A Comparison of Two Predator-Prey Models with Holling's Type I Functional Response

** Joint work with **Mark Kot** at the University of Washington **

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York University / Ryerson University

Model Formulation

intrinsic rate of growth of the prey

Functional Response

$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \Phi(N)P$$

Carrying capacity

$$\frac{dP}{dT} = G(N,P)P$$

Numerical Response

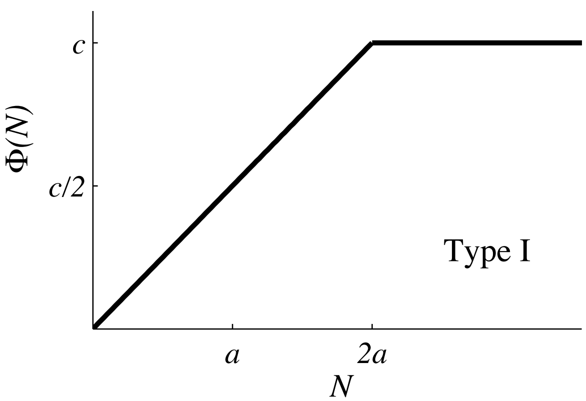
$N(T) = \text{Prey population}$

$P(T) = \text{Predator population}$

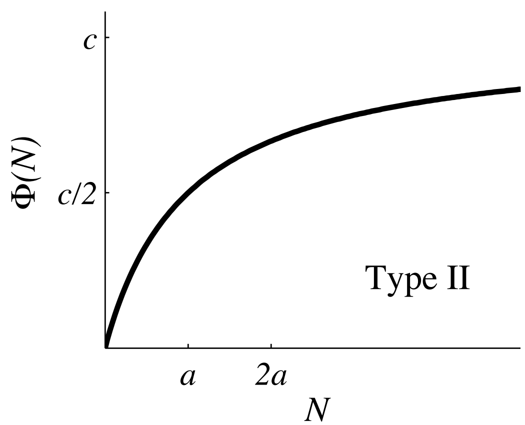
Model Formulation

$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \Phi(N)P$$
$$\frac{dP}{dT} = G(N,P)P$$

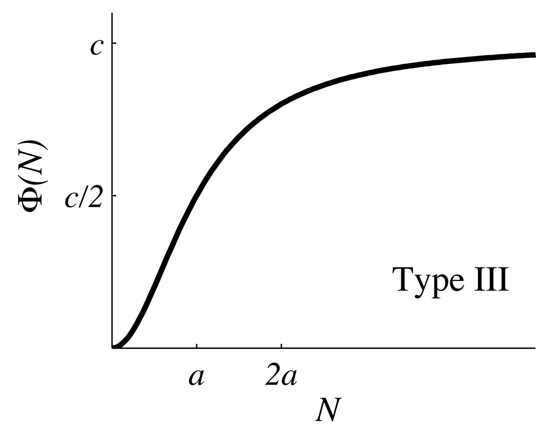
Functional Responses: identified by C. S. Holling (1959, 1965, 1966)



$$\Phi(N) = \begin{cases} \frac{c}{2a}N & \text{if } N < 2a \\ c & \text{if } N \geq 2a. \end{cases}$$



$$\Phi(N) = \frac{cN}{a+N}$$



$$\Phi(N) = \frac{cN^2}{a+N^2}$$

Model Formulation

$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \Phi(N)P$$

$$\frac{dP}{dT} = G(N, P)P$$

Numerical Responses

Laissez-faire

$$G(N, P) = \frac{b}{c}\Phi(N) - m$$

Leslie

$$G(N, P) = s\left(1 - \frac{P}{hN}\right)$$

Outline

$$\Phi_{\mathrm{I}}(N) = \begin{cases} \frac{c}{2a} N, & N < 2a, \\ c, & N \geq 2a. \end{cases}$$

- **Laissez-faire Model with a type I functional response.**
- **Leslie-type Model with a type I functional response.**
  - Nondimensionalization.
  - Stability analyses of equilibria:
    - performing a linearized stability analysis,
    - constructing a Lyapunov function .
  - Numerical studies.

if time permits

- **Laissez-faire and Leslie-type models with arctan functional responses.**
- **Discussion**

