CANADIAN APPLIED
MATHEMATICS QUARTERLY
Volume 14, Number 2, Summer 2006

NICHOLSON'S BLOWFLIES EQUATION WITH A DISTRIBUTED DELAY

ELENA BRAVERMAN AND DAMIR KINZEBULATOV

Dedicated to Jack W. Macki and James S. Muldowney on the occasion of their retirement

ABSTRACT. For the Nicholson's blowflies equation with a distributed delay

$$\dot{N}(t) = -\delta N(t) + p \int_{h(t)}^{t} N(s)e^{-aN(s)} d_s R(t,s), \quad t \geq 0,$$

we obtain existence, positiveness and permanence results for solutions with positive initial conditions. We prove that all nonoscillatory about the positive equilibrium N^* solutions tend to N^*. In the case $\delta < p < \delta e$ there are no slowly oscillating solutions and the positive equilibrium is globally asymptotically stable. Some generalizations to other nonlinear models of population dynamics with a distributed delay in the recruitment term and a nondelayed linear death term are considered.

1 Introduction It is usually believed that equations with a distributed delay provide a more realistic description for models of population dynamics and mathematical biology in general. For example, if the delay involved in the equation is a maturation delay, then the maturation time is generally not constant, but is distributed around its expectancy value.

Historically, Volterra considered the logistic equation with a distributed delay in 1926 [**34**]

$$\dot{N}(t) = rN(t) \int_0^\infty k(\tau) \left[1 - \frac{N(t-\tau)}{K}\right] d\tau, \tag{1}$$

The authors were partially supported by the NSERC Research Grant and the AIF Research Grant.

AMS subject classification: 34K11, 34K45, 92B.

Keywords: Distributed delay, Nicholson blowflies equation, oscillation, permanence, global attractivity.

first, before the Hutchinson's equation (the logistic equation with a concentrated delay)

$$\dot{N}(t) = rN(t)\left[1 - \frac{N(t-\tau)}{K}\right] \tag{2}$$

was introduced in 1948 [**19**]. Here N is the size of the population, K is the carrying capacity of the environment, the function $k(\tau) \geq 0$ in (1) satisfies

$$\int_0^\infty k(\tau)d\tau = 1. \tag{3}$$

This can be interpreted in the following way: the present growth rate depends on the state in the past, where $\int_{\tau_1}^{\tau_2} k(\tau)\,d\tau$ is the probability that delay τ is between τ_1 and τ_2.

The Nicholson's blowflies equation

$$\dot{x}(t) = -\delta x(t) + px(t-\tau)e^{-ax(t-\tau)} \tag{4}$$

was used in [**13**] to describe the periodic oscillation in Nicholson's classic experiments [**27**] with the Australian sheep blowfly, *Lucila cuprina*.

The main object of the present paper is the generalization of (4) to the case of a distributed delay

$$\dot{x}(t) = -\delta x(t) + p\int_{h(t)}^t x(s)e^{-ax(s)}d_sR(t,s), \quad t \geq 0, \tag{5}$$

where $\int_{h(t)}^t d_sR(t,s) = 1$ for any t. The distributed delay involved in (5) is more general than one in (1) in the following sense: if we interpret the delay as probability, then the probabilistic measure is not necessarily non-atomic. For example, (4) is a special case of (5), while (2) cannot be obtained from (1). However, unlike (1), we do not consider infinite delays.

As an additional generalization, we consider a nonlinear differential equation with a distributed delay in the recruitment term and instantaneous death

$$\dot{x}(t) = \delta\int_{h(t)}^t f(x(s))d_sR(t,s) - \delta x(t), \quad t \geq 0. \tag{6}$$

The delay we consider is the most general type of delay. As special cases, (6) includes

The integro-differential equation

$$\dot{x}(t) = -\delta x(t) + \delta \int_{h(t)}^{t} K(t,s) f(x(s))\, ds \tag{7}$$

corresponding to the absolute continuous $R(t,\cdot)$ for any t. Here

$$\int_{h(t)}^{t} K(t,s)\, ds = 1 \quad \text{for any } t, K(t,s) = \frac{\partial}{\partial s} R(t,s) \geq 0$$

is defined almost everywhere.

The equation with several concentrated delays

$$\dot{x}(t) = -\delta x(t) + \delta \sum_{k=1}^{m} a_k(t) f\left(x[h_k(t)]\right), \tag{8}$$

with $a_k(t) \geq 0$, $k = 1, \ldots, m$, where $\sum_{k=1}^{m} a_k(t) = 1$ for any t. This corresponds to $R(t,s) = \sum_{k=1}^{m} a_k(t) \chi_{(h_k(t),t]}(s)$, where $\chi_{[a,b]}(t)$ is the characteristic function of the interval $[a,b]$.

For various models of Mathematical Biology with distributed and concentrated delays see the monographs [**6, 11, 20, 21**]. We also refer the reader to [**1–5, 7, 10, 14, 17, 18, 24–26, 28–33, 35, 37**] and to the references therein for the recent progress in the theory of delay differential equations with a distributed delay, especially asymptotics and stability, as well as justification of various applied models including a distributed delay. Here we deliberately do not mention recent developments in neural networks and control theory for equations with distributed delays. Many publications on equations with a distributed delay refer to partial differential equations, however we mention here only [**15**], where the diffusive Nicholson's blowflies equation with distributed delays was considered. The delay in [**15**], as in most of the above publications, was of the integral type (7).

2 Preliminaries

Together with (6) and (5) we consider initial conditions

$$x(t) = \varphi(t), \quad t \leq 0. \tag{9}$$

Let us assume that the parameters of the equation (5) satisfy

(a1) $p > \delta > 0$;

(a2) $h : [0, \infty) \to \mathbb{R}$, is a Lebesgue measurable function, $h(t) \le t$, $\lim_{t\to\infty} h(t) = \infty$;
(a3) $R(t, \cdot)$ is a left continuous nondecreasing function for any t, $R(\cdot, s)$ is locally integrable for any s, $R(t, s) = 0$, $s \le h(t)$, $R(t, t^+) = 1$.

Here $u(t^+)$ is the right side limit of the function u at the point t.

Now let us proceed to conditions for the initial function φ. The integral in the right hand side of (6) should exist almost everywhere. In particular, for (7) with a locally integrable kernel, φ should be a Lebesgue measurable essentially bounded function. For (8) φ should be a Borel measurable bounded function. For any distribution R the integral exists if φ is bounded and continuous (here we either consider the model (5) or assume f is continuous). Besides, we consider a population dynamics model, so the initial value is nonnegative and the value at the initial point is positive. Thus, we assume

(a4) $\varphi : (-\infty, 0] \to \mathbb{R}$ is a continuous function, $\varphi(t) \ge 0$, $\varphi(0) > 0$.

However we keep in mind that the condition (a4) can be relaxed for certain types of $R(t, s)$.

