A Consumer-Resource Model with Synchronized Reproduction

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Based on Pachepsky, Nisbet, and Murdock, *Ecology*, 2008

With helpful contributions and accuracy checks
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Discrete or Continuous?

- A number of issues influence whether a modeler chooses discrete time or continuous time:
  - Data is often collected at discrete times. (Red herring.)
  - Discrete models are easier to understand conceptually. (Red herring.)
  - **Life history events are synchronized for some systems.**
  - **Discrete time models can exhibit instabilities that cannot happen in continuous time.**
- **We should use discrete time when life history events are synchronized and continuous time when they are not.**

Mixed Time Model, components

- Suppose a consumer that stores resources for an annual reproductive event consumes a resource that grows continuously.
- To achieve the right time choices, we need
  - A discrete model that tracks resource level and consumer population at an annual census, with
  - An embedded continuous model that tracks resource levels and consumer population during the time between census events.

	continuous	discrete
Time	$0 < s < 1$	$t = 0, 1, \ldots$
Resource Biomass	$F(s)$	U_t
Consumer Population	$X(s)$	V_t

Mixed Time Model, discrete system overview

- U_t and V_t are the resource level and consumer population after the birth pulse between year t and year $t+1$.
  - U_0 and V_0 are the initial conditions for year 1.
- The (U, V) system is then defined by a discrete map

$$U_{t+1} = P(U_t, V_t); \qquad V_{t+1} = Q(U_t, V_t),$$

where the functions P and Q are determined by the continuous dynamics of year t along with the birth pulse between years t and $t+1$.

Mixed Time Model, continuous time equations

- The continuous model must track the resource level F, the consumer population X, and the cumulative resource acquisition per consumer b.

$$\frac{dF}{ds} = \rho F\left(1 - \frac{F}{K}\right) - aFX, \qquad F(0) = U_t; \tag{1}$$

$$\frac{dX}{ds} = -\mu X, \qquad X(0) = V_t; \tag{2}$$

$$\frac{db}{ds} = \theta a F, \qquad b(0) = 0. \tag{3}$$

- θ is the number of offspring that can be produced from one unit of resource consumption.

Mixed Time Model, birth pulse

- Resource levels carry over from discrete time t to $s = 0$ and from $s = 1$ to discrete time $t + 1$.

$$F(0) = U_t, \qquad U_{t+1} = F(1); \tag{4}$$

- Adult consumers carry over from discrete time t to $s = 0$ and from $s = 1$ to discrete time $t + 1$, while stored biomass becomes new consumers at discrete time t.

$$X(0) = V_t, \qquad V_{t+1} = [1 + b(1)]\, X(1); \tag{5}$$

Dimensionless Version

$$\frac{dF}{ds} = \rho F\left(1 - \frac{F}{K}\right) - aFX, \quad F(0) = U_t, \quad U_{t+1} = F(1);$$
$$\frac{dX}{ds} = -\mu X, \quad X(0) = V_t, \quad V_{t+1} = [1 + b(1)]\, X(1);$$
$$\frac{db}{ds} = \theta a F, \qquad b(0) = 0.$$

Scale F, U by K and X, V by ρ/a; time is already scaled.

$$\frac{df}{ds} = \rho f(1 - f - x), \quad f(0) = u_t, \quad u_{t+1} = f(1); \tag{6}$$
$$\frac{dx}{ds} = -\mu x, \quad x(0) = v_t, \quad v_{t+1} = [1 + b(1)]\, x(1); \tag{7}$$
$$\frac{db}{ds} = \alpha f, \qquad b(0) = 0. \tag{8}$$

Analysis Overview

- There are three types of possible fixed points:
  1. Extinction
  2. Resource only
  3. Coexistence
- With careful analysis, we will
  1. Show that the resource always persists.
  2. Determine a simple criterion for consumer persistence.
  3. Show that the consumer persistence criterion guarantees a unique coexistence fixed point.
  4. Identify the [**least complicated**] pair of inequalities for stability of the coexistence fixed point.

Resource Persistence

- In the absence of the consumer, the resource level simply satisfies the logistic growth equation

$$\frac{df}{ds} = f(1 - f),$$

for all time, there being no need for a discrete time structure.
- The consumer gains in population only through consumption of the resource.
- Therefore, the model includes no mechanism for driving the resource level to 0.
    - We'll see that the resource level can be very low for some parameter regimes.