Laissez-faire Model

$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \Phi_I(N)P$$

$$\frac{dP}{dT} = P\left(\frac{b}{c}\Phi_I(N) - m\right)$$

Leslie-type Model

$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \Phi_I(N)P$$

$$\frac{dP}{dT} = sP\left(1 - \frac{P}{hN}\right)$$

Models with Type I Functional Responses

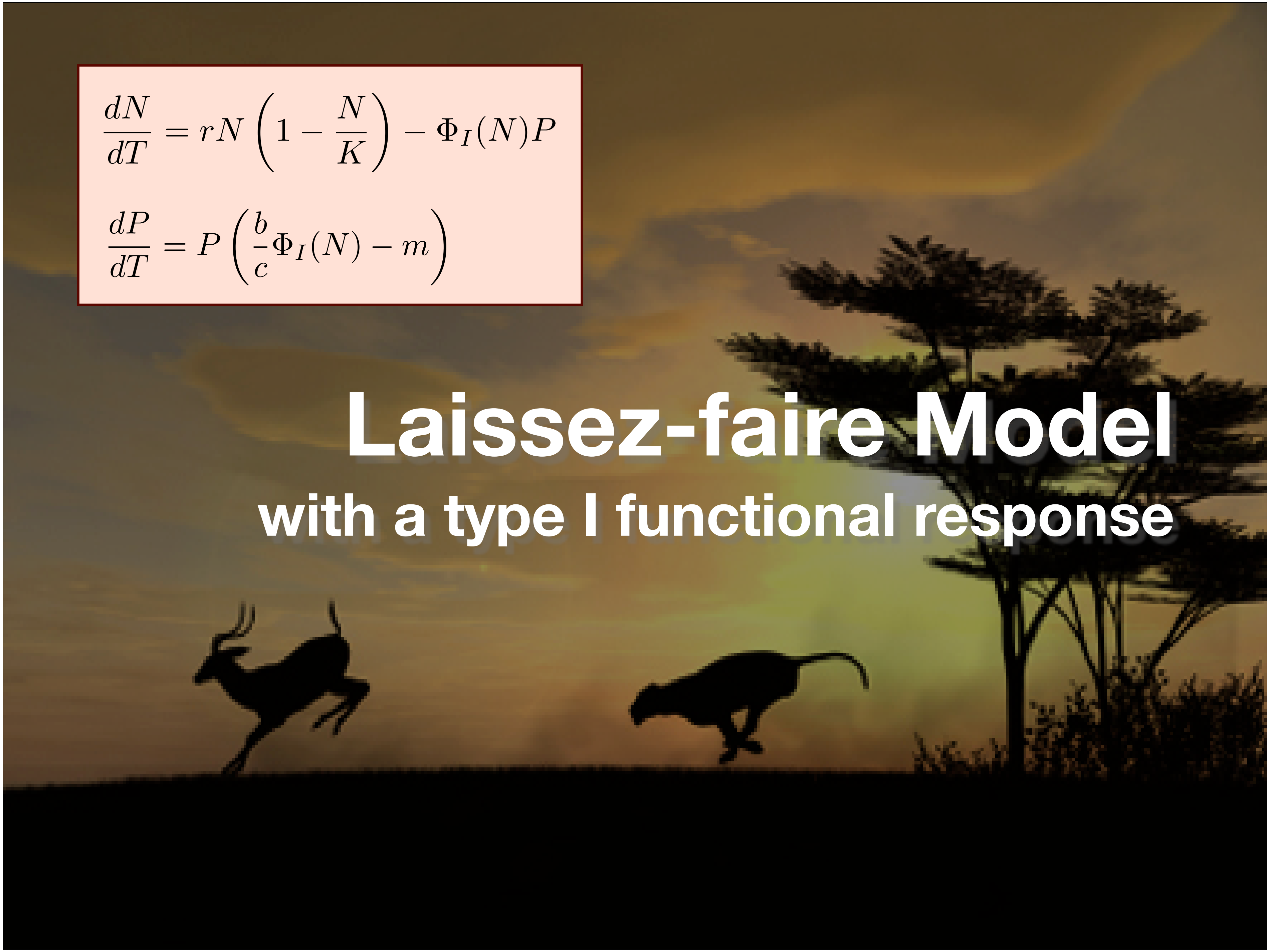
- **D. M. Dubois and P. L. Closset.** Patchiness in primary and secondary production in the Southern Bight: a mathematical theory. In G. Persoone and E. Jaspers, editors, Proceedings of the 10th European Symposium on Marine Biology, pp. 211–229, Universa Press, Ostend, 1976.
- **Y. Ren and L. Han.** The predator prey model with two limit cycles. Acta Math. Appl. Sinica (English Ser.), 5: 30–32, 1989.
- **J. B. Collings.** The effects of the functional response on the bifurcation behavior of a mite predator–prey interaction model. J. Math. Biol., 36: 149–168, 1997.
- **G. Dai and M. Tang.** Coexistence region and global dynamics of a harvested predator–prey system. SIAM J. Appl. Math., 58: 193–210, 1998.
- **X. Y. Li and W. D. Wang.** Qualitative analysis of predator–prey system with Holling type I functional response. J. South China Normal Univ. (Natur. Sci. Ed.), 29: 712–717, 2004.
- **B. Liu, Y. Zhang, and L. Chen.** Dynamics complexities of a Holling I predator–prey model concerning periodic biological and chemical control. Chaos Solitons Fractals, 22: 123–134, 2004.
- **Y. Zhang, Z. Xu, and B. Liu.** Dynamic analysis of a Holling I predator–prey system with mutual interference concerning pest control. J. Biol. Syst., 13:45–58, 2005.

$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \Phi_I(N)P$$

$$\frac{dP}{dT} = P\left(\frac{b}{c}\Phi_I(N) - m\right)$$

Laissez-faire Model

with a type I functional response



Laissez-faire Model with a type I functional response

Nondimensionalization & Equilibria

$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \Phi_I(N)P$$

$$\frac{dP}{dT} = P\left(\frac{b}{c}\Phi_I(N) - m\right)$$

$$\text{where} \quad \Phi_I(N) = \begin{cases} \frac{c}{2a}N & \text{if } N < 2a \\ c & \text{if } N \geq 2a \end{cases}$$

$$x = \frac{N}{a}, \quad y = \frac{c}{ra}P, \quad t = rT$$

$$\alpha = \frac{b}{r}, \quad \beta = \frac{m}{b}, \quad \gamma = \frac{K}{a}$$

$$\frac{dx}{dt} = x\left(1 - \frac{x}{\gamma}\right) - \phi_I(x)y$$

$$\frac{dy}{dt} = \alpha y(\phi_I(x) - \beta)$$

$$\text{where } \phi_I(x) = \begin{cases} x/2, & x < 2 \\ 1, & x \geq 2 \end{cases}$$

Assuming $\alpha > 0, \quad 0 < \beta < 1, \quad \text{and} \quad \gamma > 2$

Equilibria

$$E_0 = (0, 0),$$

$$E_1 = (\gamma, 0),$$

$$E_2 = (2\beta, g(2\beta)) \quad \text{where } g(x) = \frac{x}{\phi_I(x)}\left(1 - \frac{x}{\gamma}\right)$$

Laissez-faire Model with a type I functional response

Linearized Stability Analysis

Assuming $\alpha > 0, \quad 0 < \beta < 1, \quad \text{and} \quad \gamma > 2$

Equilibria

$E_0 = (0, 0)$, **saddle point**

$E_1 = (\gamma, 0)$, **saddle point if** $\phi_I(\gamma) > \beta$

stable node if $\phi_I(\gamma) < \beta$

$$E_2 = (2\beta, g(2\beta)) \quad \text{where } g(x) = \frac{x}{\phi_I(x)}\left(1 - \frac{x}{\gamma}\right)$$

$$J = \begin{pmatrix} \phi_I'(x)\,(g(x) - y) + \phi_I(x)g'(x) & -\phi_I(x) \\ \alpha y \phi_I'(x) & \alpha\,(\phi_I(x) - \beta) \end{pmatrix}$$

Laissez-faire Model with a type I functional response

Linearized Stability Analysis

Assuming $\alpha > 0, \quad 0 < \beta < 1, \quad \text{and} \quad \gamma > 2$

Equilibria

$E_0 = (0, 0),$ **saddle point**

$E_1 = (\gamma, 0),$ **saddle point if** $\phi_I(\gamma) > \beta$

stable node if $\phi_I(\gamma) < \beta$

$$E_2 = (2\beta, g(2\beta)) \quad \text{where } g(x) = \frac{x}{\phi_I(x)}\left(1 - \frac{x}{\gamma}\right)$$