Throughout the paper, our main object is the Nicholson's blowflies equation and we assume in (6)

$$f(x) = \frac{p}{\delta} x e^{-ax}.$$

In Section 6 we discuss some possible generalizations, where f is a continuous function. Conditions on $f(x)$ will be specified later.

Let us notice that the condition $R(t, h(t)) = 0$ means that the delay is finite, while $R(t, t^+) = 1$ corresponds to any delay equation, which is "normalized" with the coefficient p. Thus R has a probabilistic meaning: $R(t, s)$ is the probability that at point t the delay does not exceed s.

Definition 1. An absolutely continuous in $[0, \infty)$ function $x : \mathbb{R} \to \mathbb{R}$ is called *a solution of the problem* (6),(9) if it satisfies equation (6) for almost all $t \in [0, \infty)$ and conditions (9) for $t \le 0$.

Definition 2. Equation (6) has *a nonoscillatory about the positive equilibrium x^* solution* $x(t)$ if the difference $x(t) - x^*$ is either eventually positive or eventually negative. Otherwise, all solutions of (5), (9) are *oscillatory about x^**.

The Nicholson's blowflies equation (5) has the positive equilibrium

$$x^* = \frac{1}{a} \ln\left(\frac{p}{\delta}\right). \tag{10}$$

Similar to the general case, we can specify particular cases of (5): the integrodifferential Nicholson's blowflies equation

$$\dot{x}(t) = -\delta x(t) + p \int_{h(t)}^{t} K(t,s)x(s)e^{-ax(s)}\, ds, \tag{11}$$

the Nicholson's blowflies equation with several variable delays

$$\dot{x}(t) = -\delta x(t) + p \sum_{k=1}^{m} a_k(t) x[h_k(t)] e^{-ax[h_k(t)]}, \tag{12}$$

and the equation with a constant delay [**13, 27**]

$$\dot{x}(t) = -\delta x(t) + px(t-\tau)e^{-ax(t-\tau)}. \tag{13}$$

Finally, we comment that we still consider the equation with constant coefficients and a constant equilibrium and our results do not involve some recent developments in the theory of Nicholson's blowflies equations with variable (periodic) coefficients [**8**].

3 Existence, positiveness and permanence of solutions Let $C([c,d])$ be the space of continuous in $[c,d]$ functions with sup-norm, $L^2([c,d])$ be the space of Lebesgue measurable functions $y(t)$, such that

$$Q = \int_c^d (y(t))^2\, dt < \infty, \qquad \|y\|_{L^2([c,d])} = \sqrt{Q}.$$

We will use the following result from the book of Corduneanu [**9,** Theorem 4.5, p. 95].

Lemma 1. *Consider the equation*

$$\dot{y}(t) = (Ly)(t) + (Ny)(t), \quad t \in [c,d], \tag{14}$$

where L is a linear bounded causal operator, $N : C([c,d]) \to L^2([c,d])$ is a nonlinear causal operator which satisfies

$$\|Nx - Ny\|_{L^2([c,d])} \le \lambda \|x - y\|_{C([c,d])} \tag{15}$$

for λ sufficiently small. Then there exists a unique absolutely continuous solution of (14) *in $[c,d]$, with the initial function equal to zero for $t < c$.*

Let us note that the function

$$f(x) = \frac{p}{\delta}\, x e^{-ax} \tag{16}$$

attains its maximum at the point

$$x_M = \frac{1}{a}, \tag{17}$$

which equals

$$M = \max_{x \geq 0} f(x) = f(x_M) = \frac{p}{\delta a e}. \tag{18}$$

Its first derivative

$$f'(x) = \frac{p}{\delta}\, e^{-ax}(1 - ax) \tag{19}$$

satisfies $f'(0) = p/\delta$, then the derivative decreases in $[0, 2/a]$, where at $x = 2/a$ it equals $-(p/\delta)e^{-2}$, in $[2/a, \infty)$ the derivative increases and tends to zero. Thus $|f'(x)| \leq K = p/\delta$ for any $x > 0$ and

$$|f(x) - f(y)| \leq K|x - y| = \frac{p}{\delta}|x - y|, \quad x, y > 0, \quad K = \frac{p}{\delta}. \tag{20}$$

Theorem 1. *Suppose* (a1)–(a4) *hold. Then there exists a unique solution of* (5), (9).

Proof. To reduce (5) to the equation with the zero initial function, for any $c \geq 0$ we can present the integral as a sum of two integrals

$$\dot{y}(t) = -\delta y(t) + \delta \int_c^t f(y(s))\, d_s R(t,s) + \delta \int_c^t f(\varphi(s))\, d_s R(t,s), \tag{21}$$

where

$$y(t) = 0, \quad t < c, \qquad \varphi(t) = 0, \quad t \geq c.$$

Here $c \geq 0$ is arbitrary, so we begin with $c = 0$ and proceed to a neighbouring c to prove the existence of a local solution. Then in (14)

$$Ly = -\delta y, \quad Ny = \delta \int_c^t f(y(s))\, d_s R(t,s) + F(t),$$

$$\text{where } F(t) = \delta \int_c^t f(\varphi(s))\, d_s R(t,s)$$

and for any $\lambda > 0$ there is d, such that

$$\begin{aligned}\|Nx - Ny\|_{L^2([c,d])} &\le \delta \left\| \int_c^t |f(x(s)) - f(y(s))| \, d_s R(t,s) \right\|_{L^2([c,d])} \\ &\le \delta K \max_{\tau \in [c,d]} |x(s) - y(s)| \left\| \int_c^t d_s R(t,s) \right\|_{L^2([c,d])} \\ &\le \delta K \|x(s) - y(s)\|_{C([c,d])} |d - c| \\ &\le \lambda \|x - y\|_{C([c,d])}\end{aligned}$$

for $|d - c| \le \lambda/p$ due to (20), here λ can be chosen small enough. By Lemma 1 this implies the uniqueness and the existence of a local solution for (5). This solution is either global or there exists such t_1 that either

$$\liminf_{t \to t_1} x(t) = -\infty \tag{22}$$

or

$$\limsup_{t \to t_1} x(t) = \infty. \tag{23}$$

The initial value is positive, so as far as $x(t) > 0$, the solution is not less than $x(0)e^{-\delta t}$, which solves $\dot{x} = -\delta x$. The solution is continuous, so to become negative, it should first intersect the curve $x(0)e^{-\delta t}$, thus the solution is positive and the former case (22) is impossible. In addition, $\dot{x}(t) < 0$ for any $x(t) > M$, which contradicts (23). Thus there exists a unique global solution, which completes the proof. $\square$

Theorem 2. *Suppose* (a1)–(a4) *hold. Then the solution of* (5), (9) *is positive for* $t \ge 0$.

