Persistence and stability for some cooperative population models with delays

Teresa Faria

University of Lisbon
teresa.faria@fc.ul.pt

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Outline:

1. Introduction: biological models with delay

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2. Stability and permanence for cooperative scalar DDEs

3. Applications: *an alternative model for the delayed logistic equation*;
   a non-autonomous Nicholson's equation

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2. Stability and permanence for cooperative scalar DDEs

3. Applications: *an alternative model for the delayed logistic equation*;
   a non-autonomous Nicholson's equation

4. Persistence and permanence for n-dim DDEs

5. Applications to structured populations models (Lotka-Volterra)

1. Introduction: biological models with delays

Delay Differential Eqns (DDEs) vs Ordinary Differential Eqns (ODEs)

$$\dot{x}(t) = f(t, x(t), x(t-\tau)) \quad \text{vs} \quad \dot{x}(t) = f(t, x(t))$$

or

$$\dot{x}(t) = f(t, x_{|_{[t-\tau,t]}}) \quad \text{vs} \quad \dot{x}(t) = f(t, x(t))$$

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Time-delays:

⋆ maturation period of a biological species
⋆ hunting delay in predator-prey systems
⋆ incubation time in epidemic models
⋆ synaptic transmission time among neurons
⋆ maturation time of blood cells
⋆ "splitting" delay of cell organisms in chemostat models
⋆ delays in control systems, number theory, stochastic models, mechanical engineering, ...

$\tau > 0$ **time delay**

"Initial data" at a time t_0: past history of the system over the interval $[t_0 - \tau, t_0]$.

Phase Space: $C := C([-\tau, 0]; \mathbb{R}^n)$, $\quad \|\varphi\| = \max_{-\tau \leq \theta \leq 0} |\varphi(\theta)|$

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Standard notation:

$$x_t \in C, \quad x_t(\theta) = x(t + \theta), \; -\tau \leq \theta \leq 0$$

DDE in C: $\boxed{\dot{x}(t) = f(t, x_t)}$

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Initial Condition at e.g. $t_0 = 0$: $x(\theta) = \varphi(\theta),\ -\tau \le \theta \le 0$

i.e., $x_0 = x_{|[-\tau,0]} = \varphi, \quad \varphi \in C$

Some basic population models:

$n = 1$:

Delayed Logistic Eq.

$\dot{N}(t) = rN(t)\big[1 - N(t-\tau)/K\big]$ (**one discrete** delay)

$\dot{N}(t) = rN(t)\big[1 - a_1 N(t-\tau_1) - \cdots - a_n N(t-\tau_n)\big]$ (n **discrete** delays)

$\dot{N}(t) = rN(t)\Big(1 - \frac{1}{K}\int_{-\tau}^{0} k(\theta)N(t+\theta)\,d\theta\Big)$ (**distributed** delay)

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$n > 1$

Kolmogorov-type n-dimensional population models:

$$\dot{x}_i(t) = x_i(t) f_i(t, x_t), \quad 1 \le i \le n$$

As a particular case, LV models:

$$\dot{x}_i(t) = x_i(t)[b_i(t) - g_i(t, x_t)], \quad 1 \le i \le n$$

$infinite\ delay$

Systems with infinite memory: Volterra's population models

Typically the "memory functions" appear as integral kernels:
e.g., consider the predator-prey model

$$\dot{x}(t) = x(t)[a - bx(t) - cy(t) - \int_0^\infty k_1(s)x(t-s)ds - \int_0^\infty k_2(s)y(t-s)ds]$$
$$\dot{y}(t) = y(t)[-d + px(t) - qy(t) + \int_0^\infty k_3(s)x(t-s)ds - \int_0^\infty k_4(s)y(t-s)ds]$$

$a, b, c, d, p, q > 0$
$k_i(s) \geq 0$ continuous, $k_i \in L^1[0, \infty)$

(the delay effects diminish gradually when going back in time)

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IC at $t = 0$:
$x(s) = \phi(s), \quad s \leq 0, \quad \text{i.e.,} \quad x|_{(-\infty,0]} = \phi \in C((-\infty, 0]; \mathbb{R}^n)$

Initial conditions

$C^+ = C([-\tau, 0]; R^n_+)$

Initial conditions: For our results, **initial conditions** are taken in C^+ or in

$$C_0 = \{\varphi \in C^+ : \varphi(0) > 0\}.$$

C_0 is an admissible set of IC: $\varphi \in C_0 \Rightarrow x_t(\cdot; t_0, \varphi) \in C_0$

Standard definitions:

In a set $S \subset C^+ \setminus \{0\}$ of IC:

- An equilibrium $x^* \geq 0$ of $\dot{x} = f(t, x_t)$ is **globally attractive (GA)** if

$$\lim_{t \to \infty} x(t, \varphi) = x^* \quad \forall \varphi \in S$$

- An equilibrium $x^* \geq 0$ of $\dot{x} = f(t, x_t)$ is **globally asymptotically stable (GAS)** if it is stable and globally attractive

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• $\dot{x} = f(t, x_t)$ is **persistent** (respec. **uniformly persistent**) if

$$\liminf_{t \to \infty} x_i(t, \varphi) > 0 \quad (\text{respec. } \geq m_0 > 0) \quad \forall i,\ \varphi \in S$$

• $\dot{x} = f(t, x_t)$ is **permanent** if $\exists\, m, M > 0$:

$$m \leq \liminf_{t \to \infty} x_i(t, \varphi) \leq \limsup_{t \to \infty} x_i(t, \varphi) \leq M, \quad 1 \leq i \leq n, \varphi \in S$$

Cooperative Systems:

- $\dot{x} = f(t, x_t)$ is **cooperative** if $f = (f_1, \ldots, f_n)$ satisfies Smith's[1] *quasi-monotonicity condition*:

$$\varphi, \psi \in C^+, \varphi \leq \psi \text{ and } \varphi_i(0) = \psi_i(0) \Rightarrow f_i(t, \varphi) \leq f_i(t, \psi), \forall t \geq 0, 1 \leq i \leq n \quad (Q)$$

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- comparison of solutions: consider two DDEs

$$x'(t) = f(t, x_t) \quad \text{and} \quad x'(t) = g(t, x_t)$$

and assume that <u>either</u> f <u>or</u> g satisfies (Q). If $f \leq g$, then

$$x(t; t_0, \varphi; f) \leq x(t; t_0, \varphi; g).$$

[1] H. Smith: book on *Monotone Dynamical systems*, AMS 1995; SIAM J Math Anal (1986)

2. Cooperative scalar DDEs

Goal:

1. To develop a method to establish the **permanence** for a large class of non-autonomous **cooperative** scalar DDEs (answering some open problems..), along the following lines:

⋆ Compare (below and above) the positive solutions of the DDE with solutions of two DDEs with globally attractive equilibria

⋆ $\Rightarrow$ *permanence* of the DDE

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2. To carry out this method to study (a class of) non-autonomous cooperative n**-dim DDEs**

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- cooperative scalar model with autonomous coefficients:

$$\dot{x}(t) = R\big(x(t-\tau_1(t)), \dots, x(t-\tau_m(t))\big) - D(x(t)) \qquad (1)$$

$\tau_k : [0,\infty) \to \mathbb{R}$ continuous, $0 \le \tau_k(t) \le \tau$ for some $\tau > 0$
$R : \mathbb{R}_+^m := [0,\infty)^m \to [0,\infty), D : [0,\infty) \to [0,\infty)$ *smooth* ($\exists\,!$ of solutions for $t \ge 0$), $R(0,\dots,0) = 0$ (not essential), $D(0) = 0$.