By Routh-Hurwitz criterion,

the coexistence equilibrium is asymptotically stable.

$$J_{E_2} = \begin{pmatrix} \beta g'(2\beta) & -\beta \\ \alpha g(2\beta)\phi_I'(2\beta) & 0 \end{pmatrix}$$

Characteristic Equation

$$\lambda^2 - \beta g'(2\beta)\lambda + \alpha\beta g(2\beta)\phi_I'(2\beta) = 0$$

Laissez-faire Model with a type I functional response

Global Stability Analysis of E2

Using **Harrison's "Gedankenexperiment"** (1979), construct ***Lyapunov function***

$$V(x,y) = \int_{x^*}^{x} \frac{\alpha(\phi_I(\xi) - \beta)}{\phi_I(\xi)} d\xi + \alpha \int_{y}^{g(x^*)} \frac{g(x^*) - \xi}{\alpha\xi} d\xi$$

where $g(x) = \dfrac{x}{\phi_I(x)}\left(1 - \dfrac{x}{\gamma}\right)$ and $x^* = 2\beta$

$$V(x,y) = V_1(x) + V_2(x) \quad \text{where} \quad V_1(x) = \alpha \begin{cases} (x - x^*) - x^* \ln \frac{x}{x^*} & x < 2, \\ (2 - x^*) - x^* \ln \frac{2}{x^*} + (1-\beta)(x-2), & x \geq 2 \end{cases}$$

$$V_2(x) = g(x^*) \ln \frac{g(x^*)}{y} + y - g(x^*)$$

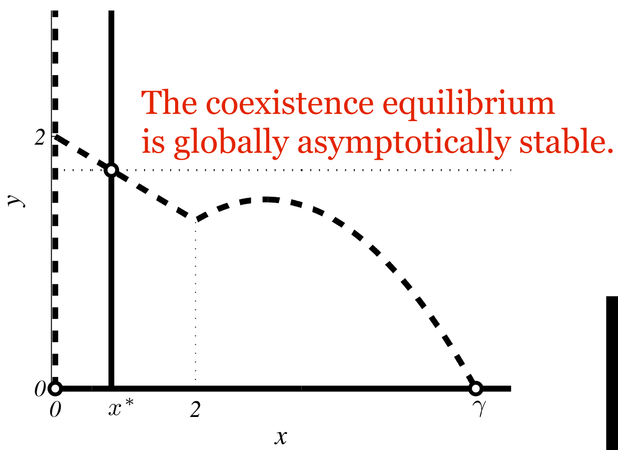
$\dot{V} \left(= \dfrac{dV}{dt} \right) = \alpha\left(\phi_I(x) - \beta\right)\left(g(x) - g(x^*)\right)$ is continuous at $x = 2$

- $V(x,y)$ is continuous at $x = 2$ and is zero at the coexistence equilibrium
- For all positive x and y, $V(x,y)$ is positive, except at coexistence equilibrium E_2.
- $\dot{V} < 0$ in a neighborhood of E_2 if $g(x) > g(x^*)$ for $x < x^*$ AND $g(x) < g(x^*)$ for $x > x^*$.

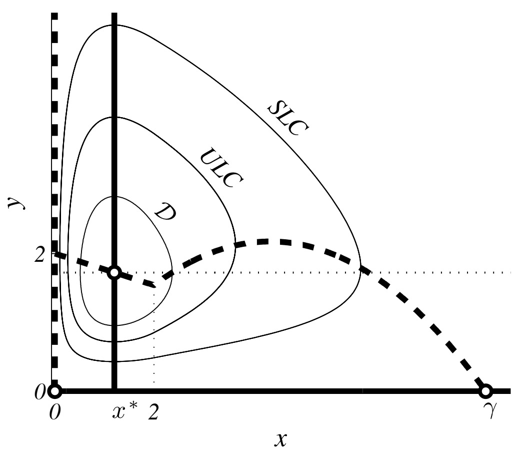
Laissez-faire Model with a type I functional response

Global Stability Analysis of E_2

(a)



(b)



A subset of the basin of attraction

$$\mathcal{D} = \{(x,y) \mid V(x,y) < u\}$$

where

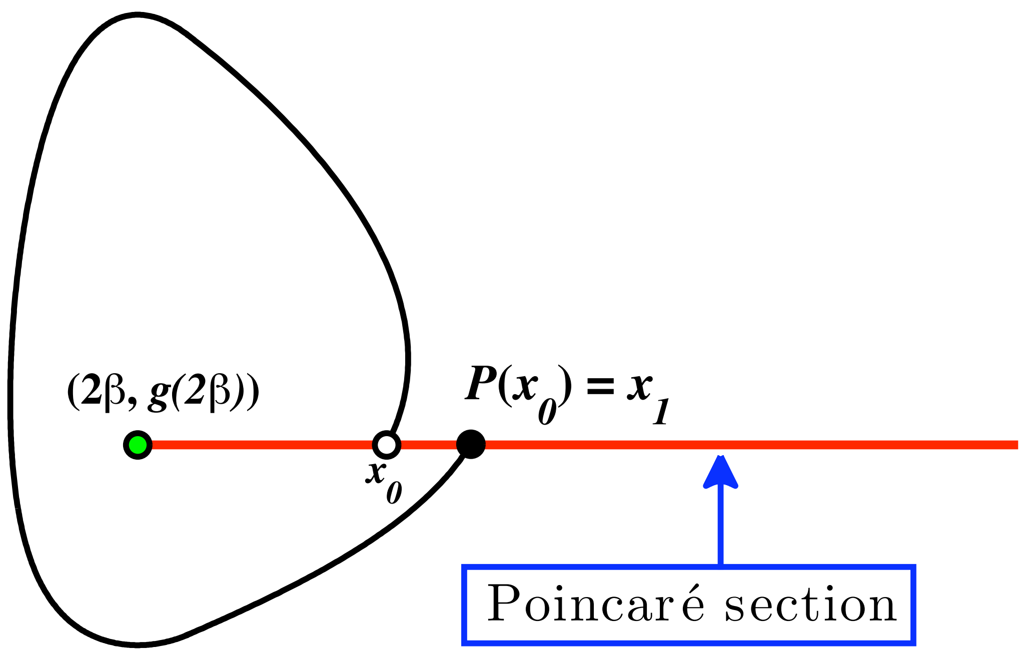
$$u = \min \{V(0, g(x^*)),\ V(x_M, g(x^*)),\ V(x^*, 0),\ V(x^*, +\infty)\}$$

with $x_M = \dfrac{\gamma - \sqrt{\gamma^2 - 8(\gamma - 2\beta)}}{2}$ when $\gamma > 4 + 4\sqrt{1-\beta}$.