Consumer Persistence

- The consumer persists if and only if the resource-only fixed point $f = u = 1$, $x = v = 0$ is asymptotically stable.
- An equivalent but much simpler approach is to just check whether the resource-only fixed point is stable with respect to an initial perturbation in the consumer population.
- The continuous time problem for x reduces to

$$\frac{dx}{ds} = -\mu x, \quad x(0) = v_0 = \epsilon, \quad v_1 = [1 + b(1)]\, x(1),$$

$$b(1) = \int_0^1 \alpha f \, ds = \alpha[1 - O(\epsilon)].$$

- Persistence is defined by $v_1/v_0 \geq 1$, or

$$(\alpha + 1)e^{-\mu} > 1. \tag{9}$$

Analysis Plan [assuming $(\alpha+1)e^{-\mu} > 1$]

1. Use the differential equations and birth pulse equations to obtain the functions g and h for the map

$$u_{t+1} = u_t \, g(u_t, v_t), \qquad v_{t+1} = v_t \, h(u_t, v_t) \tag{10}$$

   - This form focuses on the growth factors u_{t+1}/u_t and v_{t+1}/v_t, which simplifies the derivation of the map and computation of the fixed points.

2. Solve $g(u^*, v^*) = 1$, $h(u^*, v^*) = 1$, where $u^*, v^* > 0$.
3. Find the Jacobian, its trace T, and its determinant D.
   - Use extensive algebraic simplification!
4. Identify stability conditions from the Jury criteria,

$$D < 1, \qquad D + T + 1 > 0, \qquad D - T + 1 > 0. \tag{11}$$

Analysis Results

- There is a unique coexistence fixed point when $\alpha + 1 > e^{\mu}$. Key quantities are yearly averages $(\bar{f}, \bar{x})$ rather than (u^*, v^*):

$$\bar{f} = \frac{e^{\mu_1} - 1}{\alpha_1} < 1, \qquad \bar{x} = 1 - \bar{f} < 1. \tag{12}$$

- Key parameters are q, M, δ:

$$q = \frac{\int_0^1 (1 - e^{-\mu s}) G^*(s, \mu, \bar{x}, \rho)\, ds}{\int_0^1 (1 - e^{-\mu}) G^*(s, \mu, \bar{x}, \rho)\, ds} < 1, \quad G^* = \cdots > 0. \tag{13}$$

$$M = (\alpha + 1)e^{-\mu} - 1 > 0, \qquad \delta = e^{-\rho \bar{f}} < 1, \tag{14}$$

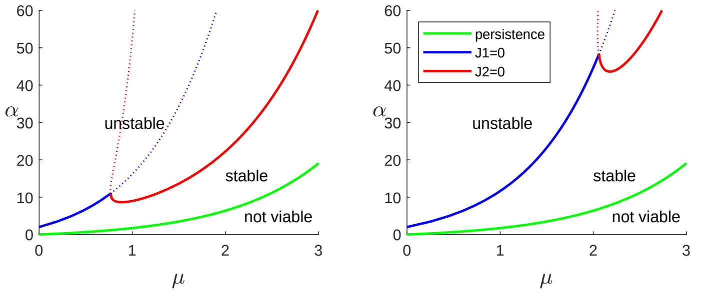
- Stability criteria require M small enough:

$$\frac{1}{M} > 1 - q, \qquad \frac{1}{M} > \frac{1 - \delta}{1 + \delta}\left(q - \frac{1}{2}\right), \tag{15}$$