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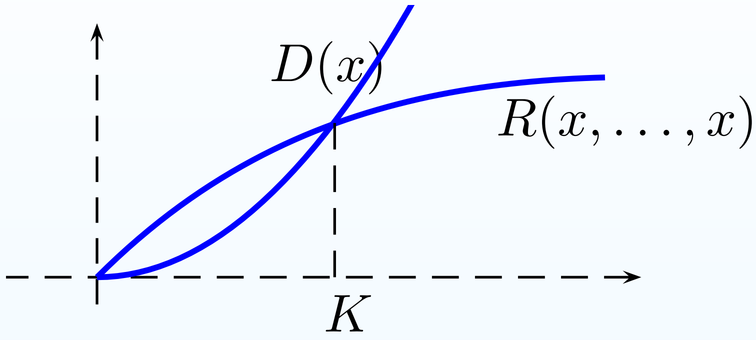
(A1) $R(y_1, \ldots, y_m)$ is nondecreasing in $y_k \ge 0, \forall k$
(A2) there exists $K \ge 0$ such that

$$(x-K)(R(x,\ldots,x) - D(x)) < 0 \quad \text{for} \quad x > 0, x \ne K.$$

With $K = 0$ in (A2), 0 is the unique equilibrium; otherwise, 0, K are equilibria.



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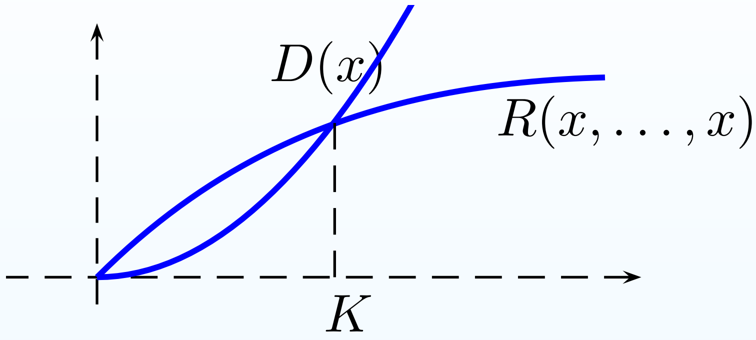

Theorem 1. Assume (A1)–(A2).
Then K is globally asymptotically stable (GAS), in the set of solutions with IC in $C_0 := \{\varphi \in C^+ : \varphi(0) > 0\}$.

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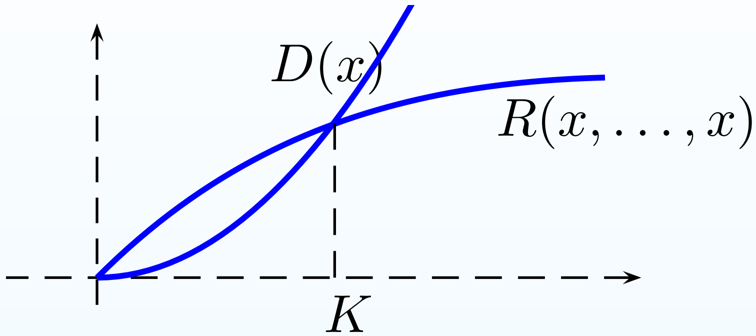

Theorem 1. Assume (A1)–(A2).
Then K is globally asymptotically stable (GAS), in the set of solutions with IC in $C_0 := \{\varphi \in C^+ : \varphi(0) > 0\}$.

($K = 0$: extinction; vs with $K > 0$: K is GAS)

Remark.
For the autonomous case: related results in Kuang's monograph on DDEs; with simple delay in Arino et al. (2006): $\dot{x}(t) = R(x(t-\tau)) - D(x(t)),\ t \geq 0.$

Step 2: scalar DDEs with non-autonomous coefficients

Theorem 2. *Consider*

$$\dot{x}(t) = R\big(t, x(t - \tau_1(t)), \ldots, x(t - \tau_m(t))\big) - D(t, x(t)), \quad t \geq 0, \quad (2)$$

with $R(t, y), D(t, x), \tau_k(t)$ *continuous,* $0 \leq \tau_k(t) \leq \tau$, *for* $t, x \geq 0, y \in \mathbb{R}_+^m$

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with $R(t,y), D(t,x), \tau_k(t)$ *continuous,* $0 \leq \tau_k(t) \leq \tau$*, for* $t, x \geq 0, y \in \mathbb{R}_+^m$

Assume that:

(H) *there are (locally Lipschitz) continuous functions* $R^l, R^u : \mathbb{R}_+^m \to \mathbb{R}_+, D^l, D^u : \mathbb{R}_+ \to \mathbb{R}_+$ *with* $R^l(0,\ldots,0) = R^u(0,\ldots,0) = D^l(0) = D^u(0) = 0$*, such that:*

$$R^l(y) \leq R(t,y) \leq R^u(y)$$
$$D^l(x) \leq D(t,x) \leq D^u(x), \quad t \geq 0, y \in \mathbb{R}_+^m, x \geq 0$$

and the pairs $(R^u, D^l), (R^l, D^u)$ **satisfy (A1)-(A2)** *with* $K = K^u, K^l > 0$*, respec. THEN,* (2) *is* **permanent** *(in* C_0*): in fact, all positive sol.* $x(t)$ *satisfy*

$$K^l \leq \liminf_{t\to\infty} x(t) \leq \limsup_{t\to\infty} x(t) \leq K^u.$$

$$\dot{x}(t) = R\big(t, x(t-\tau_1(t)), \dots, x(t-\tau_m(t))\big) - D(t, x(t)), \quad t \geq 0, \qquad (2)$$

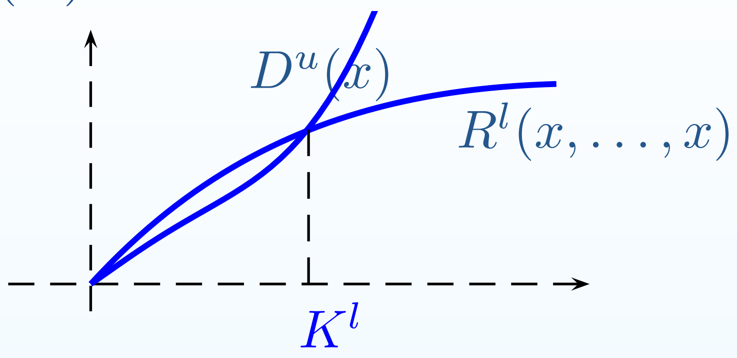
A very simple argument: A solution $x(t)$ of (2) satisfies the inequalities

$$R^l\big(x(t-\tau_1(t)), \dots, x(t-\tau_m(t))\big) - D^u(x(t)) \leq \dot{x}(t) \quad \text{and}$$
$$\dot{x}(t) \leq R^u\big(x(t-\tau_1(t)), \dots, x(t-\tau_m(t))\big) - D^l(x(t))$$

We compare the solutions $x(t;\varphi)$ ($\varphi \in C_0$) of (2) with the solutions of the two auxiliary cooperative DDEs:

$$\dot{v}(t) = R^l\big(v(t-\tau_1(t)), \dots, v(t-\tau_m(t))\big) - D^u(v(t)) \qquad (2^l)$$
$$\dot{u}(t) = R^u\big(u(t-\tau_1(t)), \dots, u(t-\tau_m(t))\big) - D^l(u(t)) \qquad (2^u)$$