Laissez-faire Model with a type I functional response

Numerical Studies

Poincaré or first return map



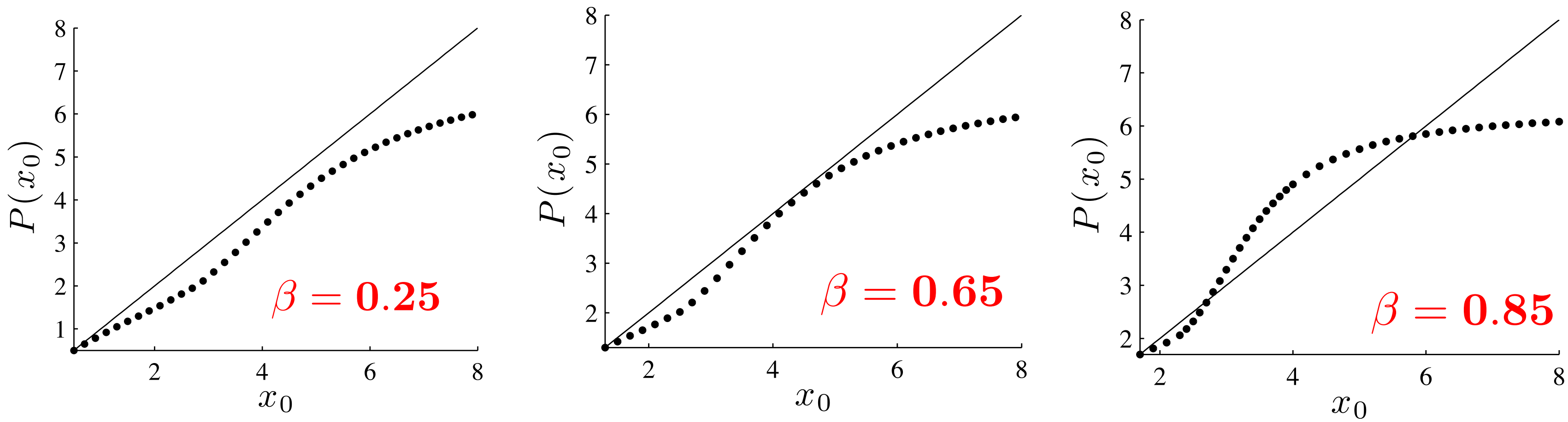
$: \; y = 2\left(1 - \frac{2\beta}{\gamma}\right) \quad \text{for } x > 2\beta$

Laissez-faire Model with a type I functional response

Numerical Studies

$\alpha = 2, \ \gamma = 8$

Poincaré or first return map

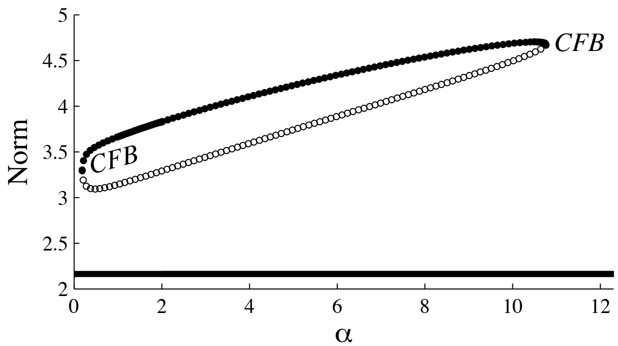


Laissez-faire Model with a type I functional response

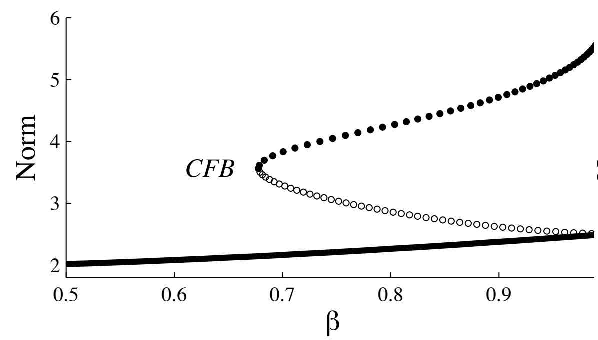
Numerical Studies

Bifurcation Diagrams (using XPPAUT)

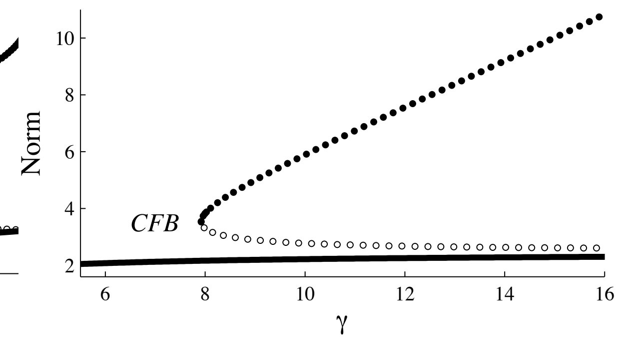
$\beta = 0.7, \ \gamma = 8$



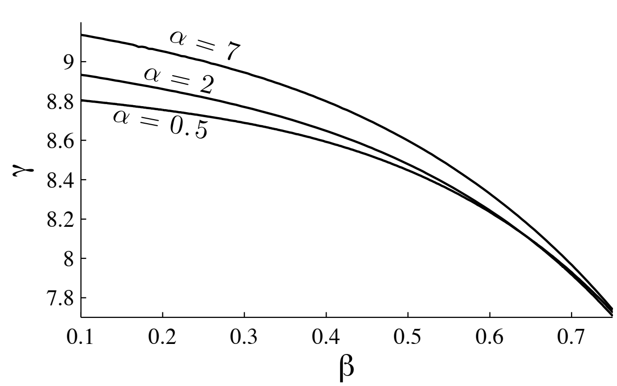
$\alpha = 2, \ \gamma = 8$



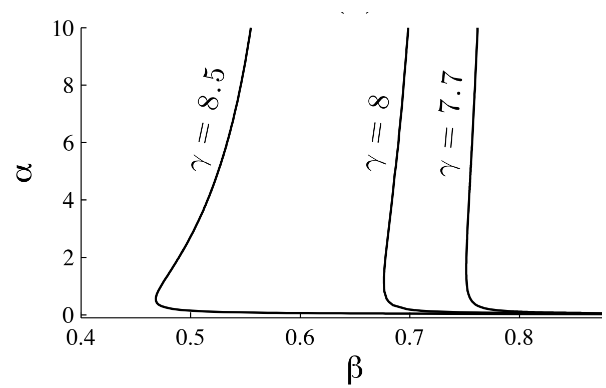
$\alpha = 2, \ \beta = 0.7$



Two limit cycles occur above each curve.



