Numerical approach to an age-structured Lotka-Volterra model

Jordi Ripoll & Jordi Font

Universitat de Girona

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Age-structured Lotka-Volterra

Outline

- PDE predator-prey model in $L^1(\mathbb{R}_+) \times \mathbb{R}$.
- Non-linear renewal equation (consumer-resource model).
- Asymptotic age-profile and limit ODE system.
- Long term predator-prey dynamics for age-independent interaction.
- Stability analysis via *pseudospectral* methods. Accuracy.
- Long transient dynamics via predictor-corrector methods. Numerical accuracy.
- Realistic scenario for age-dependent interaction.

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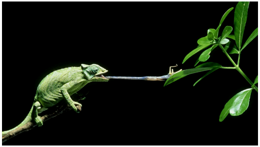
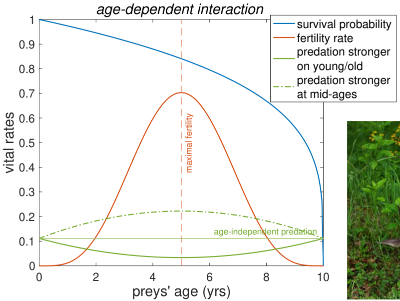
Some predator species eat all ages of prey indiscriminately and some others select their preys.

Preys' vulnerability changes along their lives, e.g. mature preys can employ aggressive defense against predators.





Predation rates depend on preys' age, season of the year, spatial distribution of species, predators' hunting patterns, etc...

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Introduction

- Age structure is important for predator-prey dynamics. Key-feature: **age or body-size** profiles of the preys.
- Simple **Lotka-Volterra** model: neither density-dependent prey growth nor functional response of the predators.
- Age-specific predation is enough to trigger a **Hopf** bifurcation. Long transient oscillations towards a limit cycle.
- *Partial differential equations* (PDE) vs *Renewal equations*. **Efficient numerical** methods for stability & time-evolution.
- We take advantage of exact solutions when interaction is considered age-independent. Accuracy analysis of the **computational methods** is achieved. *FW: convergence.*

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PDE predator-prey model in $L^1(\mathbb{R}_+) \times \mathbb{R}$

$u(a,t)$ age-density of the preys and $v(t)$ predator population.

$$\begin{cases} \partial_t u(a,t) + \partial_a u(a,t) = -\left(\mu(a) + \gamma(a)v(t)\right) u(a,t) \\ v'(t) = \left(\alpha \int_0^\infty \gamma(a)u(a,t)\,da - \delta\right) v(t) & , \ t \geq 0 \\ u(0,t) = \int_0^\infty \beta(a)u(a,t)\,da \end{cases}$$

- Predator mortality $\delta > 0$, ingestion coefficient $0 < \alpha < 1$ and age-specific per capita rates: $\mu, \beta, \gamma \in L^\infty_+(\mathbb{R}_+)$ as prey mortality, prey fertility and **species interaction**, resp.
- Model limitations: *deterministic*, *autonomous* (constant environment), no predators' age and no *spatial distribution*.

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PDE predator-prey model in $L^1(\mathbb{R}_+) \times \mathbb{R}$ (cont')

$u(a,t)$ age-density of the preys and $v(t)$ predator population.

$$\begin{cases} \partial_t u(a,t) + \partial_a u(a,t) = -\left(\mu(a) + \gamma(a) v(t)\right) u(a,t) \\ v'(t) = \left(\alpha \int_0^\infty \gamma(a) u(a,t)\, da - \delta\right) v(t) & , \ t \geq 0 \\ u(0,t) = \int_0^\infty \beta(a) u(a,t)\, da \end{cases}$$

- **Basic reproduction number** for the preys in absence of predators: $R_0 = \displaystyle\int_0^\infty \beta(a)\, e^{-\int_0^a \mu(s)\, ds}\, da > 1$.
- Equivalently, positive **Malthusian parameter** $r > 0$: prey asynchronous exponential growth in absence of predators.

