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Delay effect in models of population growth

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Abstract

First, we systematize earlier results on the global stability of the model $\dot{x} + \mu x = f(x(\cdot - \tau))$ of population growth. Second, we investigate the effect of delay on the asymptotic behavior when the nonlinearity f is a unimodal function. Our results can be applied to several population models [Elements of Mathematical Ecology, 2001 [7]; Appl. Anal. 43 (1992) 109–124; Math. Comput. Modelling, in press; Funkt. Biol. Med. 256 (1982) 156–164; Math. Comput. Modelling 35 (2002) 719–731; Mat. Stos. 6 (1976) 25–40] because the function f does not need to be monotone or differentiable. Specifically, our results generalize earlier result of [Delay Differential Equations with Applications in Population Dynamics, 1993], since our function f may not be differentiable.

Keywords: Delay differential equations; Comparison theorem; ω-limit set of a persistent solution; One-parameter semi-group; Convergence to equilibrium; Nicholson's blowfly model; Periodic solutions

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1. Introduction

Given a continuous function $f:\mathbb{R}_+ \to \mathbb{R}_+$ and a nonnegative function $\xi \not\equiv 0$ on $[-\tau, 0]$, we consider the delay differential equation

$$\dot{x} + \mu x = f\big(x(\cdot - \tau)\big), \qquad x(s) = \xi(s) \quad \text{for } s \in [-\tau, 0]. \tag{1.1}$$

For simplicity, we assume throughout that ξ is bounded. It follows that (1.1) has a unique solution—e.g., one can proceed by intervals of length τ—with $x_{f,\xi}(\cdot)$ nonnegative and continuous for $t \geqslant 0$. We denote the solution of the delay differential equation (1.1) by $x(\cdot) = x_{f,\xi}(\cdot)$. It is easily seen that one has the equivalent integrated formulation:

$$x(t) = e^{-\mu(t-a)}x(a) + \int_a^t e^{-\mu(t-s)} f\big(x(s-\tau)\big)\, ds \tag{1.2}$$

for $t \geqslant 0$. (Actually, continuity of f is not needed for (1.2), only enough regularity to ensure the requisite integrability.) We further note the following

Lemma 1. *Given real constants μ, ν and $\tau > 0$, there is a function $X = X(t)$ such that the solution y of the autonomous linear delay differential equation*

$$\dot{y} + \mu y + \nu y(t-\tau) = g(t), \quad y|_{[-\tau,0]} = \eta, \tag{1.3}$$

has the integral representation

$$y(t) = y_0(t;\eta) + \int_0^t X(t-s) g(s)\, ds, \tag{1.4}$$

where $y_0 = y_0(\cdot;\eta)$ is the solution of the associated homogeneous initial value problem. Both $X(\cdot)$ and y_0 decay exponentially if

$$h(z) := z + \mu + \nu e^{-\tau z} = 0 \quad \Rightarrow \quad \Re(z) < 0, \tag{1.5}$$

i.e., if every root of the characteristic equation has (*strictly*) *negative real part, and grow exponentially if $h(\cdot)$ has any root with positive real part.*

Proof. See, e.g., [6]. Note that

$$\|X\|_1 = \int_0^\infty \big|X(t)\big|\, dt < \infty \tag{1.6}$$

when X decays exponentially. □

A standard calculation shows that (1.5) holds for all $\tau > 0$ when $|\nu| < \mu$ and, conversely, fails when $|\nu| > \mu$ unless τ is restricted so that

$$\tau < \tau_* = \tau_*(\mu, \nu) = \frac{\arccos[-\mu/\nu]}{\sqrt{\nu^2 - \mu^2}} \tag{1.7}$$

(cf., e.g., [1,5]). We will later focus our attention on delay equations of the form (1.1) in which the nonlinearity f satisfies:

- $f:\mathbb{R}_+ = [0,\infty) \to \mathbb{R}_+$ is continuous.
- There is a unique equilibrium $\bar{r} > 0$, so $\mu\bar{r} = f(\bar{r}) > 0$.
- $$\begin{cases} f(r) > \mu r & \text{for } 0 < r < \bar{r}, \\ f(r) < \mu r & \text{for all } r > \bar{r}. \end{cases} \tag{1.8}$$

2. Comparison theorem and consequences

An easy argument then provides the following basic comparison theorem.