For (2^l):



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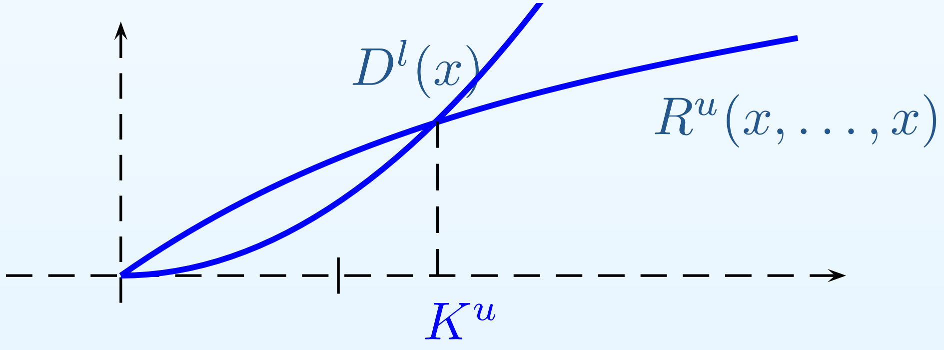

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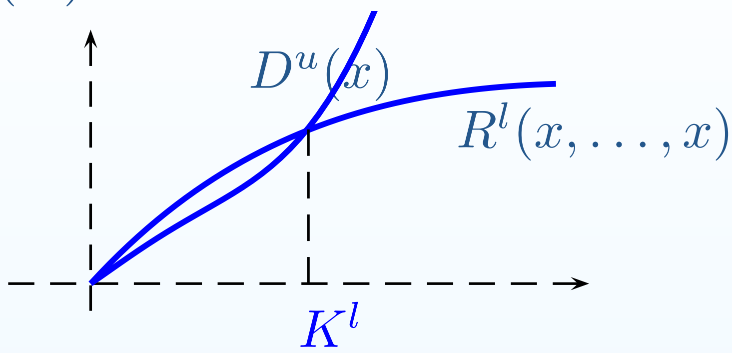

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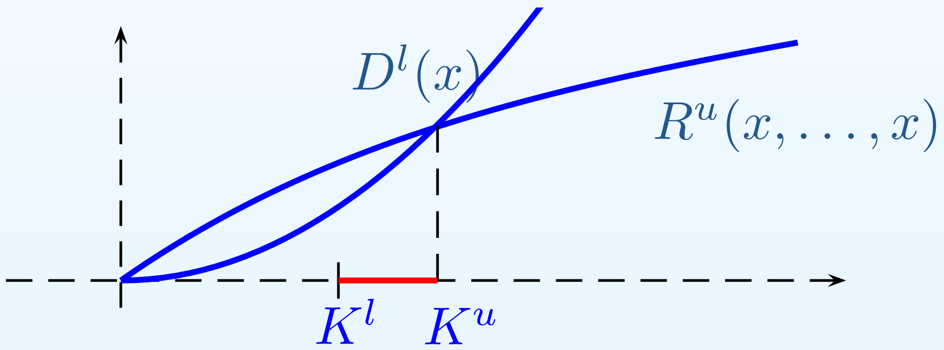

We get

$$v(t;\varphi) \leq x(t;\varphi) \leq u(t;\varphi), \quad t \geq 0,$$

and Theorem 1 implies that $v(t;\varphi) \to K^l, u(t;\varphi) \to K^u$ as $t \to \infty$.

Particular case: $R(t, y_1, \ldots, y_m) = \sum_{k=1}^{m} y_k r_k(t, y_k)$, $D(t,x) = xd(t,x)$:

$$\dot{x}(t) = \sum_{k=1}^{m} x(t-\tau_k(t)) r_k\big(t, x(t-\tau_k(t))\big) - x(t) d\big(t, x(t)\big) \qquad (3)$$

with $r_k(t,y), d(t,x), \tau_k(t)$ continuous, $0 \le \tau_k(t) \le \tau, 1 \le k \le m$

Note that $R(t, x, \ldots, x) - D(t,x) = x\Big(\sum_{k=1}^{m} r_k(t,x) - d(t,x)\Big)$.

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Corollary: Permanence IF there are continuous fcs. $r_k^l, r_k^u, d^l, d^u \ge 0$ such that with $r^u(x) = \sum_{k=1}^{m} r_k(x), r^l(x) = \sum_{k=1}^{m} r_k^l(x)$ we have:

(i) $r^l(x) \le \sum_{k=1}^{m} r_k(t,x) \le r^u(x), d^l(x) \le d(t,x) \le d^u(x), t \ge 0, x \ge 0$

(ii) $xr_k^l(x), xr_k^u(x)$ nondecreasing

(iii) the functions $r^u(x) - d^l(x)$ and $r^l(x) - d^u(x)$ are (strictly) decreasing on $[0, \infty)$

(iv) $r^l(0) - d^u(0) > 0$ and $r^u(\infty) - d^l(\infty) < 0$.

3. Aplications

Example 1. *A delayed logistic model:*

$$\dot{x}(t) = \sum_{k=1}^{m} \frac{\alpha_k(t)x(t-\tau_k(t))}{1+\beta_k(t)x(t-\tau_k(t))} - \mu(t)x(t) - \kappa(t)x^2(t) \qquad (L)$$

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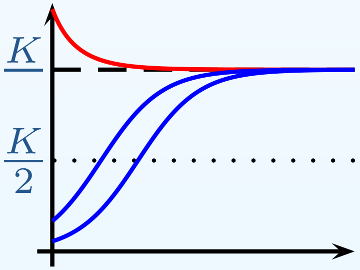
- Classic logistic ODE: $N'(t) = rN(t)\left[1 - \frac{N(t)}{K}\right]$



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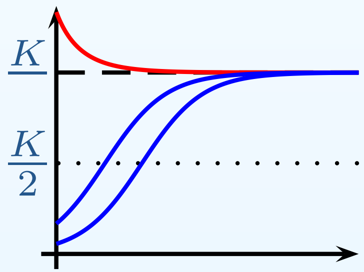

- Classic logistic DDE (Hutchinson, 1948):

$$N'(t) = rN(t)\left[1 - \frac{N(t-\tau)}{K}\right] \qquad (H)$$

r is the intrinsic growth rate, K is the carrying capacity, $N(t)$ is the adult population size at time t, τ is the maturation delay

Wright's equation

- With $\boxed{y(t) = -1 + N(\tau t)/K}$ and $\boxed{\alpha = \tau r}$, (H) becomes

$$y'(t) = -\alpha y(t-1)[1 + y(t)] \qquad (W)$$

Thm [Wright,1955]

- if $0 < \alpha < \pi/2$, then the $y = 0$ is a LAS solution of (W)
- if $\alpha > \pi/2$: $y = 0$ is unstable

- if $0 < \alpha \leq 3/2$, $\lim_{t\to\infty} y(t) = 0$, for all solutions $y(t)$ of (W) with IC with $y(0) > -1$, i.e., the steady solution $N(t) \equiv K$ of (H) is globally attractive in the set of its *positive* solutions.

