A Competition Model with Seasonal Reproduction

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Collaborators

- The research portion of this work was done as part of a research group that included
  - Richard Rebarber, University of Nebraska-Lincoln
  - Amanda Laubmeier, then of UNL, now of Texas Tech University
  - Terrance Pendleton, Drake University
- The project started as a Research Experience for Undergraduate Faculty project.
  - Thanks to Leslie Hogben, ISU, and the rest of the REUF leadership team.

Talk Structure

- Slides whose titles start with a number are overviews that summarize an idea or tell you what to look for in the coming slides.
- Slides whose titles do not start with a number are the main presentation.
- Contrasting colors are used to call attention to distinctions and to help you form mental connections between related words and symbols.

1. Instability in Ecological Models

- There are two main types of instabilities:
  - Overcompensation
  - Consumer-Resource
- Overcompensation instability only happens in discrete models.
  - This fact is important for model selection.
- Consumer-resource instability can happen in either discrete or continuous models, but is easier to identify in continuous models.

1.1 Single-Species Population Models

- We compare the characteristics of continuous-time and discrete-time dynamical systems.
- For the comparison, it is important to write discrete-time systems in a way that is analogous to continuous-time systems.
- Done right, the comparison makes overcompensation instability easy to explain.

Single-Species Population Models (as usually presented)

- Continuous-Time Model $y' = f(y)$
  - An equilibrium solution y^* [$f(y^*) = 0$] is asymptotically stable iff

$$f'(y^*) < 0.$$

- Discrete-Time Model $N_{t+1} = g(N_t)$
  - A fixed point N^* [$g(N^*) = N^*$] is asymptotically stable iff

$$-1 < g'(N^*) < 1.$$

- These criteria look very different, but the difference is misleading.

Single-Species Population Models

- Continuous-Time Model $\quad y' = f(y)$
  - $f(y)$ is the *rate of change*.
- Discrete-Time Model $\quad N_{t+1} = g(N_t)$
  - $g(N)$ is the *updated population*.
    - **The model forms are not comparable.**
  - The *rate of change* is

$$\frac{N_{t+1} - N_t}{(t+1) - t} = N_{t+1} - N_t.$$

  - For comparison with the continuous model form, we should use the form

$$N_{t+1} - N_t = F(N_t).$$

Single-Species Population Models (as they should be presented)

- Continuous-Time Model $\quad y' = f(y)$
  - An equilibrium solution y^* $[f(y^*) = 0]$ is asymptotically stable iff
$$f'(y^*) < 0.$$
- Discrete-Time Model $\quad N_{t+1} - N_t = F(N_t)$
  - A fixed point N^* $[F(N^*) = 0]$ is asymptotically stable iff
$$-2 < F'(N^*) < 0.$$
- Overcompensation instability is what happens when $F'(N^*) < -2$. (The discrete rate $N_{t+1} - N_t$ updates too slowly.)
  - *Overcompensation cannot occur in continuous models because y' changes continuously.*

1.2 Overcompensation Instability Examples

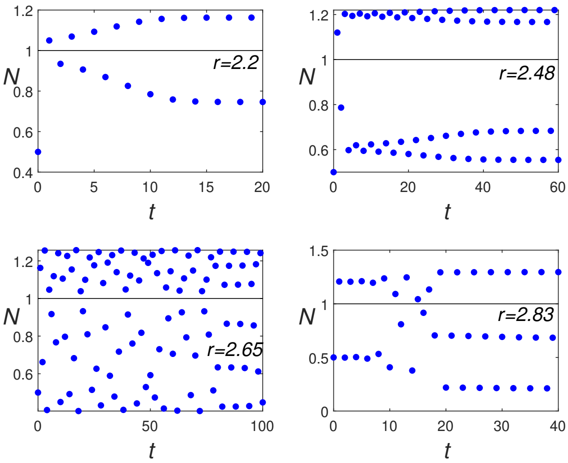
- The well-known behavior of the discrete logistic map serves as a canonical example of overcompensation.
- Some examples show the variety of behaviors exhibited by discrete models with overcompensation.

Logistic Growth Models

- Continuous-Time Model $\quad y' = ry(1-y), \quad r > 0$
  - $y^* = 0$ is never asymptotically stable.
  - $y^* = 1$ is always asymptotically stable.