Bifurcation Plots

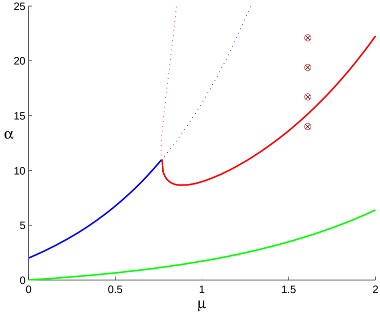
$\rho = 20$
fast resource growth

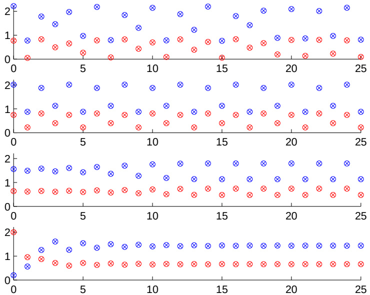
$\rho = 10$
moderate resource growth



Overcompensation (J2) Instability

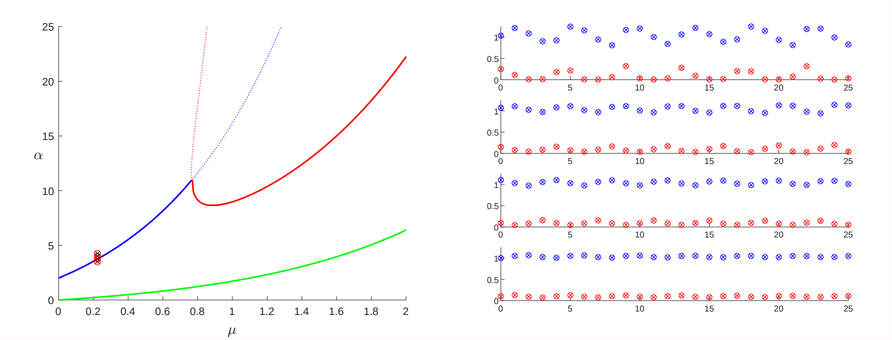
- When μ is large, the system behaves like the discrete logistic map. Greater instability leads to period doubling and chaos.





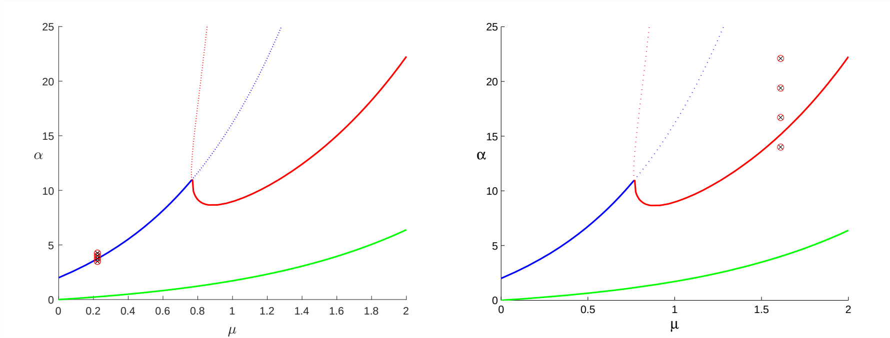
Consumer-Resource (J1) Instability

- When μ is small, the system again exhibits period doubling and chaos, but there are some important differences.



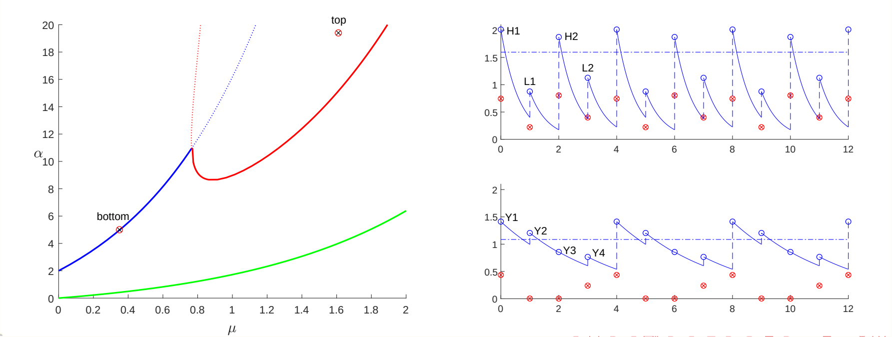
Distance to Chaos

- The top example in each sequence was just into the chaotic regime. This happens much quicker for the low μ instability.



Cycle Details

- Overcompensation 4-cycles (top) are actually a pair of 2-cycles (H1-H2 and L1-L2) inside a 2-cycle (H-L).
- Consumer-resource 4-cycles (bottom) are 4-year cycles, with periods of near extinction of the resource.



Cycle Details