Proof. Let us make the substitution

$$y(t) = x(t)e^{\delta t}, \tag{24}$$

then (5) becomes

$$\dot{y}(t) = pe^{\delta t} \int_{h(t)}^t y(s) e^{-\delta s} e^{-ay(s)\exp(-\delta s)} d_s R(t,s), \quad t \ge 0. \tag{25}$$

Thus $y(0) > 0$ and $\dot{y}(t) > 0$ as far as $y(s) > 0$, $s \le t$, consequently, $y(t) > 0$ for any $t \ge 0$. Since the signs of $y(t)$ and $x(t) = y(t)e^{-\delta t}$ coincide, then $x(t) > 0$ for any $t \ge 0$. $\square$

Definition 3. The solution $x(t)$ of (5), (9) is *permanent* if there exist A and B, $B \ge A > 0$, such that

$$A \le x(t) \le B, \quad t \ge 0.$$

In the following theorem not only we prove permanence of all solutions of (5) with positive initial conditions but also establish bounds for solutions.

Theorem 3. *Suppose* (a1)–(a4) *hold. Then the solution of* (5), (9) *is permanent.*

Proof. By Theorem 2 the solution is positive for $t \ge 0$. By (a2) there exists $t_1 > 0$, such that $h(t) > 0$, $t \ge t_1$. Below we demonstrate that in the case $0 < \delta < p \le \delta e$ if the solution is between $x_{\min}$ and $x_{\max}$ for $0 < t < t_1$ (assuming $x^* \in [x_{\min}, x_{\max}]$), then $x(t) \in [x_{\min}, x_{\max}]$ for any $t \ge 0$ (see Figures 1 and 2).

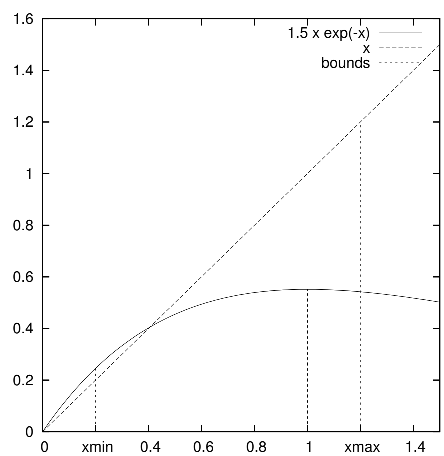

FIGURE 1: The graphs of the functions $y = px\exp(-x)$ and $y = \delta x$ for $0 < \delta < p < \delta e$. Here $p = 1.5$, $\delta = 1$, the point of intersection of two graphs is less than $x = 1$ (the maximum point). If the solution is between $x_{\min}$ and $x_{\max}$ for $t < t_1$, where the segment $[x_{\min}, x_{\max}]$ contains the equilibrium point, then the solution is in this segment for any t. If the equilibrium point x^* is not contained, then the lower (upper) bound is substituted by x^*.

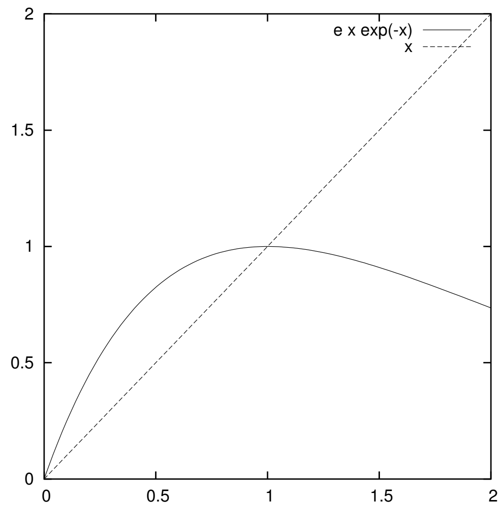

FIGURE 2: The graphs of the functions $y = px\exp(-x)$ and $y = \delta x$ for $p = \delta e$. Here $p = e$, $\delta = 1$, the point of intersection of two graphs is exactly $x = 1$ (the maximum point). If the solution is between $x_{\min}$ and $x_{\max}$ for $t < t_1$, then $x(t) \in [\min\{x_{\min}, 1\}, \max\{x_{\max}, 1\}]$ for any $t \geq 0$.

The situation in the case $p > \delta e$ is a little bit more complicated (see Figure 3). Below we consider the general case.

Let us take any $\varepsilon > 0$ and define

$$A = \min\left\{ \inf_{t\in[0,t_1]} x(t), f(M+\varepsilon), x^* \right\} \tag{26}$$

$$B = \max\left\{ \sup_{t\in[0,t_1]} x(t), M + \frac{\varepsilon}{2} \right\} \tag{27}$$

and demonstrate

$$x(t) \in [A, B], \quad t \geq 0. \tag{28}$$

By the definition of A and B we have

$$m = \inf_{A\leq x\leq B} f(x) \geq A, \qquad M = \sup_{x\geq 0} f(x) \leq B$$

and $x(t_1) \in [A, B]$.

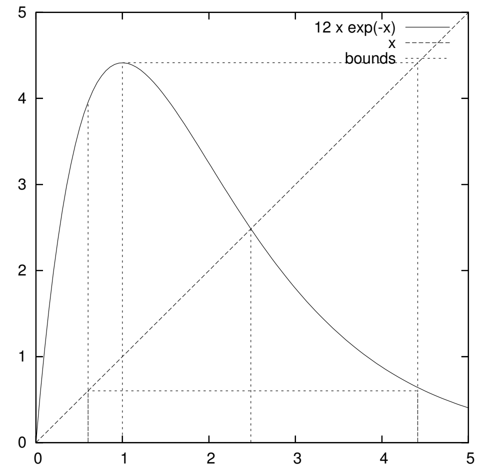

FIGURE 3: The graphs of the functions $y = f(x) = px\exp(-x)$ and $y = \delta x$ for $p > \delta e$. Here $p = 12$, $\delta = 1$, the point of intersection of two graphs is greater than $x = 1$ (the maximum point). Here $f(1)$ should be taken into account in the upper bound of a solution, as well as $f(f(1))$ in the lower bound.

Let us demonstrate (28). Suppose the contrary: $x(t) > B$ or $x(t) < A$ for some $t > t_1$.

First, let $x(t) > B$. Denote

$$S = \{t > t_1 | x(t) > B\}, \quad t^* = \inf S.$$

Then $x(t^*) = B$, $M = \sup_x f(x) < B$. Since $x(t)$ and $f(x)$ are continuous, then there exists some $\nu > 0$, such that for $t \in [t^* - \nu, t^*)$ we have $B > x(t) > (B+M)/2$, also $f(x(t)) \leq M < (B+M)/2$ for any $t \geq 0$. Thus for $t \in [t^* - \nu, t^*)$

$$\begin{aligned}\dot{x}(t) &= \delta \left[\int_{h(t)}^{t} f(x(s))\, d_s R(t,s) - x(s) \right] \\ &< \delta \left[\int_{h(t)}^{t} M\, d_s R(t,s) - \frac{B+M}{2} \right] \\ &= \delta \left(M - \frac{B+M}{2} \right) = \delta\, \frac{M-B}{2} < 0.\end{aligned}$$

Consequently, $B = x(t^*) < x(t^* - \nu)$, which contradicts the definition of t^* as the infimum of S, since $t^* - \nu \in S$. Thus $x(t) \le B$, $t \ge t_1$.