Two limit cycles occur to the right of each curve.



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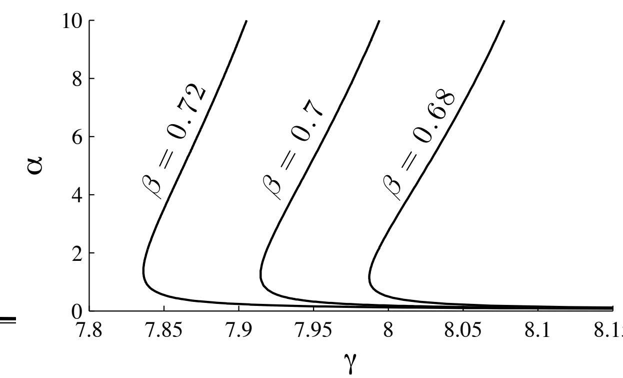
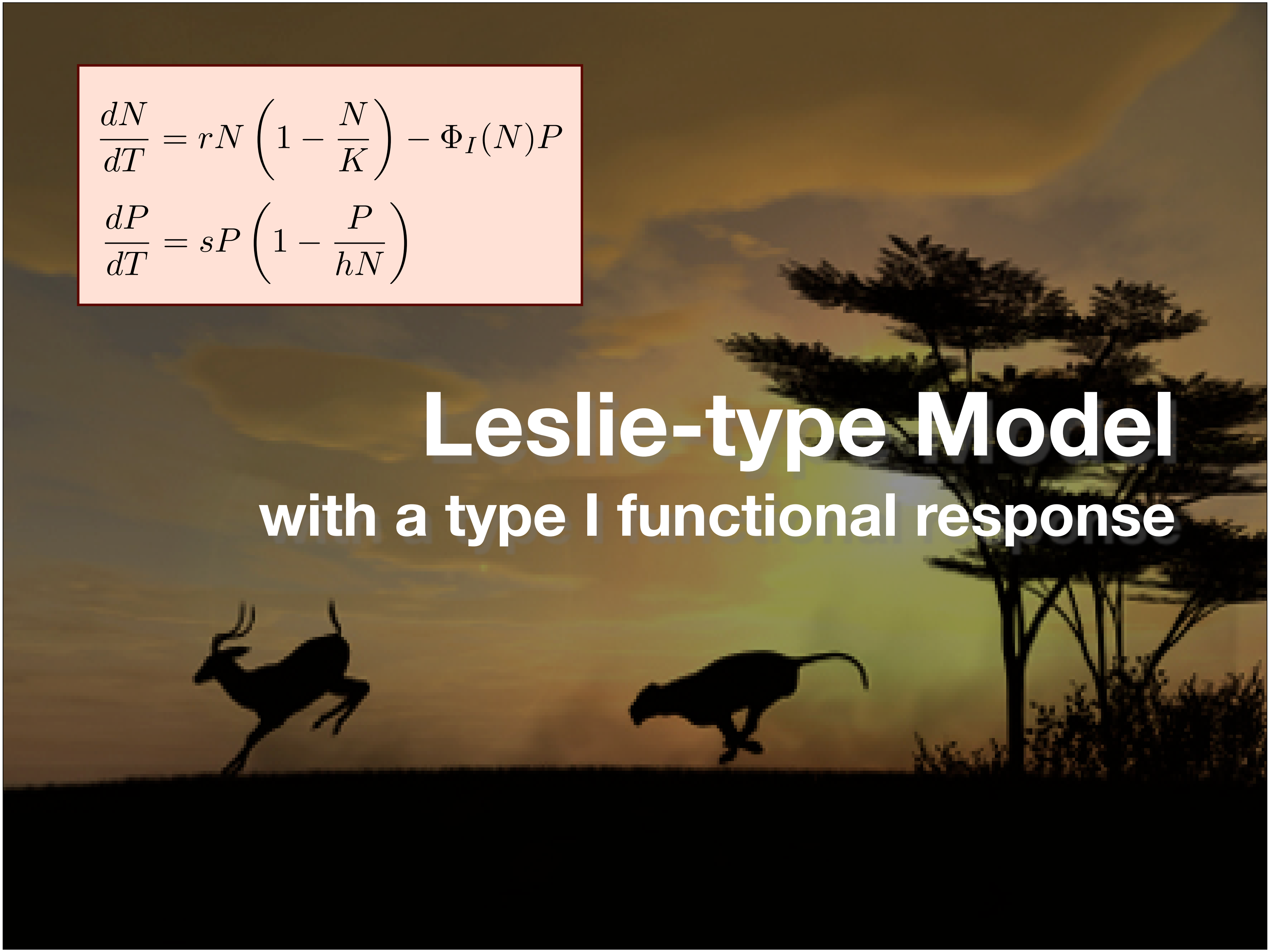




$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \Phi_I(N)P$$

$$\frac{dP}{dT} = sP\left(1 - \frac{P}{hN}\right)$$

Leslie-type Model

with a type I functional response

Leslie-type Model with a type I functional response

Nondimensionalization & Equilibria

$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \Phi_I(N)P$$
$$\frac{dP}{dT} = sP\left(1 - \frac{P}{hN}\right)$$
$$\text{where} \quad \Phi_I(N) = \begin{cases} \frac{c}{2a}N & \text{if } N < 2a \\ c & \text{if } N \geq 2a \end{cases}$$

$$x = \frac{N}{a}, \quad y = \frac{c}{ra}P, \quad t = rT$$
$$A = \frac{s}{r}, \quad B = \frac{ch}{r}, \quad \gamma = \frac{K}{a}$$

$$\frac{dx}{dt} = x\left(1 - \frac{x}{\gamma}\right) - \phi_I(x)y$$
$$\frac{dy}{dt} = Ay\left(1 - \frac{y}{Bx}\right)$$
$$\text{where } \phi_I(x) = \begin{cases} x/2, & x < 2 \\ 1, & x \geq 2 \end{cases}$$