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Hopf bifurcation:
Moreover, for $\alpha = \pi/2$ (i.e., delay $\tau = \frac{\pi}{2r}$) there is a supercritical Hopf bifurcation, with stable periodic solutions

Historical notes:

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4. The introduction of delays in differential equations goes back to Volterra's works in the 1920's and 30's, on biological growth models. To represent the incubation time of a parasite, Volterra proposed the following logistic model with distributed (possibly infinite) delay (see also Miller (1965)):

$$\dot{x}(t) = x(t)\Big(a - bx(t) - \int_c^t f(t-s)x(s)\,ds\Big),$$

where $c = 0$ or $c = -\infty,\ a, b > 0$ and $f(x) \geq 0, f \in L^1[0, \infty)$ is the *memory func.*

'Alternative' delayed logistic equation :

In J. Arino, L. Wang, G. Wolkowicz, JTB (2006):

- 'alternative' logistic DDE:

$$N'(t) = \frac{\gamma\mu N(t-\tau)}{\mu e^{\mu\tau} + K(e^{\mu\tau}-1)N(t-\tau)} - \mu N(t) - \kappa N^2(t) \qquad (\ell)$$

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Deduction of the model (ℓ) (Arino et al.):

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$\star$ at time t, the *growth* rate is proportional to the number of individuals at time $t - \tau$ that **have survived** until time t; to find the growth rate, one solves the ODE $N'(t) = -\mu N(t) - \kappa N^2(t)$, and obtains $\gamma N(t)$ replaced by $\frac{\gamma \mu N(t-\tau)}{\mu e^{\mu\tau} + K(e^{\mu\tau}-1)N(t-\tau)}$; inserting in (1),

$$N'(t) = \frac{\gamma \mu N(t-\tau)}{\mu e^{\mu\tau} + K(e^{\mu\tau} - 1)N(t-\tau)} - \mu N(t) - \kappa N^2(t) \qquad (\ell)$$

Generalization of the 'alternative' logistic DDE:

- generalization with multiple delays:

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$\alpha_k, \kappa : [0,\infty) \to (0,\infty)$ continuous, bounded below and above by positive constants, $\mu, \beta_k, \tau_k : [0,\infty) \to [0,\infty)$ continuous and bounded, $1 \leq k \leq m$

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Theorem 3. If

$$\sum_{k=1}^{m} \inf_{t\ge 0} \alpha_k(t) > \sup_{t\ge 0} \mu(t)\,, \qquad (*)$$

equation (L) is **permanent**. Moreover, all solutions $x(t) = x(t;\varphi)$ $(\varphi \in C_0)$ of (L) satisfy the uniform estimates

$$m \le \liminf_{t\to\infty} x(t) \le \limsup_{t\to\infty} x(t) \le M, \qquad \text{where}$$

$$M = \limsup_{t\to\infty} \frac{1}{\kappa(t)} \left(\sum_{k=1}^{m} \alpha_k(t) - \mu(t) \right), m = \liminf_{t\to\infty} \frac{1}{\kappa(t)} \left(\sum_{k=1}^{m} \frac{\alpha_k(t)}{1+\beta_k(t)M} - \mu(t) \right)$$

Sketch of proof.

(L) has the form (3), with $r_k(t,x) = \frac{\alpha_k(t)}{1+\beta_k(t)x}$, $d(t,x) = \mu(t) + \kappa(t)x$

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Notation: $\underline{f} = \inf_{t\geq 0} f(t), \overline{f} = \sup_{t\geq 0} f(t)$

- *Claim 1*: Permanence

It follows by the Corollary of **Theorem 2**:
with $d^u(x) = \overline{\mu} + \overline{k}x,\ d^l(x) = \underline{\mu} + \underline{k}x$ and

$$r_k^u(x) = \frac{\overline{\alpha}_k}{1+\underline{\beta}_k x}, \quad r_k^l(x) = \frac{\underline{\alpha}_k}{1+\overline{\beta}_k x} \quad \text{for} \quad x \geq 0, k = 1, \ldots, m.$$

we have $xr_k^u(x), xr_k^l(x) \nearrow, \sum_k r_k^u - d^l, \sum_k r_k^l - d^u \searrow$ on $[0,\infty)$ with

$$\sum_k r_k^u(\infty) - d^l(\infty) = -\infty < 0, \quad \sum_k r_k^l(0) - d^u(0) > 0 \ (\text{condition } (*))$$

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⋆ By Claim 1, $0 < \overline{x} < \infty$

⋆ take $t_n \to \infty$, and $\dot{x}(t_n) \to 0$ and $x(t_n) \to \overline{x}$

⋆ NOW, we use the equation: fix any $\varepsilon > 0$ small; $\exists T > 0 : x(t-\tau) \le \overline{x} + \varepsilon$ for $t \ge T_0$; for n large,

$$\begin{aligned}
\dot{x}(t_n) &= k(t_n)\left[\frac{1}{k(t_n)}\left(\sum_{k=1}^{m}\frac{\alpha_k(t_n)x(t_n-\tau_k(t_n))}{1+\beta_k(t_n)x(t_n-\tau_k(t_n))} - \mu(t_n)x(t_n)\right) - x^2(t_n)\right] \\
&\le k(t_n)\left[\frac{1}{k(t_n)}\left(\sum_{k=1}^{m}\frac{\alpha_k(t_n)(\overline{x}+\varepsilon)}{1+\beta_k(t_n)(\overline{x}+\varepsilon)} - \mu(t_n)x(t_n)\right) - x^2(t_n)\right] \\
&\le k(t_n)\overline{x}\left[\frac{1}{k(t_n)}\left(\sum_{k=1}^{m}\alpha_k(t_n) - \mu(t_n)\right) - x(t_n)\right] + O(\varepsilon)
\end{aligned}$$

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\end{aligned}$$

$\star\, n \to \infty, \varepsilon \to 0^+$:

$$0 \le \limsup_{t\to\infty}\left[\frac{1}{k(t_n)}\left(\sum_{k=1}^{m} \alpha_k(t_n) - \mu(t_n)\right) - x(t_n)\right], \quad \text{thus}$$

$$\overline{x} \le \limsup_{t\to\infty} \tfrac{1}{k(t)}\left(\textstyle\sum_{k=1}^{m} \alpha_k(t) - \mu(t)\right) = M.$$

- *Claim 3*: $\underline{x} := \liminf_{t \to \infty} x(t) \geq m$

$\star$ take $s_n \to \infty$, and $\dot{x}(s_n) \to 0$ and $x(s_n) \to \underline{x}$, etc.:

analogous procedure, where in addition the already established upper bound M is used.

Example 2: *A non-autonomous Nicholson's equation*

- Nicholson's eq with multiple discrete delays:

$$\dot{x}(t) = -d(t)x(t) + \sum_{k=1}^{m} \beta_k(t)x(t - \tau_k(t))e^{-x(t-\tau_k(t))} \qquad (N)$$

$\beta_k, \tau_k, d : [0, \infty) \to [0, \infty)$ are continuous, bounded and nonnegative.