Second, let $x(t) < A$. Again, denote

$$S = \{t > t_1 \mid x(t) < A\}, \quad t^* = \inf S.$$

$x(t^*) = A$, $x(t) \ge A$ and $f(x(t)) > A$ for $t \le t^*$. Similar to the previous case, we find some left ν-neighbourhood of t^*, where the derivative is positive; then $x(t^* - \nu) < x(t^*) = A$, so $t^* - \nu \in S$, which contradicts the definition of t^* as $\inf S$. Finally, $x(t) \in [A, B]$, so any solution with positive initial conditions is permanent, which completes the proof. $\square$

4 Oscillation

Theorem 4. *Suppose* (a1)–(a4) *hold. Then any nonoscillatory about* x^* *solution of* (5), (9) *tends to the equilibrium* (10)*:*

$$\lim_{t\to\infty} x(t) = x^*. \tag{29}$$

Proof. 1) First, suppose $0 < x(t) < x^*$, $t \ge t_1$. By (a2) there is a point t_2, such that $h(t) > t_1$, $t \ge t_2$. The solution is permanent by Theorem 3 and $x(t) \in [A, B]$, where A and B are defined in (26) and (27), respectively. In particular, denote $m_0 = A$, then $m_0 \le x(t) < x^*$, $t \ge 0$. Further, introduce

$$m_1 = \min\left\{ \min_{m_0 \le x \le x^*} f(x), x^* \right\}. \tag{30}$$

We observe $m_1 > m_0$, since $m_0 = A < x^*$ and $f(x) > x$, $x < x^*$. In addition, $\dot{x}(t) > 0$ for any $x(t)$, as far as still $0 < x(t) < m_1$ and $t \ge t_2$. Then, there are two possibilities: $x(t)$ is increasing and is less than m_1 for any $t \ge t_2$ or $x(t) \ge m_1$ for some $t^* \ge t_2$. In the former case a bounded increasing function has a limit: $K = \lim_{t\to\infty} x(t)$, $K \le m_1$, $f(K) > m_1$. Thus there exist $\bar{t}$, $\nu > 0$, such that $f(x(t)) \ge m_1 + \nu$, $t > \bar{t}$ and $\hat{t} > \bar{t}$, such that $h(t) > \bar{t}$, $t > \hat{t}$. Then for $t > \hat{t}$

$$\begin{aligned} \dot{x}(t) &= \delta \int_{h(t)}^{t} f(x(t))\, d_s R(t,s) - \delta x(t) \\ &> \delta \int_{h(t)}^{t} (m_1 + \nu)\, d_s R(t,s) - \delta m_1 = \delta\nu > 0 \end{aligned} \tag{31}$$

almost everywhere; the function with the derivative exceeding $\nu > 0$ tends to infinity, which contradicts the assumption $x(t) \le m_1$, $t \ge t_2$ (unless $m_1 = x^*$).

In the latter case ($x(t) \ge m_1$ for some $t^* \ge t_2$) let us prove that $x(t) \ge m_1$, $t \ge t^*$. Really, if for any $\sigma > 0$ we take the set $S = \{t > t^* \mid x(t) < m_1 - \sigma\}$ and consider its infimum $\bar{t}$, then $\dot{x}(t) > 0$ in some left neighbourhood of $\bar{t}$, since $\dot{x}(t) > 0$ for any $t \ge t_1$ and $x(t) < m_1$. Since $\sigma > 0$ is arbitrary, we obtain $x(t) \ge m_1$, $t \ge t^*$. Denote by t_3 the point $t_3 > t^*$, such that $h(t) \ge t^*$, $t \ge t_3$. Then $\dot{x}(t) > 0$, $t \ge t_3$, and $x(t) < m_2 = \min\{\inf_{m_1 \le x \le x^*} f(x), x^*\}$. Similar to the previous case, either $m_2 = x^*$ and the solution tends to m_3 and does not exceed it, or there is t_4, such that $x(t) \ge m_2$, $t \ge t_4$. Continuing this process, we either find a sequence

$$m_0 < m_1 < m_2 < \cdots < m_k < \cdots ,$$

such that $x(t) \ge m_k$, $t \ge t_{k+2}$ (for the case $\delta < p \le \delta e$, see Figures 1 and 2), where $m_i = f(m_{i-1})$, or $m_j = x^*$ and the process cannot be continued (for the case $p > \delta e$, see Figure 3). In the former case $\lim_{k\to\infty} m_k = \lim_{k\to\infty} f^k(m_0) = x^*$ and in the latter case we prove $\lim_{t\to\infty} x(t) = x^*$ assuming the contrary and using the same argument as in (31).

2) Suppose $x(t) > x^*$. Then in the case $p \ge \delta e$ the solution is decreasing ($f(x(t)) < x^* < x(s)$ for any t and s), thus it has a limit which coincides with x^* (we use the same argument as in (31)).

In the case $\delta < p < \delta e$, as in 1), we construct a sequence $M_0 = M$, $M_1 = f(M_0), \dots, M_{k+1} = f(M_k), \dots$ and demonstrate that there is a sequence of numbers t_k, such that $x(t) \le M_k$ for $t \ge t_k$. Since $\lim_{t\to\infty} M_k = x^*$, then $\lim_{t\to\infty} x(t) = x^*$. □

Definition 4. An oscillating solution of (5) is called *slowly oscillating* if for any $t_0 > 0$ there exist two points t_1, t_2, $t_2 > t_1 > t_0$, such that $h(t) > t_1$, $t \ge t_2$, and $x(t) - x^*$ preserves its sign in $[t_1, t_2)$ and vanishes at the point t_2:

$$(x(s) - x^*)(x(t) - x^*) > 0, \ s, t \in [t_1, t_2), \quad x(t_2) = x^*.$$

Otherwise, the solution is *rapidly oscillatory.*

The solution is rapidly oscillatory if eventually the distance between adjacent zeros of the function does not exceed the delay.

