + \left( -a \gamma - z(t_n) \right) e^{-a N^* - z(t_n - g(t_n))} < 0,$$

a contradiction. This finishes the proof.

Similarly, for $n \in \mathbb{N}$, there exists $V_n \in [v_n - \tau, v_n) \cap (q_n, v_n)$ such that

$$z(V_n) = 0 \quad \text{and} \quad z(t) < 0 \quad \text{for all} \quad t \in (V_n, v_n). \quad (13)$$

Now for any $\varepsilon > 0$, there exists $n^{**} \in \mathbb{N}$ such that

$$\lambda - \varepsilon < z(t) < \mu + \varepsilon \quad \text{for all} \quad t > \min\{t_{n^{**}}, v_{n^{**}}\} - 2\tau > t_0 + 2\tau. \quad (14)$$

For $n > n^{**}$, according to (13), (14), and the fact that

$$\left[ z(t) e^{\int_0^t \delta \beta(u) du} \right]' = -\delta \beta(t) a N^* e^{\int_0^t \delta \beta(u) du} + a \delta \beta(t) e^{\int_0^t \delta \beta(u) du} \left[ \frac{1}{a} z(t - h(t)) \right] e^{-a N^* - z(t - g(t))},$$
on \([t_0, +\infty)\), we get
\[
\begin{align*}
z(v_n) e^{\int_{t_0}^{v_n} \delta\beta(u) du} &= -aN^* \left( e^{\int_{t_0}^{v_n} \delta\beta(u) du} - e^{\int_{t_0}^{v_n} \delta\beta(u) du} \right) \\
&+ aP \int_{V_n} \beta(t) e^{\int_{t_0}^{t} \delta\beta(u) du} \left[ N^* + \frac{1}{a} z(t - h(t)) \right] e^{-aN^* - z(t - g(t))} dt \\
&> -aN^* \left( e^{\int_{t_0}^{v_n} \delta\beta(u) du} - e^{\int_{t_0}^{v_n} \delta\beta(u) du} \right) \\
&+ aP \int_{V_n} \beta(t) e^{\int_{t_0}^{t} \delta\beta(u) du} \left[ N^* + \frac{1}{a} (\lambda - \varepsilon) \right] e^{-aN^* - (\mu + \varepsilon)} dt \\
&= -aN^* \left( e^{\int_{t_0}^{v_n} \delta\beta(u) du} - e^{\int_{t_0}^{v_n} \delta\beta(u) du} \right) \\
&+ a \left[ N^* + \frac{1}{a} (\lambda - \varepsilon) \right] P \left( e^{\int_{t_0}^{v_n} \delta\beta(u) du} - e^{\int_{t_0}^{v_n} \delta\beta(u) du} \right) e^{-\int_{t_0}^{v_n} \delta\beta(u) du} \\
&> aN^* \left( 1 - e^{\int_{t_0}^{v_n} \delta\beta(u) du} \right) [e^{-(\mu + \varepsilon)} - 1] \\
&+ (\lambda - \varepsilon) \left( e^{\int_{t_0}^{v_n} \delta\beta(u) du} - e^{\int_{t_0}^{v_n} \delta\beta(u) du} \right),
\end{align*}
\]
and hence
\[
\begin{align*}
z(v_n) + (\lambda - \varepsilon)(e^{-\delta\tau\beta^+} - 1) &\geq z(v_n) + (\lambda - \varepsilon) \left( e^{\int_{t_0}^{v_n} \delta\beta(u) du} - 1 \right) \\
&> aN^* \left( 1 - e^{\int_{t_0}^{v_n} \delta\beta(u) du} \right) [e^{-(\mu + \varepsilon)} - 1] \\
&\geq aN^* \left( 1 - e^{-\delta\tau\beta^+} \right) [e^{-(\mu + \varepsilon)} - 1].
\end{align*}
\]
By taking inferior limit and letting \(\varepsilon \to 0^+\), (12) leads to
\[
\lambda \geq aN^* (e^{\delta\tau\beta^+} - 1)(e^{-\mu} - 1) \geq e^{-\mu} - 1 \geq -1.
\]
From the definition of \(T_n\) and the fact that
\[
z(t - h(t)) e^{-z(t - g(t)) < (\mu + \varepsilon) e^{-(\lambda - \varepsilon)}} \text{ for all } t \in (T_n, t_n) \text{ and } n > n^*,
\]
we obtain
\[
\begin{align*}
z(t_n) e^{\int_{t_0}^{t_n} \delta\beta(u) du} &= -aN^* \left( e^{\int_{t_0}^{t_n} \delta\beta(u) du} - e^{\int_{t_0}^{t_n} \delta\beta(u) du} \right) \\
&+ aP \int_{T_n}^{t_n} \beta(t) e^{\int_{t_0}^{t} \delta\beta(u) du} \left[ N^* + \frac{1}{a} z(t - h(t)) \right] e^{-aN^* - z(t - g(t))} dt \\
&= -aN^* \left( e^{\int_{t_0}^{t_n} \delta\beta(u) du} - e^{\int_{t_0}^{t_n} \delta\beta(u) du} \right) \\
&+ aP e^{-aN^*} \int_{T_n}^{t_n} \beta(t) e^{\int_{t_0}^{t} \delta\beta(u) du} N^* e^{-z(t - g(t))} dt \\
&+ P e^{-aN^*} \int_{T_n}^{t_n} \beta(t) e^{\int_{t_0}^{t} \delta\beta(u) du} z(t - h(t)) e^{-z(t - g(t))} dt
\end{align*}
\]
Remark 1. Suppose that \( N^\ast \) is the positive equilibrium of (5).