Theorem 2. *Let f,ξ and correspondingly g,η be as above with g nondecreasing. Set $x := x_{f,\xi}$ and $y := x_{g,\eta}$.*

(1) *Suppose $f \leqslant g$ where relevant (i.e., $f(r) \leqslant g(r)$ for each r in the range of $f(x)$) and suppose $\xi \leqslant \eta$ on $[-\tau, 0]$. Then $x(t) \leqslant y(t)$ for all t.*
(2) *Suppose $f \geqslant g$ where relevant and $\xi \geqslant \eta$ on $[-\tau, 0]$. Then $x(t) \geqslant y(t)$ for all t.*

Proof. Both cases go in essentially the same fashion, so we only consider the first case (with $f \leqslant g$, etc.). Now suppose the result were false. We could then find a largest t_* such that $x(s) \leqslant y(s)$ on $[-\tau, t_*)$. For any $t < t_* + \tau$ we would have $r = t - s - \tau < t_*$ for $0 \leqslant s < t$ whence $x(r) \leqslant y(r)$ for such r so $f(x(r)) \leqslant g(x(r)) \leqslant g(y(r))$. It follows from (1.2) and the corresponding integrated formulation involving g that $x(t) \leqslant y(t)$ for such $t \in [t_*, t_* + \tau)$ as well, contradicting the definition of t_*. $\square$

We remark that this comparison theorem generalizes to equations in partially ordered Banach spaces, etc., but we do not pursue this here.

Corollary 3. *Let f, ξ, x be as above in* (1.1).

(1) *Suppose there is some $M > 0$ such that $f(r) \leqslant \mu \max\{r, M\}$ and suppose $x \leqslant M$ on $[t_* - \tau, t_*]$. Then, also $x(t) \leqslant M$ for all $t \geqslant t_*$.*
(2) *Suppose there is some $m > 0$ such that $f(r) \geqslant \mu \min\{r, m\}$ and suppose $x \geqslant m$ on $[t_* - \tau, t_*]$. Then, also $x(t) \geqslant m$ for all $t \geqslant t_*$.*

Proof. Again, both cases go in essentially the same fashion so we need only consider the first. Further, since we can restart at any t_* it is sufficient to consider $t_* = 0$ so we may assume $\xi \leqslant M$ on $[-\tau, 0]$.

Take $\eta \equiv M$ and $g(r) := \mu \max\{r, M\}$. Clearly, g is nondecreasing and the hypotheses yield $\xi \leqslant \eta$ and $f \leqslant g$. We immediately verify that $y \equiv M$ satisfies the delay differential equation to have $y = x_{g,\eta}$ so that the result follows from Theorem 2. $\square$

We will be seeking asymptotic upper and lower bounds for solutions $x(t)$ of (1.1) and to this end it is convenient to introduce

$$\bar{m} = \bar{m}(x) = \liminf_{t\to\infty} x(t), \qquad \bar{M} = \bar{M}(x) = \limsup_{t\to\infty} x(t). \tag{2.1}$$

Lemma 4. *Let f be bounded with $0 < f(r) \leqslant B$. Then $\bar{M} \leqslant B/\mu$.*

Proof. From (1.2) we have

$$x(t) \leqslant e^{-\mu t}x(0) + \int_{-\tau}^{t} Be^{-\mu(t-s)}\,ds,$$

which gives the desired result as $t \to \infty$. □

We also note some information about the ω-limit set of a nontrivial solution x, e.g., as used in [10].

Lemma 5. *For any bounded solution $x = x_{f,\xi}$ of* (1.1), *there are functions u, v defined on $\mathbb{R}$ such that*

(i) u, v *satisfy* (1.1) *on* $\mathbb{R}$.

(ii) $\bar{m} \leqslant u(t), v(t) \leqslant \bar{M}$.

(iii) $u(0) = \bar{M}, \quad \dot{u}(0) = 0; \qquad v(0) = \bar{m}, \quad \dot{v}(0) = 0,$ (2.2)

with $\bar{m} = \bar{m}(x)$, $\bar{M} = \bar{M}(x)$ as in (2.1).

For completeness, we sketch a proof here.