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Non-linear renewal equation (consumer-resource model)

$b(t) = u(0,t)$ birth rate of preys (# of newborns per time-unit) and $v(t)$ predator population size.

$$\begin{cases} b(t) = \int_0^\infty \beta(a)\, e^{-\int_0^a \mu(s)+\gamma(s)v(s+t-a)\,ds} \cdot b(t-a)\,da \\ v'(t) = \left(\alpha \int_0^\infty \gamma(a)\, e^{-\int_0^a \mu(s)+\gamma(s)v(s+t-a)\,ds} \cdot b(t-a)\,da - \delta\right) v(t) \end{cases}$$

- Steady-states (SS): the *trivial equilibrium* $b^* = 0$, $v^* = 0$, and the *coexistence equilibrium* $b^* > 0$, $v^* \simeq \frac{2\ln(R_0)}{\int_0^\infty \gamma(s)\,ds} > 0$.
- Age-density at equilibrium: $u^*(a) = b^* e^{-\int_0^a \mu(s)+\gamma(s)v^*\,ds}$.

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Asymptotic age-profile and limit ODE system

Prey pop. size $P(t) = \int_0^\infty u(a,t)\,da$. If normalized age-density $u(a,t)/P(t) \to \bar{\omega}(a)$ then limit system of Lotka-Volterra type:

$$\begin{cases} \dfrac{dP}{dt} = \langle \beta - \mu \rangle_{\bar{\omega}} \cdot P - \langle \gamma \rangle_{\bar{\omega}} \cdot v\, P \\ \dfrac{dv}{dt} = \alpha \langle \gamma \rangle_{\bar{\omega}} \cdot v\, P - \delta v \end{cases} \quad , \; t \geq 0$$

- Weighted mean over age-span: $\langle \phi \rangle_{\bar{\omega}} = \int_0^\infty \phi(a)\, \bar{\omega}(a)\, da$.
- $b(t) \sim \bar{\omega}(0) P(t)$, SS: $b^* = \bar{\omega}(0) \frac{\delta}{\alpha \langle \gamma \rangle_{\bar{\omega}}}$, $v^* = \frac{\langle \beta - \mu \rangle_{\bar{\omega}}}{\langle \gamma \rangle_{\bar{\omega}}} > 0$ and periodic orbits in $\mathbb{R}^2$ "*prey birth-rate $\times$ predators*":

$$\left(\frac{v}{v_0} \right)^{v^*} \cdot \left(\frac{b}{b_0} \right)^{\alpha P^*} = \exp \left[v - v_0 + \frac{\alpha}{\bar{\omega}(0)} (b - b_0) \right] .$$

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Long term predator-prey dynamics for age-independent interaction

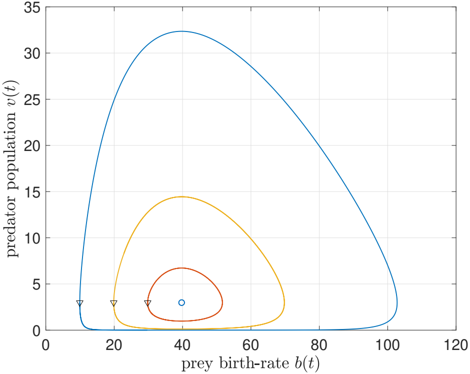

Figure: prey age-profile $\longrightarrow \bar{\omega}(a) = \bar{\omega}(0)\exp[-\int_0^a \mu(s)\,ds - r \cdot a]$. Steady-state $b^* = \bar{\omega}(0)\frac{\delta}{\alpha\bar{\gamma}}$, $v^* = \frac{r}{\bar{\gamma}}$. **Constant interaction** $\gamma(a) \equiv \bar{\gamma}$, mortality $\mu(a) = \mu_0(1 + k\,a)$, fertility $\beta(a) = \bar{\beta}\,\mu(a)$, $R_0 = \bar{\beta} = 2$ and $r = 0.43 > 0$.