Theorem 5. *Suppose* (a1)–(a4) *hold and* $\delta < p < \delta e$. *Then the equation* (5) *has no slowly oscillatory about* x^* *solutions.*

Proof. First, let us assume: $x(t) < x^*$, $t \in [t_1, t_2]$. Let us prove: $x(t) < x^*$ for any $t \geq t_1$. We recall that $f(x)$ is monotone increasing for $x \in [0, x^*]$. For the continuous solution $x(t)$ consider the function $u(t) = \max_{s \in [t_1,t]} x(s)$ for $t \geq t_2$. If $u(t) > x(t)$ for any $t > t_2$, then the maximum was attained in $[t_1, t_2]$ and $x(t) < \max_{s \in [t_1,t_2]} x(s) < x^*$ for any $t \geq t_1$. Now let us assume for some $\bar{t}$ we have $x(\bar{t}) = \max_{s \in [t_1,\bar{t}]} x(s)$. By (a3) the solution of the equation (5) does not exceed the solution of the following initial value problem (here $\max_{s \in [t_1,t]} f(y(s)) = f(\max_{s \in [t_1,t]} y(s))$)

$$(32) \quad \dot{y} = \delta f\big(\max_{s \in [t_1,t]} y(s)\big) - \delta y(t), \quad t \geq \bar{t}, \qquad y(t) = x(t), \quad t \in [t_1, \bar{t}].$$

Since $f(x) > x$, $x < x^*$, then y is increasing, as far as $y < x^*$, and thus $\max_{s \in [t_1,t]} y(s) = y(t)$, so the solution of (32) coincides with the solution of the initial value problem for the ordinary differential equation

$$(33) \qquad \dot{z} = \delta[f(z) - z], \qquad z(\bar{t}) = x(\bar{t}),$$

which by the existence and uniqueness theorem never intersects the equilibrium solution $y = x^*$. Thus $y(t) < x^*$ and

$$x(t) \leq y(t) < x^*, \quad t \geq t_1.$$

Second, let $x(t) > x^*$, $t \in [t_1, t_2]$. By Theorem 3 $x(t) < M + \varepsilon$ for any $\varepsilon > 0$ for $t > t_0$ large enough. Since $M < x^*$, it is possible to choose $\varepsilon > 0$ small enough, such that $M + \varepsilon < x_M$, where x_M is the maximum point of $f(x)$. Let us take $t_1, t_2 > t_0$. Then $f(x)$ is increasing in x for any $x(t)$, $t > t_0$. For the continuous solution $x(t)$ consider the function $u(t) = \min_{s \in [t_1,t]} x(s)$ for $t \geq t_2$. If $u(t) < x(t)$ for any $t > t_2$, then $x(t) > \min_{s \in [t_1,t_2]} x(s) > x^*$, which completes the proof. Let us assume for some $\bar{t}$ we have $x(\bar{t}) = \min_{s \in [t_1,\bar{t}]} x(s)$. By (a3) the solution of the equation (5) is not less than the solution of the following initial value problem (here $\min_{s \in [t_1,t]} f(y(s)) = f(\min_{s \in [t_1,t]} y(s))$)

$$(34) \quad \dot{y} = \delta f(\min_{s \in [t_1,t]} y(s)) - \delta y(t), \quad t \geq \bar{t}, \qquad y(t) = x(t), \quad t \in [t_1, \bar{t}].$$

Similar to the previous case $x(t) \geq y(t) > x^*$, which completes the proof. $\square$

Remark 1. The proof of Theorem 5 in addition demonstrates that if the solution is either between x_1 and x^*, where $0 < x_1 < x^*$, or between x^* and x_2, where $x^* < x_2 < M$ for some "remembered memory", then the same relation is valid for the solution, beginning with this point. However, let us demonstrate that the fact that the solution exceeds the equilibrium point at the segment of the length exceeding the delay does not imply the solution stays above the equilibrium. This is due to the fact that some part of the prehistory is above M.

Example 1. The equilibrium point of the equation

$$\dot{x}(t) = 1.5\, x(h(t))e^{-x(h(t))} - x(t) \tag{35}$$

is $x^* \approx 0.4055$. Let the delay be

$$h(t) = \begin{cases} 0, & 0 \le t < 2.8, \\ 1, & 2.8 \le t < 3.5, \\ t, & t \ge 3.5. \end{cases} \tag{36}$$

Consider the initial value problem, with $x(0) = 8$. Then $x(t) = A + (8 - A)e^{-t}$ for $t \in [0, 2.8]$, where $A = 1.5 \cdot 8e^{-8} \approx 0.0040255$. Since $x(t) \approx 0.0040255 + 7.9995975e^{-t}$, then $x(1) \approx 2.9455801$ and $x(2.8) \approx 0.4902612 > x^*$, so $x(t) > x^*$ on the segment of the length exceeding 2.8 (the maximal delay of h). Denote $B = 1.5x(1)e^{-x(1)} \approx 0.2322806$. The solution in the segment $[2.8, 3.5]$ is

$$x(t) = B + (x(2.8) - B)e^{-(t-2.8)} \approx 0.2322806 + 0.2579806e^{-(t-2.8)},$$

so $x(3.3) < 0.2322806 + 0.258e^{-0.5} \approx 0.38877 < x^* \approx 0.4055$, thus the solution becomes less than the equilibrium.

Remark 2. Theorem 5 generalizes the known result [**12**] for the Nicholson blowflies equation with a constant concentrated delay, with $\delta < p < \delta e$. In addition, under the latter condition, for (13) there is an infinite number of rapidly oscillating solutions, see [**12**]. For the equation with a variable delay this is, generally speaking, not true, as the following example demonstrates.

Example 2. Consider the equation (35) with the delay $h(t) = t - \max\{\sin(\pi t), 0\}$, which can be rewritten as

$$h(t) = \begin{cases} t - \sin(\pi t), & 0 \le t \le 1, \\ t, & 1 \le t \le 2, \\ \dots & \dots \\ t - \sin(\pi t), & 2n \le t \le 2n+1, \\ t, & 2n+1 \le t \le 2n+2. \end{cases}$$

For any initial conditions there is t_0 such that $x(t) \le M$, $t \ge t_0$. For any t_0 we have a nonoscillatory part of solution for $t > t_0$ in the segment $[2n+1, 2n+2]$ (as a solution of the ordinary differential equation with the equilibrium x^*) and the delay does not exceed one, so by Theorem 5 and Remark 2 $x(t)$ is nonoscillatory for $t \ge 2n+1$, unless $x(t) \equiv x^*$, $t \ge 2n+1$. Thus (35) has no rapidly oscillatory solutions.

Theorem 6. *Suppose* (a1)–(a4) *hold. Let* $p = \delta e$. *Then* (5) *has no oscillatory about* x^* *solutions, other than identically equal to* x^* *for all* $t \ge t_0$.

Proof. Suppose $x(t)$ is oscillating. Let us consider two cases: 1) $x(t_0) < x^*$ for some $t_0 > 0$ and 2) $x(t) \ge x^*$ for any $t \ge 0$, but there exists $t_0 > 0$, such that $x(t_0) = x^*$. We demonstrate that in the first case the solution is nonoscillatory, while in the second case $x(t) \equiv x^*$, $t > t_0$.

1) Suppose $x(t_0) < x^*$ for some $t_0 > 0$. Since for $p = \delta e$ we have $f(x) \le x^* = f(x_M)$ (see Figure 2), then the solution of (5) for $t \ge t_0$ does not exceed the solution y of the initial value problem for the ordinary differential equation

$$\dot{y}(t) = \delta x^* - \delta y(t), \quad t \ge t_0, \quad (t_0) = x(t_0) < x^*, \tag{37}$$

which is nonoscillatory about its equilibrium state x^*: $y(t) < x^*$. Thus $x(t) \le y(t) < x^*$, so $x(t)$ is nonoscillatory about x^*.