Proof. By the definition of $\bar{M}$ there is a sequence $t_k \to \infty$ such that $x(t_k) \to \bar{M}$ and we set $u_k(t) = x(t_k + t)$—e.g., for $t \geqslant -t_k$. The set $\{u_k(\cdot)\}$ is uniformly bounded with uniformly bounded derivatives, so there is a function u such that $u_k \to u$ uniformly on compact sets in $\mathbb{R}$. Since the derivatives also converge uniformly on compact subsets and each u_k satisfies (1.1), so does u. Since, for compact set $\mathcal{I}$ and any $\varepsilon > 0$, the definition of $\bar{M}$ gives $\bar{m} - \varepsilon < u_k < \bar{M} + \varepsilon$ for large enough k, we have (ii) in the limit. Since $u_k(0) = x(t_k) \to \bar{M}$, we have $u(0) = \bar{M}$ and, as that is necessarily a maximum, we also have $\dot{u}(0) = 0$. The construction of $v(\cdot)$ is similar. □

3. Asymptotic bounds and attraction

Theorem 6. *Let f, ξ, and x be as above in* (1.1).

(1) *Suppose there is some $\bar{r} \geqslant 0$ such that*

$$\begin{aligned} &f(r) \leqslant \mu\bar{r} \quad \text{for } 0 < r \leqslant \bar{r}, \\ &f(r) < \mu r \quad \text{for all } r > \bar{r}. \end{aligned} \tag{3.1}$$

Then, $\bar{M} \leqslant \bar{r} < \infty$ *and there is a nonincreasing positive function* z_+ *such that*

$$x(t) := x_{f,\xi}(t) \leqslant z_+(t) \quad \text{with } z_+(t) \to \bar{r} \text{ as } t \to \infty. \tag{3.2}$$

(2) *Suppose there is some* $\bar{r} \geqslant 0$ *such that*

$$\begin{aligned} f(r) &\geqslant \mu\bar{r} \quad \text{for } r \geqslant \bar{r}, \\ f(r) &> \mu r \quad \text{for all } 0 < r < \bar{r}. \end{aligned} \tag{3.3}$$

Then, $\bar{m} \geqslant \bar{r}$ *and there is a nondecreasing nonnegative function* z_- *such that*

$$x(t) := x_{f,\xi}(t) \geqslant z_-(t) \quad \text{with } z_-(t) \to \bar{r} \text{ as } t \to \infty. \tag{3.4}$$

Proof. Yet again, both cases go in essentially the same fashion. For the first case we begin by fixing $M > \bar{r}$, $M \geqslant \xi$, and any $\varepsilon = \varepsilon_0 > 0$ with $\bar{r} + \varepsilon < M$. We then let

$$\gamma_\varepsilon := \max\bigl\{f(r)/r\colon \bar{r} + \varepsilon \leqslant r \leqslant M\bigr\} < \mu \tag{3.5}$$

and, choosing γ so $\gamma_\varepsilon \leqslant \gamma < \mu$, set

$$g(r) = g_\varepsilon(r) := \max\bigl\{\mu(\bar{r} + \varepsilon), \gamma r\bigr\}. \tag{3.6}$$

Now, let $\lambda_\varepsilon > 0$ satisfy the characteristic equation

$$\lambda_\varepsilon + \gamma e^{\lambda_\varepsilon \tau} = \mu \tag{3.7}$$

and set

$$y^*(t) := y^*_\varepsilon(t) := M e^{-\lambda_\varepsilon t}. \tag{3.8}$$

If we did not have ξ bounded on $[-\tau, 0]$, we note that x is continuous for $t \geqslant 0$ so we could restart at τ with bounded initial data. Note also that, since f was assumed continuous and $[\bar{r} + \varepsilon, M]$ is compact and nonempty, the 'max' in (3.5) is achieved and $\gamma_\varepsilon < \mu$.

Moreover, one easily sees that (3.7) has a unique positive solution since $\gamma < \mu$.

The construction yields y^* which satisfies the delay differential equation

$$\dot{y}(t) = -\mu y(t) + \gamma y(t - \tau) \tag{3.9}$$

so, taking $\eta = \eta_\varepsilon$ to be y^* on $[-\tau, 0]$, this y^* must coincide with $y = x_{g,\eta}$ so long as $y^*(t - \tau) \geqslant \bar{r} + \delta$, where $\gamma(\bar{r} + \delta) = \mu(\bar{r} + \varepsilon)$. Note that we can—and do—choose γ close enough to μ to ensure that $\delta \leqslant 2\varepsilon$.