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Remark.
We could consider more general models with distributed delay: e.g.,

$$\dot{x}(t) = -d(t)x(t) + \beta(t) \int_{-\tau(t)}^{0} x(t + s)e^{-x(t+s)}\, ds$$

Historical notes:

Sheep pest and Nicholson's data:

In the 1950's, Alexander J. Nicholson carried out a series of experiments to study a sheep pest, the blowfly. The flies were kept in several cages in laboratory, and observations made for several years. Nicholson's data were collected in a series of publications, namely in his celebrated paper

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Lucilia Cuprina (Australian sheep blowfly)

● 4 stages of growth: eggs, larvae, pupae, and adults

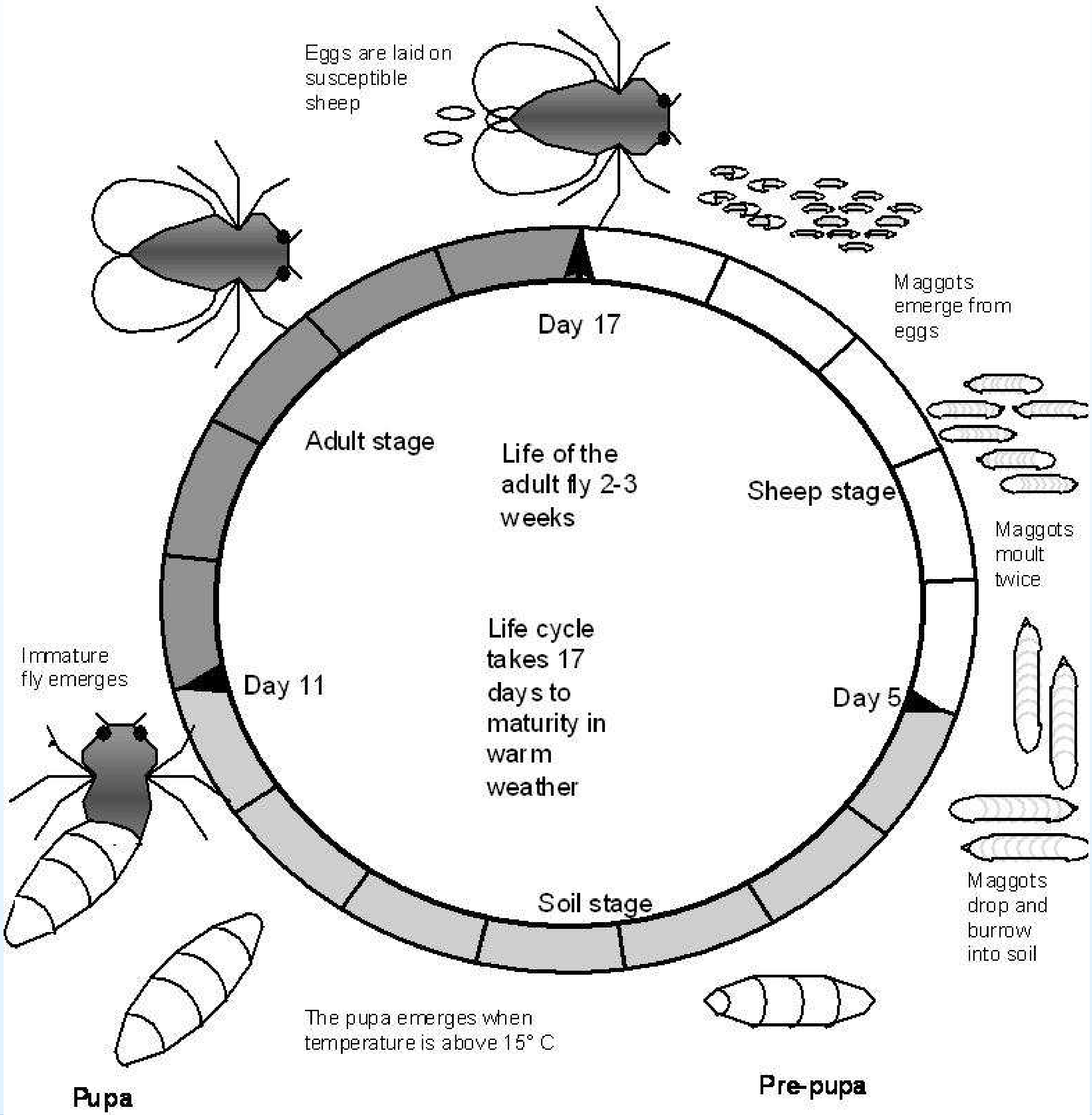
● It's known as the Australian sheep blowfly, but Lucilia cuprina is a worldwide sheep pest (mostly in dry climates).

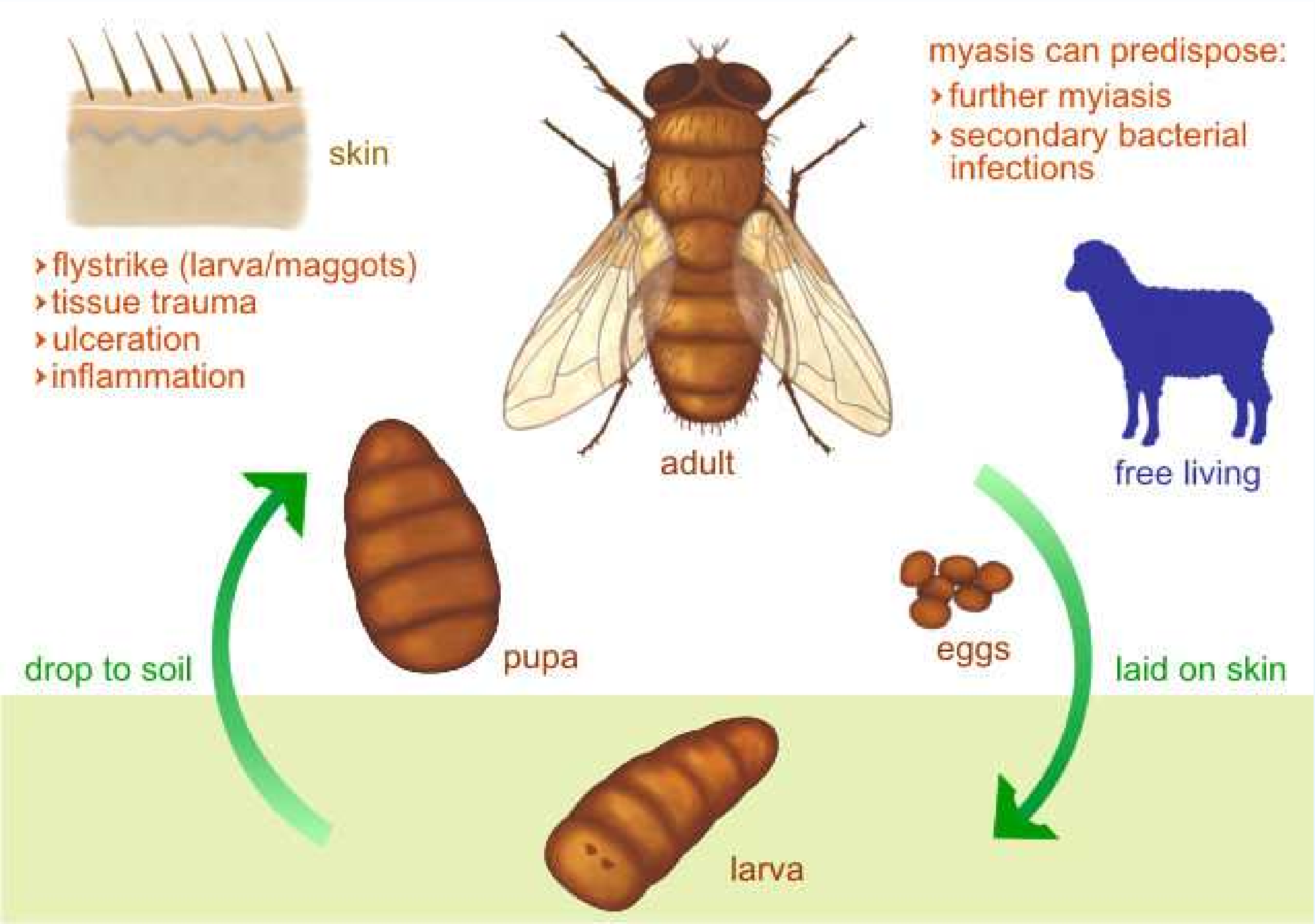
● It causes cutaneous myiasis (i.e., infestation of the body by the larvae of flies), which leads to death when left untreated. A female fly locates a sheep with an open wound in which she lays her eggs; the maggots of L. cuprina rapidly grow while eating the living flesh of the sheep, poisoning the sheep.