- Discrete-Time Model $\quad N_{t+1} - N_t = rN(1 - N_t), \quad r > 0$
  - $N^* = 0$ is never asymptotically stable.
  - $N^* = 1$ is asymptotically stable when $r < 2$.
  - There is an asymptotically stable 2-cycle when $2 < r < \sqrt{6}$.
  - As r increases further, we see
    - period doubling up to a point,
    - then chaos, mixed with some unusual stable cycles.

Overcompensation Examples ($r = 2.2, 2.48, 2.65, 2.83$)



1.3 Consumer-Resource Instability

- Consumer-resource instability can occur in continuous systems with two or more state variables.
- There needs to be nonlinearity of a sort that has a destabilizing influence.
- The Lotka-Volterra model has an unstable equilibrium point; however, it does not have enough nonlinearity to produce CR instability.
  - *Instead, its instability is due to its being a bad model.*[1]

[1] Feel free to ask me about the Lotka-Volterra model later.

Rosenzweig-MacArthur / Holling Type 2 Model

Rosenzweig-MacArthur Model:

$$X' = rX\left(1 - \frac{X}{K}\right) - F(X)Y,$$

$$Y' = cF(X)Y - mY.$$

X is resource biomass
Y is consumer biomass
$F(X)$ is the consumption rate per unit consumer
$c < 1$ is the resource→consumer biomass conversion factor

Holling type 2 dynamics: linear for small X, saturates for large X

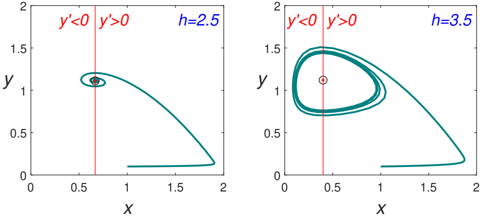
$$F(X) = \frac{QX}{K + X}$$

Consumer-Resource Instability

Dimensionless R-M/H2 model:

$$x' = x\left(1 - \frac{x}{k} - \frac{y}{1+x}\right),$$

$$y' = \epsilon y\left(\frac{hx}{1+x} - 1\right).$$



- Higher consumer efficiency (h) is destabilizing ($h > 3$ for CR instability).

1.4 Model Selection: Discrete or Continuous?

- A variety of issues are used by modelers to select between discrete time and continuous time.
- Some of these are "red herrings" (ideas that lead us in the wrong direction).
- We can identify two crucial criteria that almost always make the correct choice clear.

Model Selection: Discrete or Continuous?

- Discrete is better when data is collected at discrete times. (Red herring.)
- Discrete is better because discrete time models are easier to understand conceptually. (Red herring.)
- **Continuous is better because discrete time models can exhibit instabilities that cannot happen in continuous time.**
- **Life history events in some systems are synchronized.**
- **We should use discrete time when life history events are synchronized and continuous time when they are not.**

2. A Consumer-Resource Model with Synchronized Reproduction

- We consider a consumer-resource system that differs from that of R-M/H2 in two ways:
  1. Reproduction of consumers is seasonal.
  2. The interaction term is *less* nonlinear (not enough for CR instability in a 2D continuous model).

  - Any instabilities will be due to the discrete nature of the model.

- The model is from Pachepsky, Nisbet, and Murdock, *Ecology*, 2008. The analysis is my reworking of their problem, found in Ledder, Rebarber, Pendleton, Laubmeier, and Weisbrod, *J Biol Dyn*, 2021, doi 10.1080/17513758.2020.1862927

2.1 Model Development

- We have to think carefully about model design, using a mix of discrete and continuous time.

- Resource growth and consumption happen continuously.

- But consumer reproduction happens seasonally (we'll assume it is instantaneous).

Mixed Time Model, components

- Suppose resource growth and consumption happen continuously, but the consumer stores the resources for an annual reproductive event.

- 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.

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

Modeling Note

- To a mathematician, it would (probably?) seem most reasonable to embed the discrete model into the continuous one.
  - We would have a single set of state variables $(F, X)(t)$, and the discrete part of the model would contribute jump conditions at integer times.
- To a modeler (well, at least for the original authors and me), it seems much better to think of the model as fundamentally discrete, but with a continuous model needed to define the discrete map.
- The plan for analysis is completely different for these two visions of how the model components fit together.

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 subsequent birth pulse.

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, which we measure in terms of new consumers rather than resource units.