To apply Theorem 2, we note that g, as given by (3.6), is clearly nondecreasing and observe that our hypotheses ensure directly that $f(r) \leqslant g(r)$ for $r \leqslant \bar{r}$ and for $\bar{r} \leqslant r \leqslant \bar{r} + \varepsilon$, while choosing $\gamma \geqslant \gamma_\varepsilon$ ensures that $f(r) \leqslant g(r)$ for $\bar{r} + \varepsilon \leqslant r \leqslant M$. Since Corollary 3 ensures $x(t) \leqslant M$, it follows that $f \leqslant g$ where relevant and that $\xi \leqslant M \leqslant \eta$. Thus, Theorem 2 applies and we have $x \leqslant y := x_{g,\eta}$—whence $x \leqslant y^*$ as long as y^* coincides with y. Noting that this includes an interval of length τ on which $y \leqslant \bar{r} + \delta \leqslant \bar{r} + 2\varepsilon$, we can apply Corollary 3 again (now restarting at the end of this interval) to see that x thereafter remains below $\bar{r} + 2\varepsilon$—i.e., we have shown that

$$x(t) \leqslant z_\varepsilon(t) := \max\{M e^{-\lambda_\varepsilon t}, \bar{r} + 2\varepsilon\}$$

for all t. Since this holds for arbitrarily small $\varepsilon > 0$, we have (3.2), as desired, with $z_+(t) := \inf\{z_\varepsilon(t)\colon \varepsilon > 0\}$. This completes the proof for the first case.

Using the second case in Theorem 2, we will get a corresponding lower bound. First, however, we note that (1.2) gives

$$x(\tau) = e^{-\mu\tau} x(0) + \int_{-\tau}^{0} e^{-\mu(\tau+s)} f\bigl(\xi(s)\bigr)\, ds,$$

which will be strictly positive for nonnegative, nontrivial ξ—and then $x(t)$ will be strictly positive for all $t \geqslant \tau$. We can therefore assume, restarting if necessary, that $\xi \geqslant m$ for some $m > 0$. The rest of the proof is then almost exactly like that for the first case. □

Theorem 7. *Let f, ξ, x be as above in* (1.1) *and suppose there is some $\bar{r} \geqslant 0$ such that*

$$\begin{aligned} &f(r) > \mu r \quad \text{for } 0 < r < \bar{r}, \\ &f(r) < \mu r \quad \text{for all } r > \bar{r}. \end{aligned} \tag{3.10}$$

Suppose, also, that

$$\begin{aligned} &\text{either} \quad f(r) \leqslant \mu\bar{r} \quad \text{for } 0 < r < \bar{r} \\ &\text{or} \quad\quad\ f(r) \geqslant \mu\bar{r} \quad \text{for all } r \geqslant \bar{r}. \end{aligned} \tag{3.11}$$

Then, $x_{f,\xi}(t) \to \bar{r}$ as $t \to \infty$ for every nontrivial initial data $\xi \geqslant 0$—i.e., $\bar{m} = \bar{r} = \bar{M}$.

Proof. We consider explicitly only the first alternative in (3.11). Since this with (3.10) include (3.1), the first case of Theorem 6 applies to give $\bar{M} \leqslant \bar{r}$. If $\bar{r} = 0$, we are now done so we need only show $\bar{m} \geqslant \bar{r}$ when $\bar{r} > 0$. For any $\varepsilon > 0$ we can choose $\delta > 0$ so $f(r) \geqslant f(\bar{r}) - \mu\varepsilon$ on $[\bar{r}, \bar{r} + \delta]$ and there is some t_δ such that $x(t) \leqslant \bar{r} + \delta$ for all $t \geqslant t_\delta - \tau$. Setting $\tilde{r} = \bar{r} - \varepsilon$, this gives $f(r) \geqslant \mu\tilde{r}$ for $\tilde{r} \leqslant r \leqslant \bar{r} + \delta$. Restarting at t_δ, and noting that only values of r below $\bar{r} + \delta$ are relevant, we thus have the hypotheses for the second case of Theorem 6 for the restarted problem with $\bar{r}$ replaced by $\tilde{r}$. Thus, $\bar{m} \geqslant \tilde{r} = \bar{r} - \varepsilon$ for arbitrary $\varepsilon > 0$ so $\bar{m} \geqslant \bar{r}$. Combining these upper and lower asymptotic bounds is just the desired result. □

We henceforth will consider equations of the form (1.1) subject to the hypotheses (1.8). If $\max\{f(r)\colon\ r > 0\} = B \leqslant \mu\bar{r}$, giving the first case of (3.11), then we already know from Theorem 7 that all solutions converge to the equilibrium $\bar{r}$, so we will also assume henceforth that $B > \mu\bar{r}$ with $y_0 < \bar{r}$: (1.8) then gives (3.10) but we have neither case of (3.11).