● It is a serious problem in the animal industry, in spite of several forms of prevention (regular inspections during the fly season, insecticides, fly traps...)

The Life Cycle of the Sheep Blowfly

(Lucilia cuprina)




skin
›flystrike (larva/maggots)
›tissue trauma
›ulceration
›inflammation
adult
myasis can predispose:
›further myiasis
›secondary bacterial infections
free living
pupa
eggs
drop to soil
laid on skin
larva

Modelling:

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Here:
$x(t)$ size of (adult) blowfly population, d adult mortality, β maximal egg production rate, $1/a$ size at which the population produces eggs at max rate,

τ *generation time* (from egg to the final adult form)

Nicholson's blowflies equation:

For the original equation:

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- If $1 < \beta/d \leq e^2$, $K = \ln(\beta/d)$ is GAS for all delays $\tau > 0$.
- If $\beta/d > e^2$, K is GAS if $\tau < \tau^*$; $\exists \tau^{**} \geq \tau^*$, at τ^{**} a Hopf bif occurs

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Using Thm 2 and similar techniques to the ones above:

Theorem. Define
$\underline{\beta}_k = \inf_{t\geq 0} \beta_k(t), \overline{\beta}_k = \sup_{t\geq 0} \beta_k(t), \underline{d} = \inf_{t\geq 0} d(t), \overline{d} = \sup_{t\geq 0} d(t)$, and assume

$$\overline{d} < \sum_{k=1}^{m} \underline{\beta}_k \leq \sum_{k=1}^{m} \overline{\beta}_k < e\,\underline{d}. \qquad (*)$$

Then, (N) is **permanent** and any positive solution satisfies

$$\begin{cases} \limsup_{t\to\infty} x(t) \leq M := \limsup_{t\to\infty} \log\left(\frac{1}{d(t)} \sum_{k=1}^{m} \beta_k(t)\right) \\ \liminf_{t\to\infty} x(t) \geq m := \liminf_{t\to\infty} \log\left(\frac{1}{d(t)} \sum_{k=1}^{m} \beta_k(t)\right). \end{cases}$$

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Note. For the autonomous case with multiple delays, $\overline{d} = \underline{d}, \overline{\beta} = \underline{\beta} = \sum_k \beta_k$: it is known that $\boxed{\beta \leq e^2 d}$ $\Rightarrow$ the positive equilibrium $K = \ln(\beta/d)$ is GA.

4. n-dimensional cooperative DDEs

4.1. Autonomous DDEs:

$$x_i'(t) = F_i(x_t) - x_i(t)G_i(x_t) =: f_i(x_t), \quad i = 1, \ldots, n, \tag{4}$$

$F = (F_1, \ldots, F_n), G = (G_1, \ldots, G_n) : C \to \mathbb{R}^n$ continuous and bdd on bdd sets, $F_i(0) \geq 0$

IC: $x_0 = \varphi$ with $\varphi \in C_0$

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(A1) F and $-G$ satisfy the quasimonotone condition (Q)

(A2) there is $v \in \mathbb{R}^n, v > 0$ such that $f(\varepsilon v) > 0$ for $0 < \varepsilon \ll 1$

(A3) there is $q \in \mathbb{R}^n, q > 0$ such that $f(Lq) < 0$ for $L \gg 1$

Recall that (A1) means that (4) is cooperative!

$$\varphi, \psi \in C^+, \varphi \leq \psi \text{ and } \varphi_i(0) = \psi_i(0) \Rightarrow f_i(t, \varphi) \leq f_i(t, \psi), \forall t \geq 0, 1 \leq i \leq n \tag{Q}$$

- IF F is <u>sublinear</u> in $\mathbb{R}^n_+$, i.e.,

$$\text{for } x \in \mathbb{R}^n_+ \text{ and } \alpha \in (0,1),\ F(\alpha x) \geq \alpha F(x)$$ [2]

(A2) there exists a vector $v \in \mathbb{R}^n_+$ such that $F(v) - Bv > 0$, where $B = diag\,(G_1(0), \ldots, G_n(0))$;

(A3) there exists a vector $q = (q_1, \ldots, q_n) \in \mathbb{R}^n_+$ such that $F_i(q) - q_i G_i(Lq) < 0$ for $L \geq 1, i = 1, \ldots, n$.

[2] Note that $f_i(cv) = F_i(cv) - cv_i G_i(cv), 1 \leq i \leq n$ for $v = (v_1, \ldots, v_n) \in \mathbb{R}^n, c \in \mathbb{R}$

Theorem 4. Under (A1)-(A3), (4) is **permanent**.

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Ideas for proof.

⋆ by (A1) (4) is cooperative, so we apply the theory of monotone dynamical systems:

⋆ by (A3), for $\varphi \in C_0$ with $\varphi \leq Lq$ ($L > 0$ large) and $f(Lq) < 0$

$$x(t;\varphi) \leq x(t;Lq) \searrow y^*$$

with $y^* = y^*(L) \geq 0$ equilibrium, thus all positive sol. are **bounded**

⋆ by (A2), for $\varphi \in int\, C^+$ with $\varphi \geq \varepsilon v$ ($\varepsilon > 0$ small), and $f(\varepsilon v) > 0$

$$x(t;\varphi) \geq x(t;\varepsilon v) \nearrow x^*$$

with $x^* = x^*(\varepsilon) > 0$ equilibrium, thus (4) is **persistent** in $\mathrm{int}\, C^+$ (thus in C_0)

⋆ more technical: one proves that the equilibria $x^*(\varepsilon), y^*(L)$ **do not depend** on $\varepsilon \in (0, \varepsilon_0), L \in (L_0, \infty)$ respec.

$$x^* \leq \liminf_{t\to\infty} x(t;\varphi) \leq \limsup_{t\to\infty} x(t;\varphi) \leq y^*.$$

Theorem 4. Under (A1)-(A3), (4) is **permanent**.

Ideas for proof.

$\star$ by (A1) (4) is cooperative, so we apply the theory of monotone dynamical systems:

$\star$ by (A3), for $\varphi \in C_0$ with $\varphi \leq Lq$ ($L > 0$ large) and $f(Lq) < 0$

$$x(t;\varphi) \leq x(t;Lq) \searrow y^*$$

with $y^* = y^*(L) \geq 0$ equilibrium, thus all positive sol. are **bounded**

$\star$ by (A2), for $\varphi \in int\, C^+$ with $\varphi \geq \varepsilon v$ ($\varepsilon > 0$ small), and $f(\varepsilon v) > 0$

$$x(t;\varphi) \geq x(t;\varepsilon v) \nearrow x^*$$

with $x^* = x^*(\varepsilon) > 0$ equilibrium, thus (4) is **persistent** in $\mathrm{int}\, C^+$ (thus in C_0)

$\star$ more technical: one proves that the equilibria $x^*(\varepsilon), y^*(L)$ **do not depend** on $\varepsilon \in (0, \varepsilon_0), L \in (L_0, \infty)$ respec.

$$x^* \leq \liminf_{t\to\infty} x(t;\varphi) \leq \limsup_{t\to\infty} x(t;\varphi) \leq y^*.$$

Corollary. Under (A1)-(A3), there is at least one positive equilibrium, which is globally attractive if it is unique.