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Stability analysis via *pseudospectral* methods

Continuous eigenvalue problem $a \geq 0$	Discrete eigenvalue problem $i = 1, \ldots, N$
$\phi(0) = \int_0^\infty \beta_*(a)\phi(a)\, da$	$\Phi_0 = \frac{a^\dagger}{2} \sum_{j=0}^N \beta_j^* \Phi_j w_j$
$\lambda\, \phi(a) = -\phi'(a) - b^*\gamma(a)\, V_0$	$\lambda\Phi_i = -\sum_{j=0}^N H_{ij}\Phi_j - b^*\gamma_i\, V_0$
$\lambda V_0 = v^* \int_0^\infty \gamma_*(a)\phi(a)\, da$	$\lambda V_0 = v^* \frac{a^\dagger}{2} \sum_{j=0}^N \gamma_j^* \Phi_j w_j$

- Linearization around the SS. $\lambda = 0$ is never an eigenvalue.
- **Differential operator** A vs **large size matrix** A_N. Spectral values of A with real part $> -\mu_0$ are actually eigenvalues.
- Chebyshev nodes in age-span $[0, a^\dagger]$, differentiation matrix H and Clenshaw-Curtis quadrature rule, weights w_j.

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Accuracy of the *pseudospectral* method for age-independent interaction

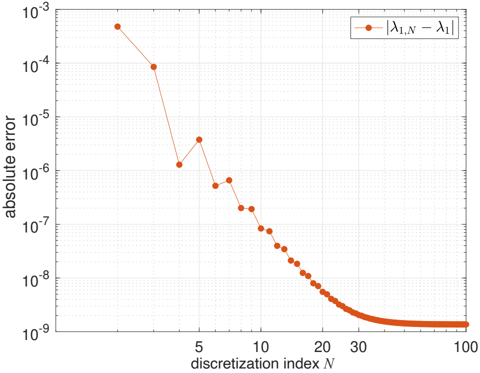

Figure: exact solution $\lambda_1 = \pm\sqrt{\delta v^* \bar{\gamma}}\, i$, spectral bound $s(A) = 0$, vs rightmost eigenvalues $\lambda_{1,N}, \bar{\lambda}_{1,N}$ of matrix A_N. Mortality $\mu(a) = \frac{\theta}{a^\dagger - a}$, fertility $\beta(a) = \bar{\beta} a(a^\dagger - a)$ and **constant interaction** $\gamma(a) \equiv \bar{\gamma}$. SS limits accuracy. Matrix spectral bound $s(A_N) = \text{Re}(\lambda_{1,N}) \sim 10^{-9}$.

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Transient dynamics via predictor-corrector methods

Integrated form of predator-prey model. [μ to avoid immortals].

$$u(a+\Delta t, t+\Delta t) = u(a,t)\, e^{-\int_a^{a+\Delta t} \mu(s)+\gamma(s) v(s+t-a)\, ds}$$
$$v(t+\Delta t) = v(t)\, e^{-\delta \Delta t + \alpha \int_t^{t+\Delta t} S(s)\, ds}, \; S(t) = \int_0^\infty \gamma(a)\, u(a,t)\, da$$

$$\begin{cases} \tilde{v}^{n+1} = v^n \exp[\Delta t(-\delta + \alpha S^n)] \;\; \textbf{predictor} \\ u_{j+1}^{n+1} = u_j^n \exp[-\Delta t(\mu_j + \gamma_j v^n + \mu_{j+1} + \gamma_{j+1} \tilde{v}^{n+1})/2] \\ u_0^{n+1} = \frac{\Delta t}{1 - w_0\, \beta_0\, \Delta t} \sum_{j=1}^{J-1} w_j\, \beta_j\, u_j^{n+1} \;\; \textbf{b.c.} \\ S^{n+1} = \Delta t \sum_{j=0}^{J-1} w_j\, \gamma_j\, u_j^{n+1} \\ v^{n+1} = v^n \exp[\Delta t\big(-\delta + \alpha(S^n + S^{n+1})/2\big)] \;\; \textbf{corrector} \end{cases}$$

- Grid points in age $j = 0, \ldots, J$ and we set $u_J^n = 0$.