4. Attraction dependent on the delay

As noted, we henceforth assume (1.8):

- $f : \mathbb{R}_+ = [0, \infty) \to \mathbb{R}_+$ is continuous.
- There is a unique equilibrium $\bar{r} > 0$, so $\mu\bar{r} = f(\bar{r}) > 0$.
- $$\begin{cases} f(r) > \mu r & \text{for } 0 < r < \bar{r}, \\ f(r) < \mu r & \text{for all } r > \bar{r}. \end{cases} \tag{4.1}$$

Lemma 8. *Assume* (4.1). *Then, for every nontrivial solution x of* (1.1) *we have*

$$e^{-\mu\tau}\bar{r} \leqslant \bar{m} \leqslant \bar{r} \leqslant \bar{M} \leqslant \max_{e^{-\mu\tau}\bar{r} \leqslant r \leqslant \bar{r}} f(r)/\mu \tag{4.2}$$

with $\bar{m} = \bar{m}(x)$, $\bar{M} = \bar{M}(x)$ as in (2.1).

Proof. From Corollary 3 we know x is bounded and let u, v be as in Lemma 5. Then, as $\dot{u}(0) = 0 = \dot{v}(0)$,

$$f\big(u(-\tau)\big) = \mu u(0) = \mu\bar{M} \geqslant \mu u(-\tau)$$

and, similarly, $f(v(-\tau)) = \mu v(0) \leqslant \mu v(-\tau)$. But $f(r) > \mu r$ if and only if $x < \bar{r}$, so $u(-\tau) \leqslant \bar{r} \leqslant v(-\tau)$. Thus,

$$v(0) = \bar{m} \leqslant u(-\tau) \leqslant \bar{r} \leqslant v(-\tau) \leqslant \bar{M}. \tag{4.3}$$

Since u, v satisfy (1.1) on all of $\mathbb{R}$, we may apply (1.2) with $t = 0$, $a = -\tau$ to get, as $f(\cdot) \geqslant 0$,

$$\bar{m} = v(0) = e^{-\mu\tau}v(-\tau) + \int_{-\tau}^{0} e^{\mu s} f\big(x(s-\tau)\big)\,ds \geqslant e^{-\mu\tau}v(-\tau) \geqslant e^{-\mu\tau}\bar{r}$$

and consequently, $u(-\tau) \geqslant v(0) \geqslant e^{-\mu\tau}\bar{r}$. Therefore,

$$u(0) = f\big(u(-\tau)\big)/\mu \leqslant \max_{e^{-\mu\tau}\bar{r} \leqslant r \leqslant \bar{r}} f(r)/\mu.$$

The proof is complete. □

Our next objective is to show global attraction to the equilibrium when the delay τ is not too large.

Theorem 9. *Assume* (4.1) *and the following pair of one-sided Lipschitz conditions*:

$$\begin{aligned} &0 \leqslant f(r) - \mu\bar{r} \leqslant L_1(\bar{r} - r) \quad \text{for } e^{-\mu\tau}\bar{r} \leqslant r < \bar{r}, \\ &0 \leqslant \mu\bar{r} - f(r) \leqslant L_2(r - \bar{r}) \quad \text{for } \bar{r} < r \leqslant B. \end{aligned} \tag{4.4}$$

Suppose τ is such that

$$(1 - e^{-\mu\tau}) < \frac{\mu}{\sqrt{L_1 L_2}}. \tag{4.5}$$

Then, every nontrivial solution of (1.1) *converges to the equilibrium $\bar{r}$.*

Proof. Let u, v be as in Lemmas 5 and 8. It then follows from (4.3) that there is some $a \in [-\tau, 0]$ such that $u(a) = \bar{r}$ and we set

$$\mathcal{A} = \big\{s \in [a, 0] \subset [-\tau, 0]\colon\ u(s-\tau) \leqslant \bar{r}\big\}.$$

Note that for $s \in [-\tau, 0] \setminus \mathcal{A}$ we have $u = u(s-\tau) > \bar{r}$ so $f(u) - \mu\bar{r} \leqslant 0$ by (4.1), while for $t \in \mathcal{A}$ we have $u \leqslant \bar{r}$ and $e^{-\mu\tau}\bar{r} \leqslant \bar{m} \leqslant u$ from (4.2) in Lemma 8 so (4.4) gives

$$f(u) - \mu\bar{r} \leqslant L_1(\bar{r} - u) \leqslant L_1(\bar{r} - \bar{m}).$$

Thus,

$$\int_{\mathcal{A}} e^{\mu s}\big[f(u)-\mu\bar r\big]\,ds \leqslant L_1(\bar r-\bar m)\int_{-\tau}^{0} e^{\mu t}\,ds = L_1(\bar r-\bar m)(1-e^{-\mu\tau}).$$