Taking superior limit and letting \( \epsilon \to 0^+ \), (12) suggests that
\[
\mu \leq \frac{e^{\delta \beta^+ \tau} - 1}{e^{\delta \beta^+ \tau} - e^{\delta \beta^- \tau}} aN^\ast(e^{-\lambda} - 1) \leq e^{-\lambda} - 1,
\]
which, together with (15), implies that
\[
e^{-\mu} - 1 \leq \lambda \leq 0 \leq \mu \leq e^{-\lambda} - 1.
\] (16)
It follows that \( G(\mu) \geq 0 \), where \( G(x) = e^{1-x} - 1 - x \). It is easy to check that \( G \) is strictly decreasing on \([0, +\infty)\) with \( G(0) = 0 \). Then we have \( \mu = 0 \) and hence \( \lambda = 0 \) by (16). This completes the proof.

Now we can state and prove our main result on the global attractivity of the positive equilibrium \( N^\ast \) follows from Lemmas 3.1-3.3.

**Theorem 3.4.** Suppose that (12) holds. Then the positive equilibrium \( N^\ast \) of (5) is a global attractor in \( \{ \varphi \in C^+| \varphi(0) > 0 \} \).

**Remark 1.** In [18], So and Yu studied the Nicholson’s blowflies equation,
\[
\dot{N}(t) = -\delta N(t) + PN(t-\tau)e^{-aN(t-\tau)},
\]
which is a special case of (5). We point out that Lemmas 3.1–3.3 and Theorem 3.4 generalize the corresponding ones in [18]. Lemma 3.1 and Lemma 3.2 tell us that the two different time-varying delays \( b(t) \) and \( g(t) \) have no impact on the asymptotical behavior of the non-oscillatory solutions about the positive equilibrium \( N^\ast \) of (5). However, the convergence of the oscillatory solutions about \( N^\ast \) depends on both the magnitudes and difference of the two delays. This means that the two delays play important roles in the global attractivity of the positive equilibrium.