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Transient dynamics via predictor-corrector methods (cont')

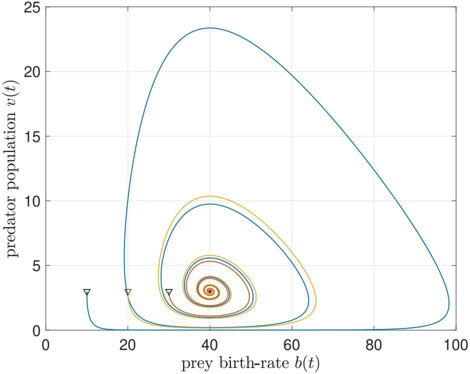

Figure: converging trajectories from 3 initial conditions ($\triangledown$) to the coexistence equilibrium $b^* = \frac{\delta\,\bar{\beta}}{\alpha\,\bar{\gamma}}$, $v^* = \frac{\bar{\beta}-1}{\bar{\gamma}} > 0$. Mortality rate $\mu(a) = \mu_0(1 + k\,a)$, fertility $\beta(a) = \bar{\beta}\,\mu(a)$, **age-specific interaction** $\gamma(a) = \bar{\gamma}\,\mu(a)$. $\mathbb{P}(\text{immortals}) \sim 10^{-10}$.

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Accuracy of predictor-corrector scheme for age-independent interaction

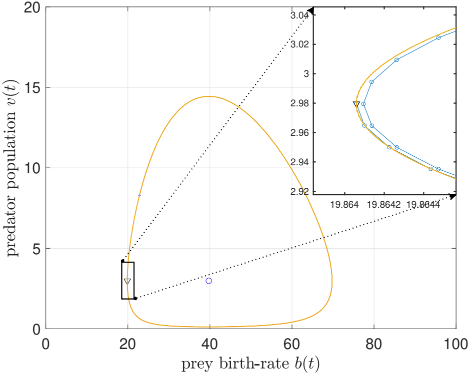

Figure: exact periodic orbit (*yellow curve*) from ODE system, vs numerical simulation of the orbit (*blue curve with dots*). Inset plot: error of the computed curve is $\sim 10^{-4}$. Step size $\Delta t = \Delta a = 0.002$ and $J = 5000$.

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Realistic scenario for age-dependent interaction

- Age-span $[0, a^\dagger]$, unbounded mortality $\mu(a) = \frac{\theta}{a^\dagger - a}$, fertility $\beta(a) = \bar{\beta} a(a^\dagger - a)$ is maximal at an intermediate age.
- Basic reproduction number $R_0 = \int_0^{a^\dagger} \beta(a) \left(\frac{a^\dagger - a}{a^\dagger}\right)^\theta da > 1$, Malthusian $r > 0$ from $1 = \int_0^{a^\dagger} \beta(a) \left(\frac{a^\dagger - a}{a^\dagger}\right)^\theta e^{-ra}\, da$ and predators $v^* > 0$, $1 = \int_0^{a^\dagger} \beta(a) \left(\frac{a^\dagger - a}{a^\dagger}\right)^\theta e^{-v^* \int_0^a \gamma(s)\, ds}\, da$.

Species interaction $\gamma(a) = \bar{\gamma}\left(1 - 4ka(a^\dagger - a)/{a^\dagger}^2\right)$, 3 scenarios:

- If $\mathbf{k} < \mathbf{0}$, *predation* is stronger at preys' intermediate ages. It's focused on the most fertile preys. If $\mathbf{k} = \mathbf{0}$, for predators, it does not matter preys' age. If $\mathbf{k} > \mathbf{0}$, *predation* is stronger at early and late ages of the preys. It's focused on the less fertile preys.

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Realistic scenario for age-dependent interaction (cont')

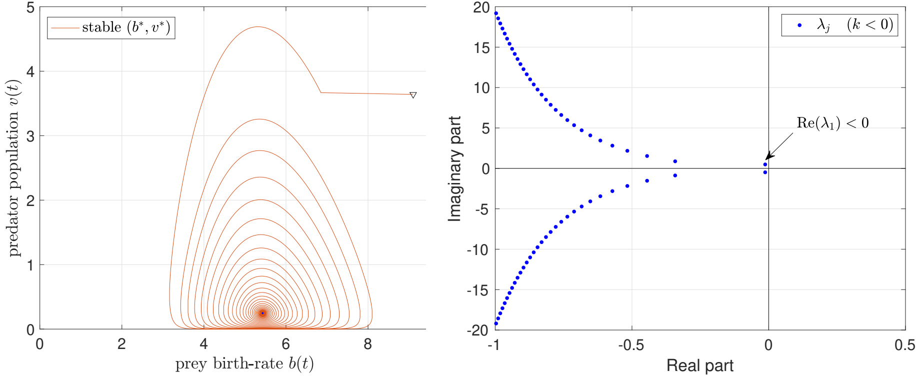

Figure: predation on intermediate preys. Long transient oscillations towards a **stable steady-state**. Pair of dominant eigenvalues: $\lambda_1 = -0.012901772 \pm 0.486759890i$. Damped oscillations.