Applying (1.2) with $t=0$ and this a, we then have

$$\begin{aligned}\bar M-\bar r &= \big[u(0)-e^{\mu a}u(a)\big]+\mu\int_a^0 e^{\mu s}\,ds = \int_a^0 e^{\mu s}\big[f\big(u(s-\tau)\big)-\mu\bar r\big]\,ds\\ &\leqslant \int_{\mathcal{A}} e^{\mu s}\big[f(u)-\mu\bar r\big]\,ds \leqslant L_1(\bar r-\bar m)(1-e^{-\mu\tau})/\mu.\end{aligned}$$

Somewhat similarly, we have some $a\in[-\tau,0]$ such that $v(a)=\bar r$ and now set $\mathcal{A}=\{s\in[a,0]\colon\ v(s-\tau)\geqslant\bar r\}$, noting that (4.4) ensures that $f(r)\geqslant\mu\bar r$ for $r\in[e^{-\mu\tau}\bar r,\bar r]$. Much as before we then get

$$\bar r-\bar m \leqslant L_2(\bar M-\bar r)(1-e^{-\mu\tau})/\mu$$

and combining gives $(\bar r-\bar m)\leqslant[L_1L_2(1-e^{-\mu\tau})^2/\mu^2](\bar r-\bar m)$. Thus, using the assumption (4.5), we have $\bar m=\bar r$ and then $\bar M=\bar r$ as well. $\square$

Essentially the same argument gives a localized version when, instead of (4.4) and (4.5), we have $|f'|$ suitably small near $\bar r$.[1]

5. Another stability result

We now return to the integral formula (1.4), noting that if x is a solution of (1.1), then $y=x-\bar r$ is a solution of (1.3) and an appropriate choice of g:

$$g(t)=f_1\big(y(t-\tau)\big)\quad\text{with } f_1(r):=\big[f(\bar r+r)-f(\bar r)\big]+\nu r, \tag{5.1}$$

where, of course, we anticipate taking $\nu=-f'(\bar r)$ for differentiable functions f, although this is not required.

It is worth noting that with this choice of ν we necessarily have $L_1,L_2\geqslant|f'(\bar r)|=\nu$ in Theorem 9 so that Lemma 1 suggests that we could not expect asymptotically stable convergence to equilibrium when $\nu>\mu$ if we do not have (1.7); indeed, as we will note in more detail in the following section, (1.1) will then have a nontrivial periodic solution. Even ignoring the constraint on τ in requiring that $f(r)\geqslant\mu\bar r$ for $r\in[e^{-\mu\tau}\bar r,\bar r]$, the assumption (4.5) taking $L_1=L_2=-f'(\bar r)=\nu$ leads to $(1-e^{-\mu\tau})<\mu/\nu$ or

$$\tau<\frac{1}{\mu}\ln\left[\frac{1}{1-\mu/\nu}\right]. \tag{5.2}$$

[1] Since we anticipate having $f(0)=0$, this part of (4.4) must be treated as a significant constraint on τ.

Clearly this, as a sufficient condition for convergence to equilibrium, is the best one can obtain using Theorem 9 and it is interesting to compare with the (necessarily weaker) condition (1.7). There is obviously a gap between these, and we now seek to handle intermediate delays under appropriate conditions.

Theorem 10. *Suppose f is a unimodal function and $\tau > 0$ satisfies* (1.7) *with $\nu = -f'(\bar{r})$. Further, suppose*

$$\left|f(\bar{r}+r) - f(\bar{r}) + \nu r\right| \leqslant L|r| \quad \text{for } e^{-\mu\tau}\bar{r} - \bar{r} \leqslant r \leqslant B - \bar{r}. \tag{5.3}$$

If f is 'flat enough near equilibrium' such that (5.3) *holds with*

$$L < 1/\|X\|_1, \tag{5.4}$$

where X is as in (1.4)*, then every nontrivial nonnegative solution of* (1.1) *converges to the equilibrium $\bar{r}$ as $t \to \infty$.*