2) Suppose $x(t) \ge x^*$ for any $t \ge 0$, but there exists $t_0 > 0$, such that $x(t_0) = x^*$. Let us demonstrate that the situation $x(t_1) > x^*$, where $t_1 > t_0$, is impossible. For almost all $t \in [t_0, t_1]$ we have $\dot{x}(t) \le 0$, since

$$\begin{aligned}\dot{x}(t) &= \delta \int_{h(t)}^{t} f(x(s))\ d_sR(t,s) - \delta x(t) \\ &\le \delta \int_{h(t)}^{t} x^*\, d_sR(t,s) - \delta x(t) \le \delta x^* - \delta x^* = 0.\end{aligned}$$

We have a contradiction: $x(t_1) > x(t_0)$, though the derivative of x is nonpositive almost everywhere in $[t_0, t_1]$. Thus $x(t) = x^*$, $t \ge t_0$, as far as $x(t_0) = x^*$ and $x(t) \ge x^*$ for any $t \ge 0$, which completes the proof. □

The following example demonstrates that the second option in the statement of Theorem 6 is possible.

Example 3. Denote $c = \ln(2)+\ln(1-e^{-1})-\ln(1-2e^{-1}) > 0$. Consider the equation

$$\dot{x}(t) = ex(h(t))e^{-x(h(t))} - x(t), \tag{38}$$

where $h(t) = t - c$, $t \le c$, $h(t) = 0$, $c \le t \le c+1$, $h(t) = t-1$, $t > c+1$. Then the solution with the initial function $\varphi(t) \equiv 2$, $t \le 0$, is

$$x(t) = 2(1-e^{-1})e^{-t} + 2e^{-1}, \quad 0 \le t \le c, x(t) \quad = 1, \quad t \ge c. \tag{39}$$

Thus this solution coincides with the equilibrium $x(t) \equiv 1$ for $t \ge c = \ln\left((2(e-1))/(e-2)\right)$.

5 Global attractivity Now let us proceed to the global attractivity in the case $\delta < p < \delta e$ (the maximum of f exceeds the equilibrium).

Theorem 7. *Suppose* (a1)–(a4) *hold and* $\delta < p < \delta e$. *Then for the solution* $x(t)$ *of* (5), (9) *we have* $\lim_{t\to\infty} x(t) = x^*$, *i.e., the positive equilibrium is globally asymptotically stable.*

Proof. By the proof of Theorem 3 for any solution in the case $\delta < p < \delta e$ there are $t_0 > 0$, $\varepsilon_1 > 0$, $\varepsilon_2 > 0$, such that

$$\varepsilon_1 \le x(t) \le M + \varepsilon_2, \quad t \ge t_0, \quad M > x^*, \quad \varepsilon_1 < x^*.$$

Here $\varepsilon_2 > 0$ is arbitrary, so without loss of generality we can assume that $M + \varepsilon_2 < x_M$, where $x_M = 1/a$ is the maximum point of $f(x)$, since $M = f(x_M) < x_M$. Denote

$$M_1 = f(M+\varepsilon_2) < M, \quad m_1 = f(\varepsilon_1) > \varepsilon_1.$$

Let $t_1 > t_0$ be such that $h(t) > t_0$, $t \ge t_1$. Then we will demonstrate that there exists $\bar{t}_1 \ge t_1$, such that $m_1 \le x(t) \le M_1$, $t \ge \bar{t}_1$. For the lower bound m_1, assume the contrary: there are points t arbitrarily large, such that $x(t) < m_1$. Then there are two possibilities:

a) $x(t) < m_1$ for any $t > t_1$, or
b) there are two points $s_2 > s_1 > t_1$, such that $x(s_2) < m_1$, $x(s_1) = m_1$.

In the case a)

$$\dot{x}(t) = \delta \int_{h(t)}^{t} f(x(s))d_sR(t,s) - \delta x(t) > \delta m_1 - \delta m_1 = 0,$$

so x is increasing and has a limit $\overline{m}$, $\varepsilon_1 < \overline{m} \le m_1$. Since $f(\overline{m}) > \overline{m}$, then

$$\dot{x}(t) = \delta \int_{h(t)}^{t} f(x(s)) d_s R(t,s) - \delta x(t) \ \to \ \delta[f(\overline{m}) - \overline{m}] > 0 \ \text{ as } t \to \infty$$

almost everywhere. Thus $\lim_{t\to\infty} x(t) = \infty$, which contradicts $\lim_{t\to\infty} x(t) = \overline{m}$.

In the case b) without loss of generality we may assume $x(t) \ge x(s_2)$, $t \in [s_1, s_2]$ (otherwise, we take the infimum $\bar{s}$ of all $s > s_1$, such that $x(s) \le x(s_2)$, and redenote it $s_2 = \bar{s}$). Then there exists $\nu > 0$, such that $x(t) < m_1$, $t \in [s_2 - \nu, s_2] \subset [s_1, s_2]$. In this interval

$$\dot{x}(t) = \delta \int_{h(t)}^{t} f(x(s))\, d_s R(t,s) - \delta x(s) > \delta m_1 - \delta m_1 > 0,$$

since $f(x(t)) > m_1$, $t \ge t_0$. This contradicts $x(t) \ge x(s_2)$, $t \in [s_1, s_2]$, thus there exists $t_2 \ge t_1$, such that $x(t) \ge m_1$ for $t \ge t_2$. We proceed with take $\bar{t}$, such that $h(t) \ge t_2$, $t \ge \bar{t}$; repeating this procedure, we obtain

$$x(t) \ge m_1, \quad t \ge t_2, \quad x(t) \ge m_2 = f(t_1), \quad t \ge t_3,$$
$$\dots, x(t) \ge m_k = f^{k-1}(m_1), \quad t \ge t_{k+1}, \dots .$$

Similarly, for the upper bound we obtain

$$x(t) \le M_1, \quad t \ge \tilde{t}_1, \quad x(t) \le M_2 = f(M_1), \quad t \ge \tilde{t}_2, \dots .$$

The sequences $m_1, m_2, m_3, m_4, m_5, m_6$ and M_1, M_2, M_3 are illustrated in Figure 4.

Since $\lim_{k\to\infty} m_k = \lim_{k\to\infty} M_k = x^*$, $\lim_{t\to\infty} x(t) = x^*$, which completes the proof. □

Remark 3. Theorem 7 claims the global attractivity for the positive equilibrium N^* of (5). in addition, its proof demonstrates the following for solutions with initial conditions satisfying (a4).

If $|N(t) - N^*| < \varepsilon < \min\{1/a - N^*, N^*\}$ for all $t \le t_1$, then $|N(t) - N^*| < \varepsilon$ for $t > t_1$ as well.