Assuming $A > 0, \quad B > 0, \text{ and } \gamma > 2$

focus on the dynamics in $0 < x(t) \leq \gamma$ **, where a unique coexistence equilibrium exists.**

Equilibria

$$\widehat{E}_1 = (\gamma, 0)$$
$$\widehat{E}_2 = (\hat{x}^*, \hat{y}^*)$$

$$\text{where } \hat{x}^* = \begin{cases} \frac{2\gamma}{B\gamma+2}, & \gamma(1-B) < 2, \\ \gamma(1-B), & \gamma(1-B) \geq 2 \end{cases}$$
$$\hat{y}^* = B\hat{x}^* = g(\hat{x}^*)$$
$$\text{with } g(x) = \frac{x}{\phi_I(x)}\left(1 - \frac{x}{\gamma}\right)$$

Leslie-type Model with a type I functional response

Stability Analysis

$$J = \begin{pmatrix} \phi_I'(x)(g(x)-y)+\phi_I(x)g'(x) & -\phi_I(x) \\ \frac{A}{B}\left(\frac{y}{x}\right)^2 & A\left(1-\frac{2y}{Bx}\right) \end{pmatrix}$$

$$\frac{dx}{dt} = x\left(1-\frac{x}{\gamma}\right) - \phi_I(x)y$$

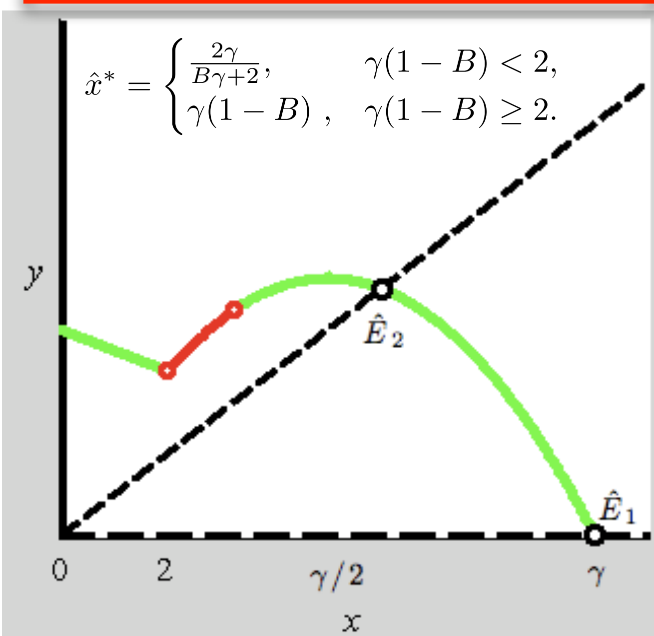
$$\frac{dy}{dt} = Ay\left(1-\frac{y}{Bx}\right)$$

$$\text{where } \phi_I(x) = \begin{cases} x/2, & x<2 \\ 1, & x \geq 2 \end{cases}$$

Equilibria

$$\hat{E}_1 = (\gamma, 0)$$ **saddle point**

$$\hat{E}_2 = (\hat{x}^*, \hat{y}^*)$$



✔ $\hat{E}_2 = (\hat{x}^*, \hat{y}^*)$

The left (J_-) and right (J_+) Jacobians evaluated at $\hat{E}_2$ where $0<\hat{x}^*<2$ or $2<\hat{x}^*<\gamma$,

$$J_\pm\Big|_{(\hat{x}^*,\hat{y}^*)} = \begin{pmatrix} \phi_I(\hat{x}^*)g_\pm'(\hat{x}^*) & -\phi_I(\hat{x}^*) \\ AB & -A \end{pmatrix}$$

with $\hat{y}^* = g(\hat{x}^*) = \dfrac{\hat{x}^*(1-\hat{x}^*/\gamma)}{\phi_I(\hat{x}^*)}$ and $\begin{cases} g_-'(\hat{x}^*) = -2/\gamma, & 0<\hat{x}^*<2, \\ g_+'(\hat{x}^*) = 1-2\hat{x}^*/\gamma, & 2<\hat{x}^*<\gamma. \end{cases}$

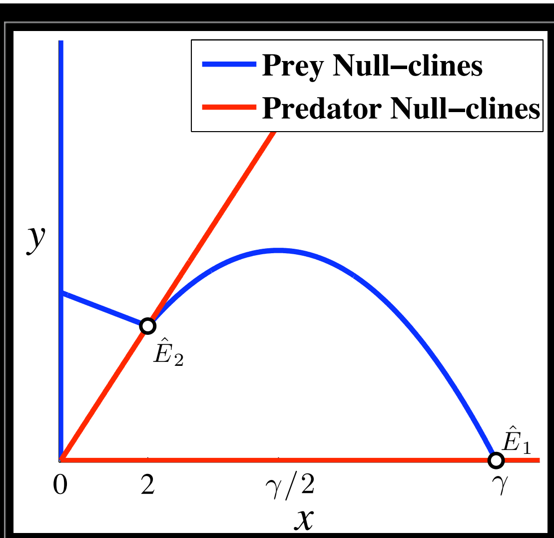
$$\lambda^2 + \lambda(A-\phi_I(\hat{x}^*)g_\pm'(\hat{x}^*)) + \underline{A\phi_I(\hat{x}^*)\left(B-g_\pm'(\hat{x}^*)\right)} = 0$$

> 0

- Asymptotically stable where $0<\hat{x}^*<2$ or $\gamma/2 \leq \hat{x}^* < \gamma$
- For $2<\hat{x}^*<\gamma/2$, Stable if $A > g'(\hat{x}^*)$
  Unstable if $A < g'(\hat{x}^*)$

Leslie-type Model with a type I functional response

Stability Analysis



The generalized Jacobian of Clarke (1998)

$$J_\Sigma = \{(1-q)J_- + qJ_+ \ , \forall\ 0 \le q \le 1\}$$

: a convex combination of the left and right Jacobian,

$$J_\pm\Big|_{(\hat{x}^*,\hat{y}^*)} = \begin{pmatrix} \phi_{\mathrm{I}}(\hat{x}^*)g'_\pm(\hat{x}^*) & -\phi_{\mathrm{I}}(\hat{x}^*) \\ AB & -A \end{pmatrix}$$

$$\Rightarrow \quad J_\Sigma = \begin{pmatrix} J_\Sigma^{11} & -1 \\ AB & -A \end{pmatrix} \text{ with } J_\Sigma^{11} = qB + (B-1) \quad \text{where} \quad 0 < B < 1 \text{ and } 0 \le q \le 1.$$

Characteristic Equation: $\lambda^2 - (J_\Sigma^{11} - A)\,\lambda + A(B - J_\Sigma^{11}) = 0$

$$\Rightarrow \lambda_{1,2} = \frac{(J_\Sigma^{11} - A) \pm i\sqrt{4AB - (J_\Sigma^{11} + A)^2}}{2}$$

☑ A discontinuous Hopf bifurcation (Leine and Nijmeijer; 2004) is expected when the eigenvalues are imaginary($J_\Sigma^{11} = A$) i.e., when $q = \dfrac{A - B + 1}{B}$ where $A \le 2B - 1 < 1$.