4.2. Non-autonomous n-dim DDEs

$$x_i'(t) = F_i(t, x_t) - x_i(t)G_i(t, x_t), \quad i = 1, \dots, n, t \geq 0 \tag{5}$$

$F, G : D \subset \mathbb{R} \times C \to \mathbb{R}^n$ continuous and bounded on bounded sets

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Theorem 5. Assume that:
(H) there are continuous functions $F^l, F^u, G^l, G^u : C \to \mathbb{R}^n$ such that

$$F^l(\phi) \leq F(t, \phi) \leq F^u(\phi)$$
$$G^l(\phi) \leq G(t, \phi) \leq G^u(\phi) \quad \text{for} \quad (t, \phi) \in D$$

with $F^l(0) \geq 0$, and the pairs (F^l, G^u) and (F^u, G^l) satisfy (A1),(A2) and (A1),(A3), respec.
THEN (5) is **permanent** in C_0.

For non-autonomous DDEs with time-dependent delays

Theorem 5 is not always easily applicable to FDEs with time-dependent delays!

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Theorem 5b. For Eq. (5), assume (A1).

In addition, suppose that the functions

$$x \mapsto F(t,x) =: \hat{F}(x), \quad x \mapsto G(t,x) =: \hat{G}(x),\ x \in \mathbb{R}^n$$

do not depend on t.

Then,

(i) if the pair $(\hat{F}, \hat{G})$ satisfies (A2), (5) is **persistent** in C_0.
(ii) if the pair $(\hat{F}, \hat{G})$ satisfies (A3), all solutions of (5) with IC in C_0 are **bounded**.

(However, in this case we cannot derive directly that (5) is **uniformly persistent** nor **dissipative**.)

5. Applications to n-dim population models

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Example 3: n populations (single or multiple species), n different patches or classes, following the 'modified' delayed logistic equation (L), with dispersal terms among the classes:

$$x_i'(t) = \sum_{k=1}^{m_i} \frac{\alpha_{ik}(t)x_i(t-\tau_{ik}(t))}{1+\beta_{ik}(t)x_i(t-\tau_{ik}(t))} - \mu_i(t)x_i(t) - \kappa_i(t)x_i^2(t) + \sum_{j=1}^{n} d_{ij}(t)x_j(t-\sigma_{ij}(t))$$

$(t \geq 0,\ i = 1, \dots, n)$

$d_{ij}(t)$ $(i \neq j)$ - dispersal rates of populations moving from patch j to patch i
$(d_{ii}(t) \equiv 0)$
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$d_{ij}(t)$ $(i \neq j)$ - dispersal rates of populations moving from patch j to patch i
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As for (L):
$\alpha_{ik}, \beta_{ik}, d_{ij}, \mu_i, \kappa_i, \tau_{ik}, \sigma_{ij} : [0, \infty) \to [0, \infty)$ continuous functions
$A_i(t) := \sum_{k=1}^{m_i} \alpha_{ik}(t)$, $\kappa_i(t)$ bounded below and above by positive constant
$\beta_{ik}, d_{ij}, \mu_i$ are bounded, $\forall k, i, j$.

Theorem 6.[3] IF there is a positive vector $v = (v_1, \ldots, v_n)$ such that

$$Hv > 0,$$

where H is the $n \times n$ matrix $H = diag\,(\underline{A}_1 - \overline{\mu}_1, \ldots, \underline{A}_n - \overline{\mu}_n) + [\underline{d}_{ij}]$ for

$$\underline{d}_{ij} = \inf_{t \geq 0} d_{ij}(t), \quad \underline{A}_i = \inf_{t \geq 0} A_i(t), \quad \overline{\mu}_i = \sup_{t \geq 0} \mu_i(t),$$

THEN the system is **permanent**, with explicit uniform lower and upper bounds m, M given by

$$m \leq \liminf_{t \to \infty} (x_i(t)/v_i) \leq \limsup_{t \to \infty} (x_i(t)/v_i) \leq M, \; i = 1, \ldots, n, \quad \text{with}$$

$$M = \max_{1 \leq i \leq n} \limsup_{t \to \infty} \frac{1}{v_i^2 \kappa_i(t)} \left[v_i \left(\sum_{k=1}^{m_i} \alpha_{ik}(t) - \mu_i(t) \right) + \sum_{j=1}^{n} d_{ij}(t) v_j \right]$$

$$m = \min_{1 \leq i \leq n} \liminf_{t \to \infty} \frac{1}{v_i^2 \kappa_i(t)} \left[v_i \left(\sum_{k=1}^{m_i} \frac{\alpha_{ik}(t)}{1 + \beta_{ik}(t) v_i M} - \mu_i(t) \right) + \sum_{j=1}^{n} d_{ij}(t) v_j \right].$$

[3] With $n = 1$ and $d_{ij} \equiv 0$, we recover Theorem 3.

Ideas for proof: The system has the form (5), with:

$$F_i(t,\phi) = \sum_{k=1}^{m_i} r_{ik}(t, \phi_i(-\tau_{ik}(t)) + \sum_{j=1}^{n} d_{ij}(t)\phi_j(-\sigma_{ij}(t)), \quad t \ge 0, \phi \in C,$$

$$G_i(t,x) = \mu_i(t) + \kappa_i(t)x, \quad t \ge 0, x \in \mathbb{R},$$

where

$$r_{ik}(t,x) := \frac{\alpha_{ik}(t)x}{1+\beta_{ik}(t)x}, \quad t \ge 0, x \ge 0, \ \forall i, k$$

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After some comparison results (..), we apply Theorem 5b:

$\star$ $F(t,\cdot)$ **sublinear**

$\star$ (A1),(A3) OK

$\star$ $Hv > 0 \ \Rightarrow$ (A2)

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⋆ (A1),(A3) OK

⋆ $Hv > 0 \ \Rightarrow$ (A2)

To get the explicit lower and upper bounds m, M:

⋆ after the scaling $x_i \mapsto \frac{x_i}{v_i}$, we proceed as in the proof of Theorem 3 for the scalar (L)

Example 4: a Cooperative Lotka-Volterra System

$$x_i'(t) = x_i(t)\left(\beta_i(t) - \mu_i(t)x_i(t) + \sum_{j=1}^{n} a_{ij}(t) \int_0^{\tau} x_j(t-s)\, d\eta_{ij}(s)\right) \qquad (LV)$$

$$+ \sum_{j=1}^{n} d_{ij}(t) \int_0^{\tau} x_j(t-s)\, d\nu_{ij}(s), \quad t \geq 0, i = 1, \ldots, n$$

with: $\mu_i(t), \beta_i(t), a_{ij}(t), d_{ij}(t)$ continuous and bounded on $[0, \infty)$,
$\mu_i(t) > 0$, $a_{ij}(t) \geq 0, d_{ij}(t) \geq 0$
$\eta_{ij}, \nu_{ij} : [0, \infty) \to \mathbb{R} \nearrow$ are bounded, with total variation one, $\forall i, j$

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$\eta_{ij}, \nu_{ij} : [0, \infty) \to \mathbb{R} \nearrow$ are bounded, with total variation one, $\forall i, j$

$x_i(t)$ - density of the i-species population
$\beta_i(t) = b_i(t) - \sum_{j=1}^{n} d_{ji}(t)$ - where $b_i(t)$ is the Malthusian growth rate
$\mu_i(t) = m_i(t)$ - self-limitation coefficient
$a_{ii}(t)$, $a_{ij}(t)\ (j \ne i)$ - (delayed) intraspecific and interspecific coefficients
$d_{ij}(t)\ (i \ne j)$ - dispersal rates of populations moving from patch j to patch i

