Qualitative Analysis of Global Dynamics in Predator-Prey Systems

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Introduction

In many predator and prey interactions, the time the predator takes to capture the prey limits the rate of predation. The phenomenon can be interpreted as a "saturation" of predators when prey levels are high enough.

The function $p(x) = \frac{ax}{1+mx}$ is called a Holling II functional response. The "p" represents the variation in prey density (x) with relation to time due to the presence of one predator. When prey density becomes large p tends to a/m, which is a constant which measures the handling ability of one predator when it can find prey everywhere.

Figure 1: Shark and shoal. From [3].

Even with high density of fish, predation rate is limited considering shark's handling velocity.

Holling-II and Stage Structure System

In the following system from [1], x represents the density of prey, y_1 of young predators (which do not hunt) and y_2 of mature predators. Preys have a negative Holling II term, while in predators it is positive. Young predators are generated in a rate e, die in a rate r_1 and become mature predators in a rate D.

$$\begin{cases} \dot{x} = x\left(r - ax - \frac{a_1 y_2}{1+mx}\right) \\ \dot{y}_1 = ey_2 - (r_1 + D)y_1 \\ \dot{y}_2 = Dy_1 - r_2 y_2 + \frac{a_2 x y_2}{1+mx} \end{cases} \quad (1)$$

- Local Stability

Linearization of the system about the predator-extinction equilibrium point $E_1 = (\frac{r}{a}; 0; 0)$ yields the following characteristic equation, with coefficients defined below:

$$(\lambda + r)(\lambda^2 + g_1\lambda + g_0) = 0,$$
$$g_0 := r_2(D + r_1) - eD - (D + r_1)\frac{a_2 r}{a+rm}$$
$$g_1 := D + r_1 + \frac{r_2(a+rm) - a_2 r}{a+rm}$$

Here, ($\lambda_1 = -r$) is a negative eigenvalue. Looking at the quadratic equation coefficients, we can show that if condition H1: $a_2 r > (a + rm)[r_2 - \frac{eD}{D+r_1} > 0$ holds, the two other roots have different signs, which implies that E_1 is unstable. If, instead,

$0 < a_2 r(D + r_1) < (a + rm)[r_2(D + r_1) - eD]$, then all roots have negative real parts, and E_1 is locally asymptotic stable.

If (H1) holds, then a coexistence equilibrium $E^* = (x^*; y_1^*; y_2^*) \in \mathbb{R}_+^3$ exists, given by:

$$x^* = \frac{r_2(D+r_1) - eD}{(a_2 - r_2 m)(D+r_1) + emD}$$
$$y_1^* = \frac{e}{D+r_1}y_2^*$$
$$y_2^* = \frac{a_2(D+r_1)(r - ax^*)x^*}{a_1[r_2(D+r_1) - eD]}$$

The characteristic equation for this coexistence equilibrium E^* is the following, with coeficients defined below it:

$$\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 = 0,$$
$$p_0 := [(a_2 - r_2 m)(D + r_1) + emD]\frac{a_1 x^* y_2^*}{(1+mx^*)^2}$$
$$p_1 := (D + r_1 + r_2)\frac{a_1 y_2^*}{(1+mx^*)^2} + (r - 2ax^*)(\frac{a_2 x^*}{1+mx^*} - (D + r_1 + r_2))$$
$$p_2 := D + r_1 + 2ax^* - r + \frac{eD}{D+r_1} + \frac{a_1 y_2^*}{(1+mx^*)^2}$$