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

$$\frac{dX}{ds} = -\mu X; \tag{2}$$

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

- aF is the resource acquisition rate per consumer;
- 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 continuous time $s = 0$ 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 $t + 1$.

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

Scaling (orange–simplifications; blue–discrete map)

$$\frac{dF}{ds} = \rho F\left(1 - \frac{F}{K}\right) - aFX, \quad F(0) = U_t, \quad U_{t+1} = F(1);$$

$$\frac{dX}{ds} = -\mu X, \quad X(0) = V_t, \quad V_{t+1} = [1 + b(1)]\, X(1);$$

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

Scale F, U by K and X, V by ρ/a; s, t, and b are already scaled.

$$\frac{df}{ds} = \rho f(1 - f - x), \quad f(0) = u_t, \quad u_{t+1} = f(1);$$

$$\frac{dx}{ds} = -\mu x, \quad x(0) = v_t, \quad v_{t+1} = [1 + b(1)]\, x(1);$$

$$\frac{db}{ds} = \alpha f, \qquad b(0) = 0.$$

2.2 Model Analysis Overview

- Think of the model as a map from (u_t, v_t) to (u_{t+1}, v_{t+1}), with parameters ρ, μ, α representing resource growth, consumer death, and consumer reproduction.

- It is mathematically superior to write the map as

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

rather than

$$u_{t+1} = p(u_t, v_t), \quad v_{t+1} = q(u_t, v_t).$$

  - Fixed points are $g = 1$, $h = 1$ rather than $p = u$, $q = v$;
  - Product rule derivatives simplify!

2.2.1 Resource Persistence

- There are three types of possible fixed points:
  1. Extinction
  2. Resource only
  3. Coexistence
- We prove resource persistence by showing that the extinction fixed point is always unstable.

Presentation Note

- Up to this point we have been using colored text to distinguish the continuous and discrete model components.
- Now we are going to use colored text to distinguish resource variables and consumer variables.

Resource Persistence

- In the absence of the consumer, the resource biomass 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.

2.2.2 Consumer Persistence

- The model is only interesting when the consumer persists.
- The criterion for consumer persistence is the same as the criterion for the resource-only fixed point to be unstable.
- The resulting criterion is easily interpreted as requiring the (mean family size at time $t+1$ from a consumer at time t) times the (continuous-time consumer survival probability) to be bigger than 1.

Consumer Persistence

- The consumer persists if and only if the resource-only fixed point $f = u = 1$, $x = v = 0$ is unstable.
- We need only check stability with respect to an initial perturbation in the consumer population.
  - Set $u_0 = 1$ and $v_0 = \epsilon \ll 1$. Solve the resulting linearized problem to determine when $v_1 > v_0$.
- Consumer persistence requires

$$(\alpha + 1)e^{-\mu} > 1. \tag{6}$$

(survivor's offspring plus survivor) * (survival probability) > 1

2.2.3 Mean Resource and Consumer Values

- If there is a stable coexistence fixed point (u^*, v^*), we can define a corresponding mean resource biomass $\bar{f}$ and mean consumer population $\bar{x}$ as averages over continuous time s.
- We can calculate these averages by eliminating $u_{t+1} = u^*$, $u_t = u^*$, etc from the continuous system.

Mean Resource and Consumer Values

Assuming $u_{t+1} = u_t = u^*$ and $v_{t+1} = v_t = v^*$:

$$f^{-1} f' = \rho(1 - f - x), \quad f(0) = f(1);$$
$$x' = -\mu x, \quad x(0) = [1 + b(1)]\, x(1);$$
$$b' = \alpha f, \qquad b(0) = 0.$$

Integrate all equations on $[0, 1]$:

$$\bar{f} + \bar{x} = 1, \quad 1 + b(1) = e^{\mu}, \quad b(1) = \alpha \bar{f}$$

$$\bar{f} = \frac{e^{\mu} - 1}{\alpha} < 1, \quad \bar{x} = 1 - \bar{f} < 1. \tag{7}$$

2.2.4 Fixed Point Analysis Plan

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

$$u_{t+1} = u_t \, g(u_t, v_t), \qquad v_{t+1} = v_t \, h(u_t, v_t) \tag{8}$$

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,

$$D < 1, \qquad D + T + 1 > 0, \qquad D - T + 1 > 0. \tag{9}$$

The Map Functions g and h

- The map functions for

$$u_{t+1} = u_t \, g(u_t, v_t), \qquad v_{t+1} = v_t \, h(u_t, v_t) \tag{8}$$

are barely manageable.

$$g(u, v) = \frac{G_1(v)}{1 + \rho u I(v)}, \quad h(u, v) = c_1 - c_2 v - c_3 g(u, v),$$

where c_k are constants, G_1 is an algebraic function, and $I(v)$ is a definite integral of a function $G(s, v)$ with respect to s.