Thus the equilibrium solution N^* of (5) is stable. Attractivity for any positive initial function implies asymptotic stability. We conjecture

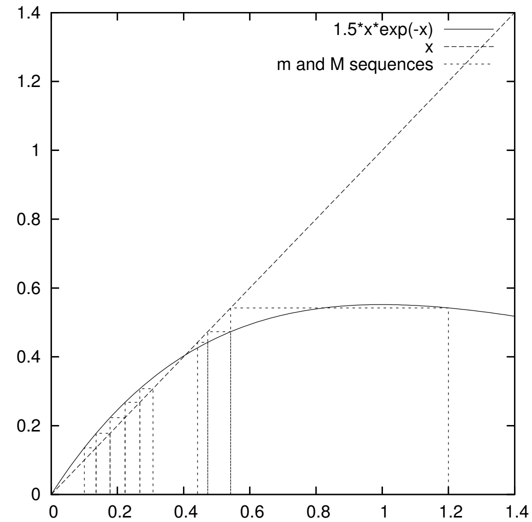

FIGURE 4: The sequences $m_1, m_2, m_3, m_4, m_5, m_6$ and M_1, M_2, M_3 illustrate the steps of convergence to the positive equilibrium

that generally, without additional restriction that the delay is globally bounded ($\sup_{t>0}[t-h(t)] < \infty$) the equation (5) is not uniformly asymptotically stable, while (5) with a bounded delay is uniformly asymptotically stable.

Remark 4. Let us note that for $\delta < p < \delta e$ the positive equilibrium solution of (13) is locally asymptotically stable [**36**]. In Theorem 7 we prove for a more general equation that this equilibrium is globally asymptotically stable.

6 Conclusions and discussion

We extended some results known for the Nicholson's blowflies equation (13) to the equation with a distributed delay. In particular, the following issues were considered for (5):

1. Existence and uniqueness of solutions;
2. Positiveness and permanence of solutions (in particular, it was proved that the solution eventually does not exceed the maximum of $f(x)$);
3. Convergence of all nonoscillatory solutions to the positive equilibrium;

4. Nonexistence of slowly oscillatory solutions in the case when the maximum of $f(x)$ exceeds the equilibrium point ($\delta < p < \delta e$);
5. Global attractivity of the positive equilibrium in the case $\delta < p < \delta e$.

However, the following issues are still to be studied:

1. If $p > \delta e$, what are sufficient oscillation and nonoscillation conditions for (5)? Relevant results for (13) are presented in [**16, 22**].
2. If $p > \delta e$, what are sufficient attractivity conditions of the positive equilibrium point x^* for (5)? The results for (13) can be found in [**16, 23**].
3. As Example 2 demonstrates, for $p < \delta e$ we cannot guarantee the existence of rapidly oscillatory solutions in the case of the general distributed delay, in contrast to (13) (see [**12**]). Which restrictions on the distributed delay will yield the existence of an infinite number of rapidly oscillatory solutions?

Let us discuss possible generalizations (6) with a reproduction function f. Everywhere below we assume that f is a continuous function; otherwise, we should impose additional constraints on the delay distribution just to provide that the integral in (6) exists. The following conjectures extend the results of the present paper to a continuous reproduction function f of a rather general form.

Conjecture 1. *Suppose $\delta > 0$, $f(x)$ is bounded, $f(x) > 0$ for $x > 0$ and there exists $K > 0$, such that $|f(x) - f(y)| \le K|x - y|$ for any $x, y \ge 0$, $\delta > 0$ and* (a2)–(a4) *hold. Then there exists a unique solution of* (6), (9).

Conjecture 2. *Suppose $\delta > 0$, $f(x)$ is continuous, $f(x) > 0$ for $x > 0$ and* (a2)–(a4) *hold. Then any solution of* (6), (9) *is positive.*

Everywhere below we assume x^* is an equilibrium point of (6), i.e., $f(x^*) = x^*$.

Conjecture 3. *Suppose $\delta > 0$, $f(x)$ is continuous, bounded, $f(x) > 0$ for $x > 0$,* (a2)–(a4) *and*

$$f(x) > x, \quad 0 < x < x^*; \qquad f(x) < x, \quad x > x^* \tag{40}$$

are satisfied. Then any solution of (6), (9) *is permanent.*

For the proof, we suggest to choose t_1, such that $h(t) \ge 0$, $t \ge t_1$, and consider the maximal $x_{\max}$ and the minimal $x_{\min}$ values of the solution for $t \in [0, t_1]$ (both values are positive). Then the upper bound A of the solution is the maximal value among the following: $x_{\max}$, x^* and M, where M is the upper bound of f. The lower bound of the solution is the minimal value among $x_{\min}$, x^* and $\inf_{x \in [a,A]} f(x)$, where $a = \min\{x^*, x_{\min}\}$.

Conjecture 4. *Suppose $\delta > 0$, $f(x)$ is continuous, $f(x) > 0$ for $x > 0$,* (a2)–(a4) *and* (40) *hold. Then any nonoscillatory about x^* solution of* (6), (9) *tends to x^*.*

Conjecture 5. *Suppose $\delta > 0$, $f(x)$ is continuous, $f(x) > 0$ for $x > 0$, $f(x) < x^*$ for $x < x^*$,* (a2)–(a4), (40) *and at least one of the following conditions hold:*

(a) *$f(x) > x^*$ for $x > x^*$;*
(b) *there exists $c > x^*$, such that $f(x)$ is increasing for $0 \le x \le c$ and is decreasing for $x > c$.*

Then the equation (6) *has no slowly oscillatory about x^* solutions.*

Conjecture 6. *Suppose $\delta > 0$, $f(x)$ is continuous, $f(x) > 0$ for $x > 0$,* (a2)–(a4) *and* (40) *hold and x^* is the global maximum of f: $f(x) < x^*$, if $x \neq x^*$. Then* (6) *has no oscillatory about x^* solutions other than identically equal to x^* for all $t \ge t_0$.*

Conjecture 7. *Suppose $\delta > 0$, $f(x)$ is continuous, $f(x) > 0$ for $x > 0$, $f(x) < x^*$ for $x < x^*$,* (a2)–(a4), (40) *and at least one of the following conditions hold:*

(a) *$f(x) > x^*$ for $x > x^*$;*
(b) *there exists $c > x^*$, such that $f(x)$ is increasing for $0 \le x \le c$ and is decreasing for $x > c$.*

Then any solution of (6), (9) *tends to the positive equilibrium.*

Let us note that in (5) the function $f(x)$ satisfies $\lim_{x\to\infty} f(x) = 0$ which is sometimes referred as a scramble competition model when limited resources are distributed uniformly [**6**]. All above conjectures are also relevant for the case of a contest competition, where the reproduction function satisfies $\lim_{x\to\infty} f(x) = K > 0$.

Acknowledgement The authors are grateful to the referee for valuable comments and suggestions.