If $p_2 > 0$ and $p_1 p_2 - p_0 > 0$, then Routh Hurwitz criterium guarantees that all roots have negative real part, implying that E^* is L.A.S.
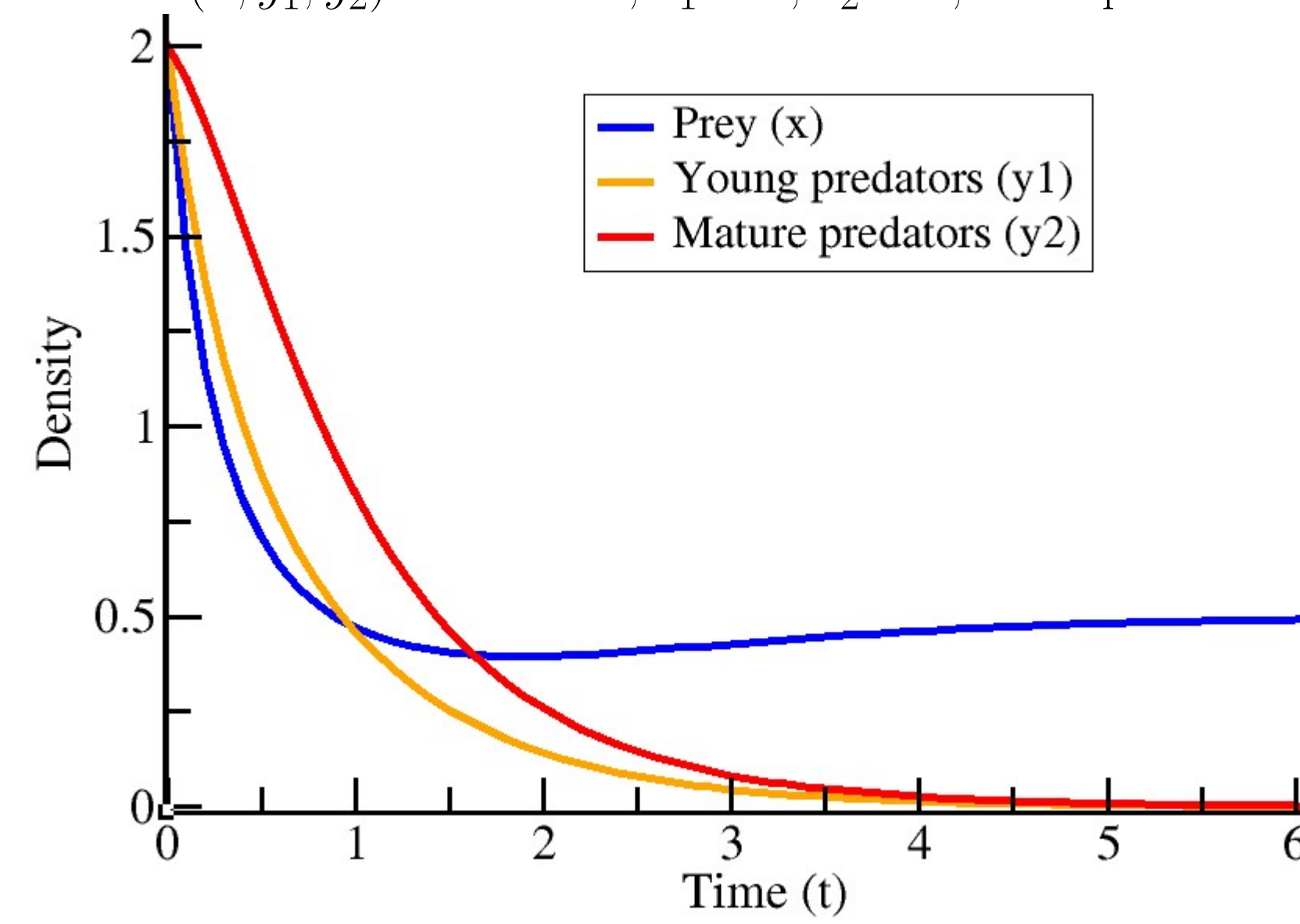
- Global Stability

Theorem If $a_2 r(D + r_1) < (a + rm)[r_2(D + r_1) - eD]$, then $E_1 =: (x_0; 0; 0)$ is globally asymptotically stable (attracts $A := (x; y_1; y_2) \in \mathbb{R}^3 : x > 0, y_1 \geq 0, y_2 \geq 0)$.

Proof: Under this hypothesis E_1 was proven to be L.A.S. The attraction of region A comes from La Salle's invariance principle, considering the following function and positive solutions of the system:

$$V_1(t) := \frac{a_2}{1+mx_0}\left(x - x_0 - x_0 ln\left(\frac{x}{x_0}\right)\right) + \frac{a_1 D}{D+r_1}y_1 + a_1 y_2$$