- This makes the Jacobian a challenge as well!

A Unique Coexistence Fixed Point

$$g(u,v) = \frac{G_1(v)}{1+\rho u I(v)} = 1, \quad h(u,v) = c_1 - c_2 v - c_3 g(u,v) = 1,$$

- It is surprisingly easy to find the fixed points for the map.
  - v^* is an explicit function of the parameters.
  - u^* is given in terms of the definite integral $I(v^*)$.
- The explicit formulas mean that uniqueness of the fixed point requires no proof.
- Existence requires some arguments to show that the result for u^* is in the required range $[0,1]$.

Stability Criteria

- Computation of the Jacobian and extensive simplification of the Jury conditions results in a pair of stability criteria.
- These are given in terms of algebraic functions $m(\mu, \alpha)$ and $d(\mu, \alpha, \rho)$ and a ratio of two definite integrals $q(\mu, \alpha, \rho)$:

$$m > 1 - q, \tag{J1}$$

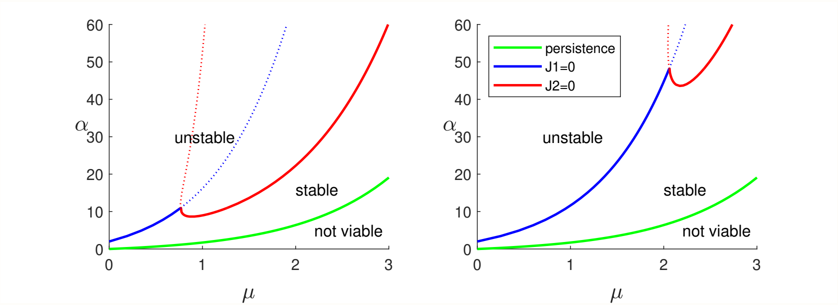
$$m > d\left(q - \frac{1}{2}\right). \tag{J2}$$

  - The definite integrals in q pose no difficulties for numerical computation.
  - The complicated model results in surprisingly simple stability criteria!

Bifurcation Plots

$\rho = 20$
fast resource growth

$\rho = 10$
moderate resource growth

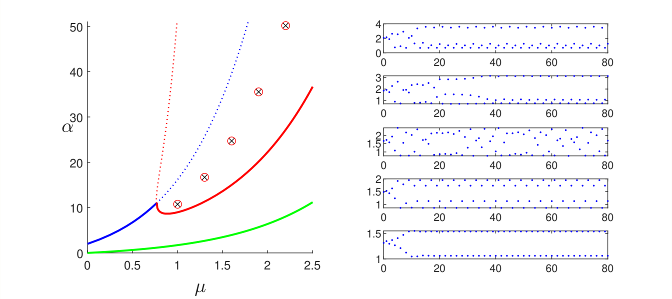


2.3 Instability Examples

- Overcompensation instability requires large α and large μ.
  - The behavior is similar to that of the discrete logistic map.
- Consumer-resource instability requires large α and small μ.
  - The behavior is much more complicated than what we saw in the R-M/H2 model.

Overcompensation (J2) Instability

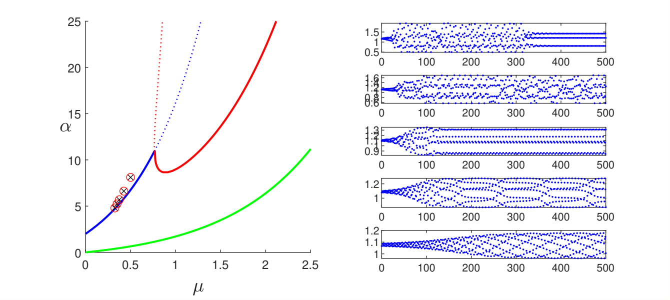
- When μ is large, the system behaves like the discrete logistic map. Greater instability leads to period doubling and chaos.