**Remark 2.** Very recently, Q. Cao et al. [6] considered the global asymptotic stability on the zero equilibrium point for Nicholson’s blowflies model with a nonlinear density-dependent mortality term
\[
x'(t) = -\frac{a(t)x(t)}{b(t) + x(t)} + \sum_{j=1}^{m} \beta_j(t)x(t - h_j(t))e^{-\gamma_j(t)}x(t - g_j(t)), \quad t \geq t_0.
\] (3.11)
where $g_j$ denotes the developmental or maturation time whereas $h_j$ represents the reproduction lag. Y. Xu et al. [21] and X. Long [14] also established the global stability on the zero equilibrium point for classical Nicholson’s blowflies models involving distinctive delays. It should be mentioned that the stability on the positive equilibrium point for the addressed models in [6, 21, 14] has not been touched. As [6, 21, 14], in [16, 11], the authors still were unable to derive any global convergence for the positive equilibrium point of (1.2). Theorem 3.1 complements the aforementioned works and this seems to be the first time that such a result is derived for this type of Nicholson’s blowflies equation. Our work partially answers an open problem proposed by [1].

4. A numerical example. In the following, we will present a numerical example to explain the theoretical result.

**Example 4.1** Consider a non-autonomous Nicholson’s blowflies equation incorporating two different time-varying delays as below,

$$x'(t) = \beta(t) \left[ -\frac{3}{20} x(t) + \frac{3}{20} e^{\frac{1}{2} x(t-h(t))} e^{-\frac{1}{20} x(t-g(t))} \right], \quad t \geq t_0 = 0, \quad (17)$$

where $\beta(t) = \frac{1+0.5 \sin t}{150}$. Clearly, $N^* = 10$ is the unique positive equilibrium point of (4.1).

Take

$$h(t) = 100 + 3 \sin t, \quad g(t) = 102 + \sin 2t. \quad (18)$$

It is easy to check that (12) is satisfied. Then, by Theorem 3.4, $N^*$ is globally attractive in $\{ \varphi \in C([-103, 0], \mathbb{R}^+) | \varphi(0) > 0 \}$, which is strongly supported by Fig. 1. However, if we take

$$h(t) = 1 + \cos^2 t, \quad g(t) = 102 + \cos^2 t, \quad (19)$$

then the third inequality in (12) does not hold whereas if we take

$$h(t) = 2001 + \cos^2 t, \quad g(t) = 2002 + \cos^2 t, \quad (20)$$

then the first inequality in (12) is violated. This time, Theorem 3.4 is inapplicable. Fig. 2 indicates the solutions might be asymptotically periodic, and maybe not tend...
to $N^*$. Since the time interval $[0, 10000]$ is long in Fig. 3, one can find that the solutions in this example can not tend to $N^*$ quickly.

From the above simulations, we can make the following observations. First, small delays with small difference will make the positive equilibrium attractive. Second, small delays with big difference will result in instability of the positive equilibrium. Finally, big delays with big difference leads to complex dynamic behavior.

5. Conclusion. In this article, we studied a non-autonomous Nicholson’s blowflies model incorporating two different time-varying delays. We briefly justified this type of model formulation from a structured population modeling point of view. With some delicate applications of differential inequality techniques and the classical Fluctuation Lemma, we established a criterion on the global attractivity of the positive equilibrium. The condition depends on all relevant parameters and is easily verifiable. This seems to be the first time that such a result is derived for this type of Nicholson’s blowflies equation. Our work partially answers an open problem proposed by [1]. Because of its complexity, the dynamic analysis for the delayed Nicholson’s blowflies model is far from complete. Further studying the dynamical
behaviors for generalized model with reaction-diffusion effects under some boundary condition \cite{12, 13} will be our future study. We believe that the approach developed here is applicable to the investigation of the long time behavior of other population models with two different time-varying delays. We hope this work will contribute to increasing the interest and research activities on delay differential systems with multiple delays (non-autonomous) in the life cycle where feedback control takes place.

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E-mail address: cxiahuang@csust.edu.cn
E-mail address: lhhuang@csust.edu.cn
E-mail address: wujh@yorku.ca