Proof. Set $\hat{M} = \max\{\bar{M} - \bar{r}, \bar{r} - \bar{m}\}$ and, again, let u, v be as in Lemmas 5 and 8. First suppose $\hat{M} = \bar{M} - \bar{r}$. We then let $y(t) = u(t-T) - \bar{r}$ so $\hat{M} = u(0) - \bar{r} = y(T)$ with $T > 0$ arbitrary. We note that $\bar{m} \leqslant y \leqslant \bar{M}$ gives $|y| \leqslant \hat{M}$. Therefore, (5.3) gives $|f_1(y)| \leqslant L\hat{M}$ uniformly. Thus, using (1.3) with (5.1), we have

$$\begin{aligned}\hat{M} &= y_0(T) + \int_0^T X(T-s) f_1\big(y(s-\tau)\big)\,ds \leqslant \bar{y}_0(T) + \int_0^T \big|X(T-s)\big| L\hat{M}\,ds \\ &\leqslant \bar{y}_0(T) + L\|X\|_1\hat{M}\end{aligned} \tag{5.5}$$

using (1.6) and letting $\bar{y}_0 = y_0(\cdot;\hat{M})$. For the alternative case $\hat{M} = \bar{r} - \bar{m}$, we let $y(t) = v(t-T) - \bar{r}$ and, similarly, again obtain (5.5) for arbitrary T. Since $\bar{y}_0(T) \to 0$ as $T \to \infty$, (5.4) ensures that $\hat{M} = 0$ so $x(t) \to \bar{r}$ as $t \to \infty$. □

6. Nonconstant periodic solution for large delay

In this section we will use Hopf bifurcation and fixed point theory to prove the existence of a nonconstant periodic solution when the delay τ is large enough. To see more clearly the effect of delay we let $\mu = 1$. The usual linearized analysis lets $x = \bar{r} + \varepsilon y$ and notes that, to first order in ε, the perturbation satisfies

$$\dot{y} + y = f'(\bar{r})y(\cdot - \tau).$$

Seeking a solution of the form $y(t) = \exp(\lambda t)$, we obtain the characteristic equation for λ:

$$\lambda + 1 = f'(r)\exp(-\tau\lambda).$$

We will have linearized stability if all complex roots of this characteristic equation have negative real parts. If $|f'(r)| < 1$ we have the local convergence to the positive equilibrium for all delays. If $|f'(r)| > 1$, the effect of delay will occur. More exactly, in this case with

$$\tau > \tau_* = \frac{1}{\sqrt{|f'(\bar{r})|^2 - 1}} \arccos\frac{1}{f'(\bar{r})}$$

there is a nonconstant periodic solution of Eq. (1.1).

Atay [1] used the Schauder fixed point theory to prove that there is a nonconstant periodic solution of the equation

$$\dot{y} = \tau h\big(y, y(\cdot - 1)\big),$$

provided

$$\tau > \tau_* = \frac{1}{\sqrt{D^2 - C^2}} \arccos\left(-\frac{C}{D}\right),$$

where $h(u, v)$ is differentiable at the origin, $h(0, 0) = 0$ and

$$0 < C := -\frac{\partial h}{\partial u}(0, 0) < D := -\frac{\partial h}{\partial v}(0, 0).$$

We let $y(t) = x(\tau t) - \bar{r}$ and

$$h(u, v) = \bar{r} - u + f(v + \bar{r}).$$

Then,

$$C = 1, \qquad D = -f'(\bar{r})$$

and we reproduce

$$\tau_* = \frac{1}{\sqrt{|f'(\bar{r})|^2 - 1}} \arccos \frac{1}{f'(\bar{r})}.$$

Here, we assume that $f'(\bar{r}) < -1$ and the function arc cosine takes its value in $[0, \pi]$.

Lemma 11. *If a positive solution x of* (1.1) *does not oscillate around the positive equilibrium $\bar{r}$ then $x(t)$ tends to $\bar{r}$ as $t \to \infty$. Consequently, every nonconstant positive periodic solution should oscillate around the positive equilibrium.*

Proof. If x does not oscillate around $\bar{r}$, then either

$$\limsup_{t\to\infty} x(t) \leqslant \bar{r} \quad \text{or} \quad \liminf_{t\to\infty} x(t) \geqslant \bar{r}.$$

From Lemma 8, in the first case, we have $\limsup x(t) = \bar{r}$. For the second case, we have $\liminf x(t) = \bar{r}$. So it is enough to consider the second case. Using the proof of Lemma 8, we get $\bar{r} \geqslant u(-\tau) \geqslant v(0) = \bar{r}$. Hence, $u(-\tau) = \bar{r}$ and $u(0) = f(u(-\tau)) = \bar{r}$. The proof is now complete. □