bottom to top: 2-cycle, 4-cycle, chaos, 3-cycle, 6-cycle

Consumer-Resource (J1) Instability

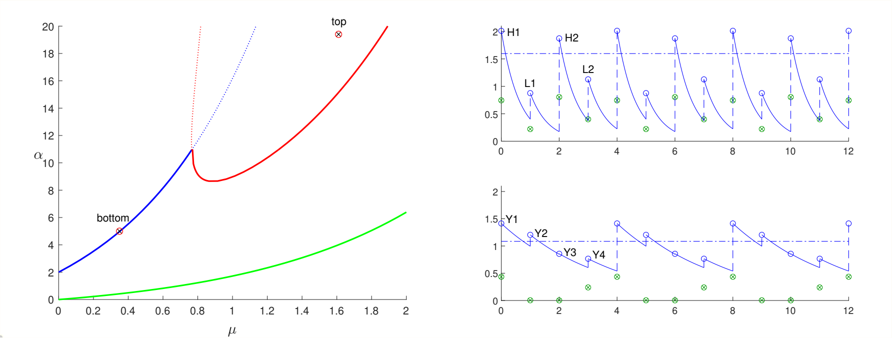
- When μ is small, the system again exhibits period doubling and chaos, but chaos begins very near the stability boundary.
  - small μ: predator is too efficient



bottom to top: ?-cycle, 101-cycle, 7-cycle, chaos, 3-cycle

Cycle Details

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



3. Competition Between Two Consumers

- The Principle of Competitive Exclusion: Two species cannot coexist at constant population values if they occupy the same ecological niche.
    - This is not so much a scientific ‘law’ as a definition of ‘ecological niche’.
- Many competition models show stable coexistence equilibria even if both consumers require the same resource.
    - Any interactions between the consumers means that their ecological niches are different because each helps define the other’s niche.
- Limiting interaction of consumers to resource competition guarantees there is a single ecological niche.

3.1 Model Description

- We add a second consumer to the model of Section 2.
- The new consumer ($y(s)$ and $w(t)$) has parameters α_2 and μ_2.
- The new consumer's birth pulse is at time $s = \tau$. Its stored resources are continuous at the discrete census times t.

Competition Model (dimensionless)

$$\frac{df}{ds} = \rho f(1 - f - x - y), \quad f(0) = u_t, \quad u_{t+1} = f(1);$$

$$\frac{dx}{ds} = -\mu_1 x, \qquad x(0) = v_t, \quad v_{t+1} = [1 + b_1(1)]\, x(1);$$

$$\frac{dy}{ds} = -\mu_2 y, \qquad y(0) = w_t, \quad w_{\tau^+} = [1 + b_2(\tau^-)]\, y(\tau^-), \quad w_{t+1} = y(1$$

$$\frac{db_1}{ds} = \alpha_1 f, \qquad b_1(0) = 0.$$

$$\frac{db_2}{ds} = \alpha_2 f, \qquad b_2(0) = b_0, \quad b_2(\tau^+) = 0, \quad b_0 = b_2(1).$$

3.2 Model Analysis

- We can prove a few basic properties of the model:
  1. The only stable fixed points have a single consumer, except for a set of measure 0 in the $(\alpha_1, \alpha_2, \mu_1, \mu_2)$ parameter space.
     - So competitive exclusion holds with probability 1.
  2. The stronger competitor always survives if present at any starting value.
     - Strength is determined by a 'power' score that combines the reproduction strength α and the death rate μ, regardless of resource growth rate ρ.
- This leaves some interesting cases for simulations.

Model Analysis

- We define the power of a competitor with the formula

$$P_i = 1 - \frac{e^{\mu_i} - 1}{\alpha_i}.$$

  - This is the same as the formula for the average consumer population $\bar{x}$ when there is a stable fixed point, but P is useful whether the F.P. is stable or not.

Proposition 1: **Fixed points with mutual survival can only happen if $P_1 = P_2$.**

- This seems to violate competitive exclusion, since two different species (defined by μ and α) can have the same power; however . . .
  - The equation $P_1 = P_2$ is a 3D hypersurface in a 4D parameter space. An arbitrary point sits on this hypersurface with probability 0.