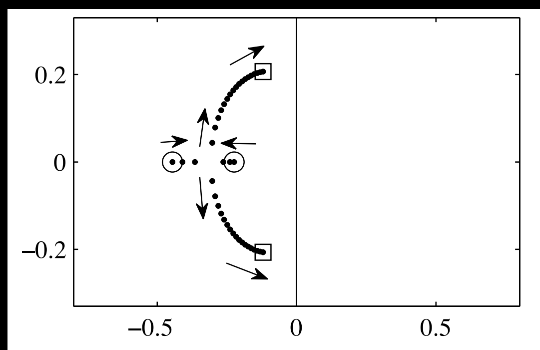
Leslie-type Model with a type I functional response

The generalized Jacobian of Clarke

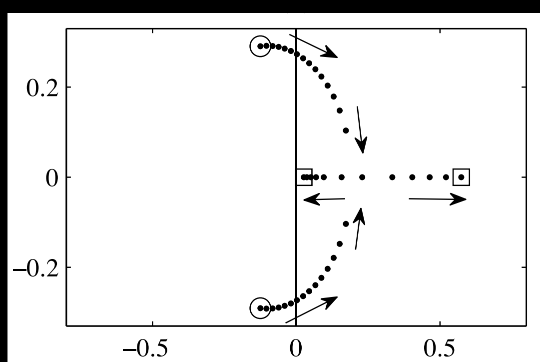
The generalized Jacobian of Clarke at $\hat{x}^* = 2$