REFERENCES

1. H. T. Banks, D. M. Bortz and S. E. Holte, *Incorporation of variability into the modeling of viral delays in HIV infection dynamics*, Math. Biosci. **183**(1) (2003), 63–91.
2. E. Beretta, R. Kon and Y. Takeuchi, *Nonexistence of periodic solutions in delayed Lotka-Volterra systems*, Nonlinear Anal. Real World Appl. **3**(1) (2002), 107–129.
3. E. Beretta and Y. Kuang, *Geometric stability switch criteria in delay differential systems with delay dependent parameters,* SIAM J. Math. Anal. **33**(5) (2002), 1144–1165.
4. L. Berezansky and E. Braverman, *Oscillation properties of a logistic equation with distributed delay,* Nonlinear Anal. Real World Appl. **4** (2003), 1–19.
5. S. Bernard, J. Bélair and M. C. Mackey, *Sufficient conditions for stability of linear differential equations with distributed delay,* Discrete Contin. Dyn. Syst. Ser. B **1**(2) (2001), 233–256.
6. F. Brauer and C. Castillo-Chavez, *Mathematical Models in Population Biology and Epidemiology,* Springer-Verlag New York, 2001.
7. T. A. Burton, *Fixed points, Volterra equations, and Becker's resolvent*, Acta Math. Hungar. **108**(3) (2005), 261–281.
8. Y. Chen, *Periodic solutions of delayed periodic Nicholson's blowflies models,* Can. Appl. Math. Q. **11**(1) (2003), 23–28.
9. C. Corduneanu, *Functional Equations with Causal Operators, Stability and Control: Theory, Methods and Applications*, **16**, Taylor & Francis, London, 2002.
10. R. V. Culshaw, S. Ruan and G. Webb, *A mathematical model of cell-to-cell spread of HIV-1 that includes a time delay,* J. Math. Biol. **46**(5) (2003), 425–444.
11. K. Gopalsamy, *Stability and Oscillation in Delay Differential Equations of Population Dynamics,* Kluwer Academic Publishers, Dordrecht, Boston, London, 1992.
12. I. Györi and S. I. Trofimchuk, *On the existence of rapidly oscillatory solutions in the Nicholson blowflies equation,* Nonlinear Analysis **48** (2002), 1033–1042.
13. W. S. C. Gurney, S. P. Blythe and R. M. Nisbet, *Nicholson's blowflies revisited,* Nature **287** (1980), 17–21.
14. M. I. Gil', *Boundedness of solutions of nonlinear differential delay equations with positive Green functions and the Aizerman-Myshkis problem,* Nonlinear Anal. **49**(8) (2002), 1065–1078.
15. S. A. Gourley, *Travelling fronts in the diffusive Nicholson's blowflies equation with distributed delays,* Math. Comput. Modelling **32**(7–8) (2000), 843–853.
16. I. Györi and G. Ladas, *Oscillation Theory of Delay Differential Equations,* Clarendon Press, Oxford, 1991.
17. R. Hinch and S. Schnell, *Mechanism equivalence in enzyme-substrate reactions: distributed differential delay in enzyme kinetics,* J. Math. Chem. **35**(3) (2004), 253–264.
18. C. Huang and S. Vandewalle, *An analysis of delay-dependent stability for ordinary and partial differential equations with fixed and distributed delays,* SIAM J. Sci. Comput. **25**(5) (2004), 1608–1632.
19. G. E. Hutchinson, *Circular causal systems in ecology,* Ann. N.Y. Acad. Sci. **50** (1948), 221–246.
20. M. Kot, *Elements of Mathematical Ecology,* Cambridge University Press, 2001.

21. Y. Kuang, *Delay Differential Equations with Applications in Population Dynamics*, Mathematics in Science and Engineering **191**, Academic Press, Boston, MA, 1993.
22. M. R. S. Kulenovic, G. Ladas and Y. S. Sficas, *Global attractivity of Nicholson blowflies,* Applicable Analysis **43** (1992), 109–124.
23. M. R. S. Kulenovic and G. Ladas, *Linearized oscillation in population dynamics,* Bull. Math. Biology **49** (1987), 615–627.
24. B. Li, G. S. K. Wolkowicz and Y. Kuang, *Global asymptotic behavior of a chemostat model with two perfectly complementary resources and distributed delay,* SIAM J. Appl. Math. **60**(6) (2000), 2058–2086.
25. S. Liu, M. Kouche and N. Tatar, *Permanence, extinction and global asymptotic stability in a stage structured system with distributed delays*, J. Math. Anal. Appl. **301**(1) (2005), 187–207.
26. E. Liz, C. Martínez and S. Trofimchuk, *Attractivity properties of infinite delay Mackey-Glass type equations,* Differential Integral Equations **15**(7) (2002), 875–896.
27. A. J. Nicholson, *An outline of the dynamics of animal populations,* Austral. J. Zool. **2** (1954), 9–65.
28. S. I. Niculescu and R. Lozano, *On the passivity of linear delay systems,* IEEE Trans. Automat. Control **46**(3) (2001), 460–464.
29. C. G. Philos and I. K. Purnaras, *Asymptotic properties, nonoscillation, and stability for scalar first order linear autonomous neutral delay differential equations,* Electronic Journal of Differential Equations **2004**(3) (2004), 1–17.
30. A. Ponosov and A. Shindiapin, *Azbelev's W-transform and its applications in mathematical modeling,* Differ. Uravn. Protsessy Upr. **4** (2003), 57–72.
31. J. P. Richard, *Time-delay systems: an overview of some recent advances and open problems,* Automatica J. IFAC **39**(10) (2003), 1667–1694.
32. X. H. Tang, *Asymptotic behavior of a differential equation with distributed delays,* J. Math. Anal. Appl. **301**(2) (2005), 313–335.
33. S. Tang and L. Chen, *Global qualitative analysis for a ratio-dependent predator-prey model with delay*, J. Math. Anal. Appl. **266**(2) (2002), 401–419.
34. V. Volterra, *Fluctuations in the abundance of species considered mathematically,* Nature **118** (1926), 558–560.
35. L. Wang, *Stabilizing Hopfield neural networks via inhibitory self-connections,* J. Math. Anal. Appl. **292**(1) (2004), 135–147.
36. J. Wei and M. Y. Li, *Hopf bifurcation analysis in a delayed Nicholson blowflies equation,* Nonlinear Anal. **60**(7) (2005), 1351–1367.
37. S. Yuan, Y. Song and M. Han, *Direction and stability of bifurcating periodic solutions of a chemostat model with two distributed delays,* Chaos Solitons Fractals **21**(5) (2004), 1109–1123.

Corresponding author: Elena Braverman

Department of Mathematics and Statistics, University of Calgary,

2500 University Drive N.W., Calgary, Alberta, Canada, T2N 1N4

E-mail address: maelena@math.ucalgary.ca

E-mail address: damir@math.ucalgary.ca