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Realistic scenario for age-dependent interaction (cont')

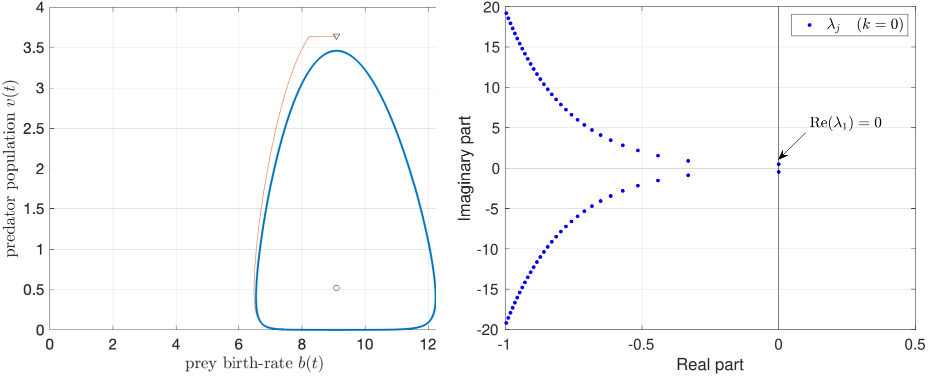

Figure: when predation becomes independent of preys' age ($k = 0$), a Hopf bifurcation occurs. Dominant eigenvalues on the imaginary axis: $\lambda_1 = \pm 0.475118407i$. **Periodic oscillations in predators and preys**.

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Realistic scenario for age-dependent interaction (cont')

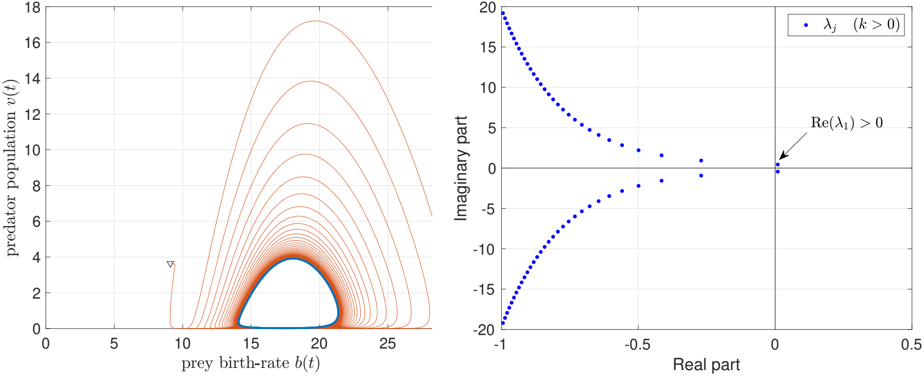

Figure: predation on vulnerable preys (young/old). Long transient oscillations towards a **stable limit cycle**. Dominant eigenvalues: $\lambda_1 = 0.009531135 \pm 0.441038955i$. Unstable steady-state.

WRAPPING UP:

Numerical approach to an age-structured Lotka-Volterra model

- **Lotka-Volterra** model, enhanced by age-structure, is a rich dynamical system to describe predator-prey interactions.
- Long-term preys' age-profile is key in our analysis.
- **Efficient numerics** for the (un)stability of SS and the long transient oscillations. *Discretization* of age and time. Approx. of differential operators by suitable matrices.
- Under the assumption that predators target preys selected by age or size, a **Hopf** bifurcation splits population behavior between damped oscillations $\rightarrow$ stable SS and sustained oscillations (stable limit cycle).

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Thank you for listening!

jordi.ripoll@udg.edu

http://imae.udg.edu/~jripoll

Girona, Spain.

Former Visiting Professor at

Dept. Ecology and Evolutionary Biology

Cornell University, Ithaca, USA.

@jripoll71