- (LV) has the form

$$x_i'(t) = F_i(t, x_t) - x_i(t) G_i(t, x_t) \quad (i = 1, \ldots, n) \tag{5}$$

with:

$$F_i(t, \phi) = \beta_i(t)\phi_i(0) + \sum_{j=1}^{n} d_{ij}(t) \int_0^\tau \phi_j(-s)\, d\nu_{ij}(s),$$

$$G_i(t, \phi) = \mu_i(t)\phi_i(0) - \sum_{j=1}^{n} a_{ij}(t) \int_0^\tau \phi_j(-s)\, d\eta_{ij}(s)$$

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For the **autonomous** case (i.e., all coefficients are constants):

$$M = diag\,(\beta_1, \ldots, \beta_n) + [d_{ij}], \quad N = diag\,(\mu_1, \ldots, \mu_n) - [a_{ij}]$$

$\star$ F is **linear**: OK

(A1) F and $-G$ satisfy (Q): OK

(A2) $\exists\, v > 0 :\ F(v) = Mv > 0$

(A3) $\exists\, q > 0 :\ F_i(q) - q_i G_i(Lq) < 0 \Leftrightarrow \exists\, q > 0 :\ Nq > 0$

$$M = diag\,(\beta_1, \ldots, \beta_n) + [d_{ij}], \quad N = diag\,(\mu_1, \ldots, \mu_n) - [d_{ij}]$$

Theorem 7. If there are positive vectors v and q such that $Mv > 0$ and $Nq > 0$, the **autonomous** system

$$x_i'(t) = x_i(t)\Big(\beta_i - \mu_i x_i(t) + \sum_{j=1}^{n} a_{ij} \int_0^{\tau} x_j(t-s)\, d\eta_{ij}(s)\Big) + \\ + \sum_{j=1}^{n} d_{ij} \int_0^{\tau} x_j(t-s)\, d\nu_{ij}(s), \quad t \geq 0, i = 1, \ldots, n$$

is **permanent** in C_0.

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About stability:

Theorem 7b. Under the assumptions of Thm 7, there exists a positive equilibrium x^*, which is **GAS** if it satisfies $Mx^* > 0$.

$$M = diag\,(\beta_1, \ldots, \beta_n) + [d_{ij}], \quad N = diag\,(\mu_1, \ldots, \mu_n) - [d_{ij}]$$

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$$+ \sum_{j=1}^{n} d_{ij} \int_0^{\tau} x_j(t-s)\, d\nu_{ij}(s), \quad t \geq 0, i = 1, \ldots, n$$

is **permanent** in C_0.

About stability:

Theorem 7b. Under the assumptions of Thm 7, there exists a positive equilibrium x^*, which is **GAS** if it satisfies $Mx^* > 0$.

Theorem 7c. The above results hold for **non-cooperative** autonomous LV models where $a_{ij} \in \mathbb{R}$, if the hypothesis $Nq > 0$ is replaced by $\hat{N}q > 0$ where $\hat{N} = diag\,(\mu_1, \ldots, \mu_n) - [|a_{ij}|]$.

For the non-autonomous LV model:

$$x_i'(t) = x_i(t)\left(\beta_i(t) - \mu_i(t)x_i(t) + \sum_{j=1}^{n} a_{ij}(t)\int_0^{\tau} x_j(t-s)\, d\eta_{ij}(s)\right) \qquad (LV)$$

$$+ \sum_{j=1}^{n} d_{ij}(t)\int_0^{\tau} x_j(t-s)\, d\nu_{ij}(s), \quad t \geq 0, i = 1, \ldots, n$$

Theorem 8. For the **non-autonomous** (LV), define

$$M^l = diag\,(\underline{\beta}_1, \ldots, \underline{\beta}_n) + \left[\underline{d}_{ij}\right],$$

$$N^u = diag\,(\underline{\mu}_1, \ldots, \underline{\mu}_n) - \left[\overline{a}_{ij}\right],$$

where $\underline{f} = \inf_{t\geq 0} f(t)$, $\overline{f} = \sup_{t\geq 0} f(t)$. If $\exists$ vectors $v > 0, q > 0$ such that $M^l v > 0$ and $N^u q > 0$, THEN (LV) is permanent in C_0.

Some References:

1. J. Arino, L. Wang, G.K. Wolkowicz, An alternative formulation for a delayed logistic equation. J. Theor. Biol. 241 (2006).

2. J.Bastinec, L.Berezansky, J. Diblik, Z. Smarda, On a delay population model with a quadratic nonlinearity without positive steady state. Appl. Math. Comput. 227 (2014).

3. T. Faria, Persistence and permanence for a class of functional differential equations with infinite delay, *J. Dyn. Diff. Equ.* (to appear)

4. T. Faria, A note on permanence of nonautonomous cooperative scalar population models with delays, *Appl. Math. Comput.*, 240 (2014).

5. T. Faria, Global Dynamics for Lotka-Volterra Systems with Infinite Delay and Patch Structure, *Appl. Math. Comput.*, 245 (2014).

6. T. Faria and Y. Muroya, Global Attractivity and Extinction for Lotka-Volterra systems with infinite delay and feedback controls, *Proc.Roy.Soc. Edinb. A*, 145 (2015).

7. T. Faria and G. Röst, Persistence, permanence and global stability or an n-dimensional Nicholson system, *J. Dyn. Diff. Equ.*, 26 (2014).

8. Y. Kuang, Delay Differential Equations with Applications in Population Dynamics, Academic Press, London, 1992.

9. H.L. Smith, Invariant curves for mappings. SIAM J. Math. Anal. 15 (1986).

10. H.L. Smith, Monotone Dynamical Systems. An Introduction to the Theory of Competitive and Cooperative Systems, Amer. Math. Soc., Providence, RI, 1995

11. X.-Q. Zhao, and Z. Jing, Global asymptotic behavior in some cooperative systems of functional differential equations. Cann. Appl. Math. Quart. 4 (1996).

Some Older References

1. W.S.C. Gurney, S.P. Blythe and R.M. Nisbet, Nicholson's blowflies revisited, *Nature* 287 (1980).
2. G.E. Hutchinson, Circular causal systems in ecology, *Ann. N. Y. Acad. Sci.* (1948).
3. R. M. May, Stability and Complexity in Model Systems, Princeton Univ Press, 1975.
4. R.M. May, Simple mathematical models with very complicated dynamics, *Nature* (1976).
5. R.M. May and G. Oster, Bifurcations and dynamic complexity in simple ecological models. American Naturalist (1976).
6. A.J. Nicholson, Compensatory reactions of populations to stresses, and their evolutionary significance. Austral. J. Zool. (1954)
7. A.J. Nicholson, An outline of the dynamics of animal populations. Austral .J. Zool. (1954)
8. A.J. Nicholson, The self-adjustment of populations to change. Cold Spring Harbor Symposium on Quantitative Biology (1957)
9. G. Oster, A. Ipaktchi, Population cycles. Theoretical Chemistry: Periodicities in Chemistry and Biology (1978)
10. V. Volterra, *Leçons sur la théorie mathématique de la lutte pour la vie*, Gauthier-Villars, Paris, 1931.
11. E.M. Wright, A non-linear difference-differential equation, *J. Reine Angew. Math* (1955).