$A = 0.1$ $\quad q = 0\ (\odot), \quad q = 1\ (\boxdot)$

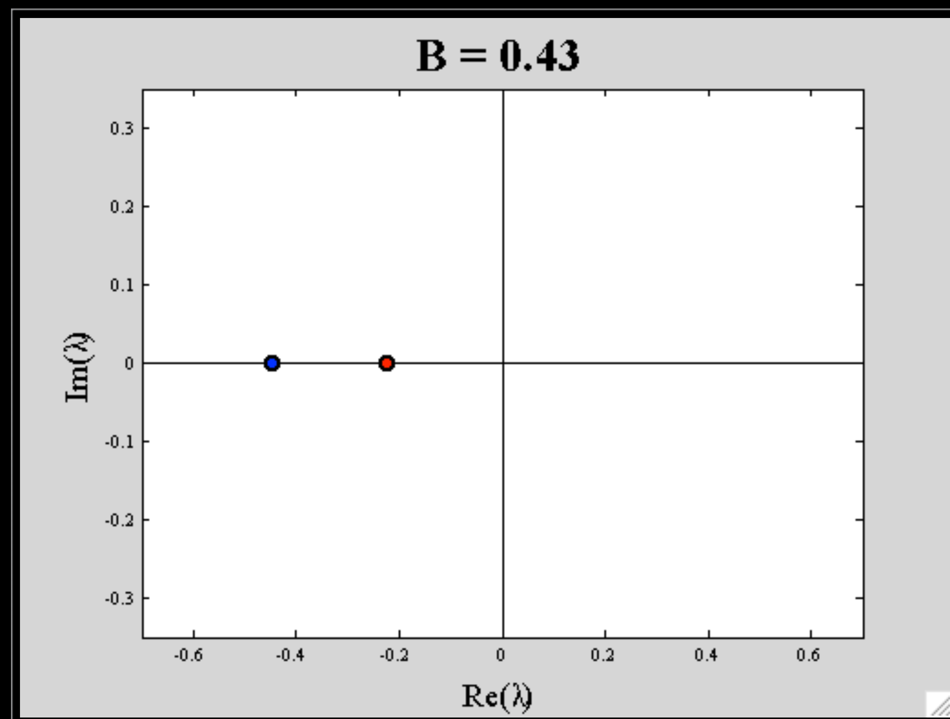
$B = 0.43$



$B = 0.85$



λ_1 λ_2



Leslie-type Model with a type I functional response

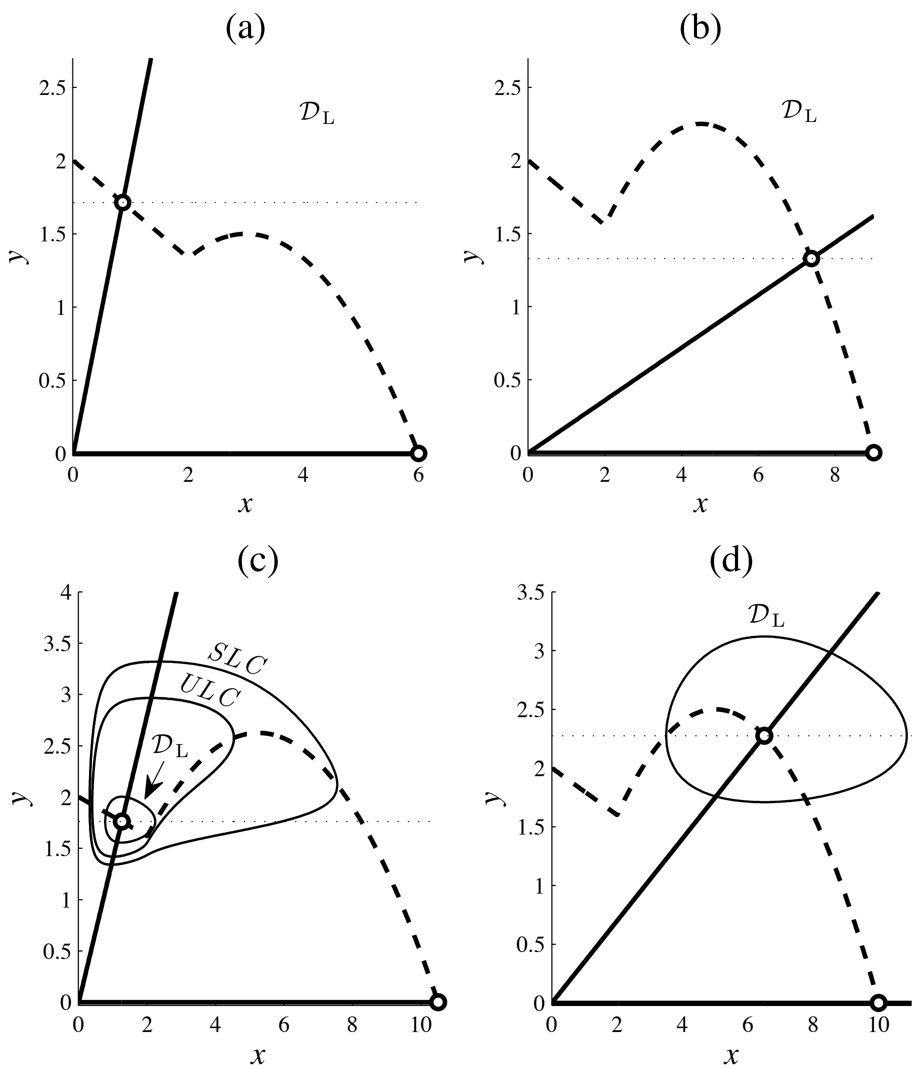
Numerical Studies

$A = 1, B = 2, \gamma = 6$

$A = 1, B = 0.18, \gamma = 9$

$A = 0.05, B = 1.4, \gamma = 10.5$

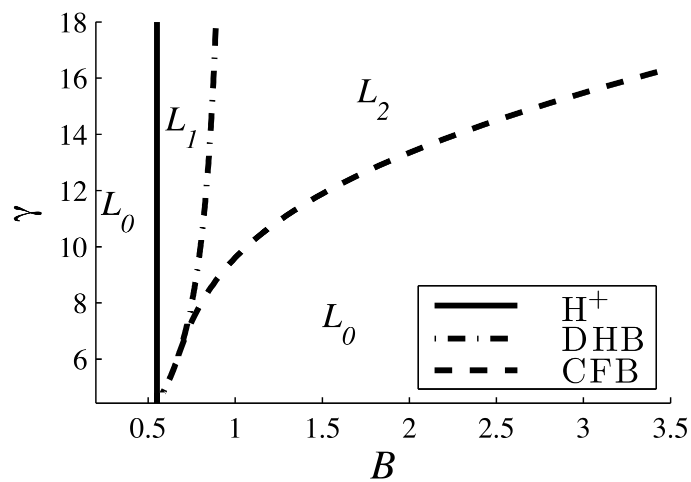
$A = 0.1, B = 0.35, \gamma = 10$



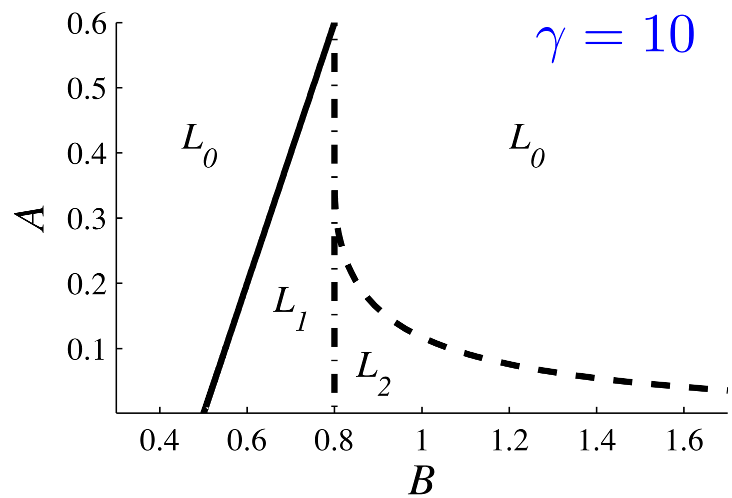
Leslie-type Model with a type I functional response

Numerical Studies: Two-parameter bifurcation diagrams

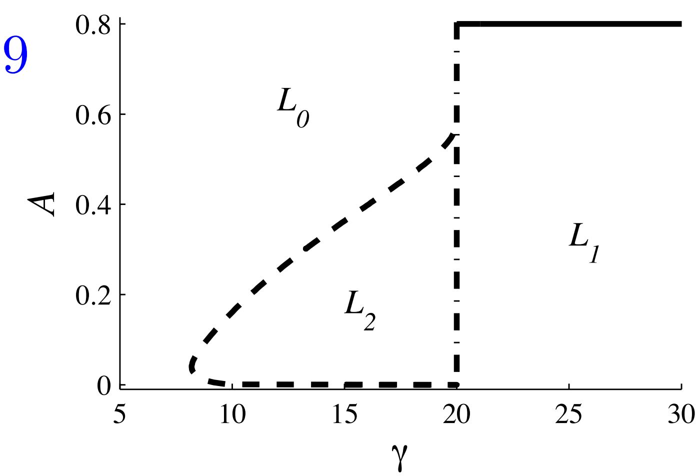
$A = 0.1$



$\gamma = 10$



$B = 0.9$



The parameter plane is divided into regions marked L_i (i = 0, 1, 2) : the subscript indicates the number of limit cycles that encircle the coexistence equilibrium

Summary

- **Laissez-faire & Leslie-type models with Type I functional Responses**
  - **Two limit cycles: Cyclic-fold bifurcations**

- **Leslie-type model with Type I functional Responses**
  - **Super-critical Hopf and Cyclic-fold bifurcations**

At $\hat{x}^* = 2$: the generalized Jacobian of Clarke (1998)

$$J_\Sigma = \{(1-q)J_- + qJ_+ \ , \forall \ 0 \le q \le 1\}$$

Discontinuous Hopf bifurcation

when $q = \dfrac{A - B + 1}{B}$ **where** $A \le 2B - 1 < 1$

Future Research Projects

- **A predator–prey model with a type I functional response including an Allee effect in the growth rate of the prey.**

- **A predator–predator–prey model with two predators characterized by type I and other possible functional responses.**

- **A Delay-differential Equation**

Thank you