Model Analysis

Proposition 2: **Suppose the FX system is stable. Consumer Y can invade only if its power is greater than that of X.**

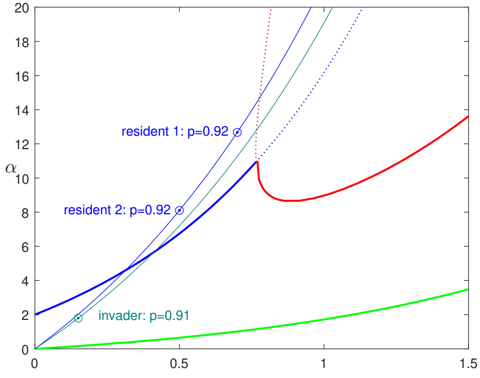
- Invasion of a stable system is possible only when the invader can coexist with a lower average resource level than that of the stable system.
- This would seem to say that the stronger competitor always wins, but it does not exclude the possibility that a weaker competitor can invade when the resident system lacks a stable fixed point.

3.3 Results

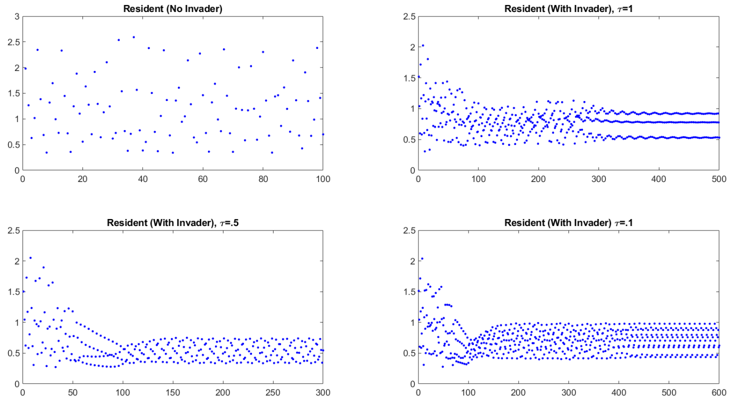
- When the stronger competitor can be part of a stable 2D consumer-resource system, then the weaker competitor always loses.
- When the stronger competitor cannot be part of a stable 2D CR system, then it may be possible for the weaker competitor to survive.
  - If this happens, the resulting coexistence must be unstable.
  - The long-term behavior may depend on the birth pulse lag time τ.

Simulations

- Resident 1 has $\mu = 0.7$, $\alpha = 12.672$, for $P = 0.92$.
- Resident 2 has $\mu = 0.5$, $\alpha = 8.1$, for $P = 0.92$.
- Invader has $\mu = 0.15$, $\alpha = 1.8$, for $P = 0.91$.
- The residents are stronger, but their CR systems are unstable.

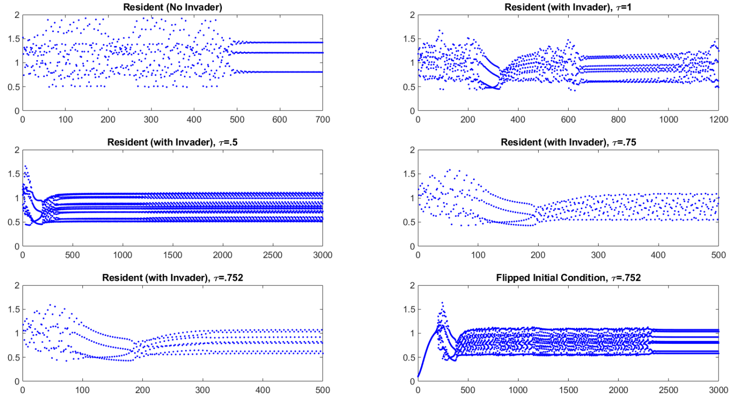


Simulations with Resident 1 and Invader



1. resident only - chaos, 2. no offset - 3-cycle, 3. 50% offset - bounded chaos, 4. $\tau = 0.1$ - 10-cycle

Simulations with Resident 2 and Invader



1. resident only - 3-cycle, 2. no offset, 3. 50% offset - large cycle,
4. $\tau = 0.75$ - bounded chaos, 5/6. $\tau = 0.752$ - 7-cycle

Reality Check

- We have seen lots of results for the mathematical model. How likely are these to be true for a real biological system?
  - Instabilities probably happen.
  - Chaos probably happens.
  - Large cycles probably don't happen.
  - Instability probably does allow slightly weaker invaders to succeed.