Y. Cao [2] proved that for $\tau \leqslant \tau_*$ there is no periodic solution which is larger than y_0 and oscillates slowly around the only positive equilibrium $\bar{r}$. For $\tau > \tau_*$, there is at most one periodic solution which is larger than y_0 and oscillates slowly around $\bar{r}$. Recall that a T-periodic solution is called *slowly oscillated around the positive equilibrium*, if $T > \tau$, $x(0) = x(T) = \bar{r}$, and there is $t_0 \in (0, T - \tau)$ such that

$$x(t_0) = \bar{r}, \qquad x(t) > \bar{r} \quad \text{for } t \in (0, t_0) \quad \text{and} \quad x(t) < \bar{r} \quad \text{for } t \in (t_0, T).$$

Cao assumes that f is decreasing from $y_0 < \bar{r}$ until $f(y_0)$. He also requires that the function $h(x) = xf'(x)/f(x)$ is monotonically increasing in $[y_0, \bar{r}]$ and decreasing in

$[\bar{r}, f(y_0)]$. Recall that $f(y_0)$ is the maximal value of $f(y)$, when $y > 0$. Without these assumptions on h one can construct several slowly oscillated periodic solutions for (1.1). Also, it is known that, if a periodic solution is not oscillated slowly, it should be unstable. Of course, Cao did not prove these results directly, but from his works one can deduce this.

7. Some applications

Equation (1.1) with unimodal f has been proposed as a model for a variety of physiological processes, where in most cases, one of the model functions

$$f(x) = kx^c \exp(-x) \tag{7.1}$$

or

$$f(x) = \frac{kx}{1 + x^c}, \tag{7.2}$$

with parameters $k > 0$ and $c > 0$, is considered [3,4,9,11–13].

The population dynamics of Nicholson's blowflies have been studied [9,12] using a function f of the form (7.1) with $c = 1$. In such a case, f is differentiable and one has

$$\bar{r} = \ln \frac{k}{\mu}, \tag{7.3}$$

and

$$\nu = -f'(\bar{r}) = \mu\left(\ln \frac{k}{\mu} - 1\right).$$

Thus, Theorem 9 yields, using (5.2),

$$\tau < \frac{1}{\mu} \ln\left[\frac{\ln(k/\mu) - 1}{\ln(k/\mu) - 2}\right]$$

as a sufficient condition for convergence to equilibrium $\bar{r}$ given in (7.3), provided $k > \mu e^2$. Moreover, there is a nonconstant periodic solution to the model equation if

$$\tau > \tau^* = \frac{1}{\mu\sqrt{(\ln(k/\mu) - 2)\ln(k/\mu)}} \arccos\left[\frac{1}{1 - \ln(k/\mu)}\right],$$

using (1.7).

In respiratory studies, (1.1) has been employed in which the response function takes the form (7.2). In such a case, one has the positive equilibrium

$$\bar{r} = \left(\frac{k}{\mu} - 1\right)^{1/c}, \tag{7.4}$$

provided $k/\mu > 1$. Then,

$$\nu = -f'(\bar{r}) = \frac{\mu}{k}\left[(c - 1)k - c\mu\right].$$

Thus, Theorem 9 yields, using (5.2),

$$\tau < \frac{1}{\mu} \ln\left[\frac{c(1 - \mu/k) - 1}{c(1 - \mu/k) - 2}\right]$$

as a sufficient condition for convergence to equilibrium $\bar{r}$ given in (7.4), provided

$$c\left(1-\frac{\mu}{k}\right) > 2.$$

Moreover, there is a nonconstant periodic solution to the model equation (1.1) with f as in (7.2) if

$$\tau > \tau^* = \frac{1}{\mu\sqrt{c(c(1-\mu/k)-2)(1-\mu/k)}}\arccos\left[\frac{1}{1-c(1-\mu/k)}\right],$$

using (1.7).

8. Conclusion

We have given a basic comparison theorem and discussed some of their consequences. The effect of delay on the asymptotic behavior has then been studied and the periodicity of positive solutions investigated for large delays. Our discussions allow the nonlinearity f to be nonmonotonic and nondifferentiable which are then more general than those of [8]. Thus, our results should be applicable to a wider range of population models; for example, models arising from the study of an optically bistable device [3,4], blood cells production, respiration dynamics, or cardiac arrhythmias [11,13]. We can also find application with a system in which the growth function is not smooth, such as a population where growth occurs in birth pulses (during the breeding season) and not continuously throughout the year.

Open problem. Investigate the stability of periodic solutions of (1.1) and the structure of ω-limit sets when the delay is large enough!

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