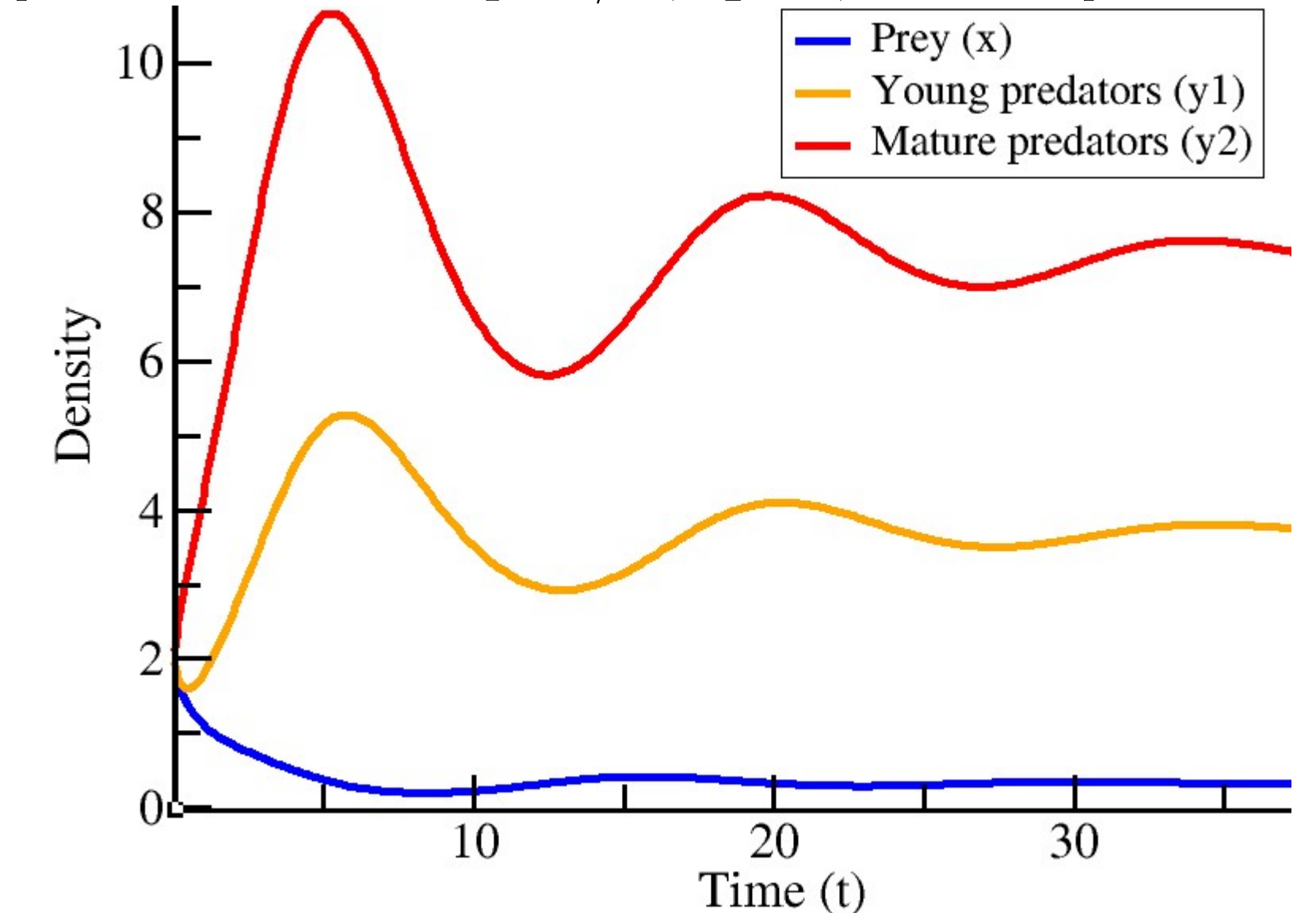Evolution of $(x; y_1; y_2)$ with $a = 2$, $r_1 = 2$, $r_2 = 2$, other parameters = 1.

Theorem If H1 holds and $\liminf_{t \to \infty} x(t) \geq l > \frac{r}{2a}$, then E^* is G.A.S. (attracts $B := (x; y_1; y_2) \in \mathbb{R}^3 : x > 0, y_1 > 0, y_2 > 0)$.

Proof: The second hypothesis implies that $x^* > r/2a$. Under this condition, we have $p_2 > 0$ and $p_2 p_1 - p_0 > 0$, and E^* is L.A.S. As before, the attraction of region B comes from La Salle's invariance principle using the function V_2.

$$V_2(t) := \frac{a_2}{1+mx^*}\left(x - x^* - x^* ln\left(\frac{x}{x^*}\right)\right) +$$

$$\frac{a_1 D}{D+r_1}\left(y_1 - y_1^* - y_1^* ln\left(\frac{y_1}{y_1^*}\right)\right) + a_1\left(y_2 - y_2^* - y_2^* ln\left(\frac{y_2}{y_2^*}\right)\right)$$

Temporal evolution with $a_1 = 3/25$, $a_2 = 2$, and other parameters = 1.

Delayed System

Next system is presented in II. Here, predator gain from hunting is delayed, i.e., depends on the results of hunting in past time: $be^{-d_j\tau}y(t - \tau)p(x(t - \tau))$. In practice, the gain from predation is converted in new young predators, and the delay is the time of incubating those, considering that d_j is their death rate during this period. The studied p functions satisfy: $p(0) = 0$, p is increasing, $p(x)/x$ is bounded and $\lim_{x \to 0} \frac{p(x)}{x} \neq 0$.

$$\begin{cases} \dot{x}(t) = x(t)(1 - x(t)) - y(t)p(x(t)) \\ \dot{y}(t) = be^{-d_j\tau}y(t - \tau)p(x(t - \tau)) - dy(t) \end{cases} \quad (2)$$

The origin is a saddle point. $\lambda_1 = 1$, $\lambda_2 = -d$.

If we linearize the system about the predator-extinction equilibrium point (1;0), the characteristic equation takes the form:

$$(\lambda + 1)(\lambda + d - be^{-d_j\tau}p(1)e^{-\lambda\tau}) = 0$$

One of the roots is negative. If (H1): $p(1) > \frac{d}{be^{-d_j\tau}}$, then the other root is real and positive, what can be ilustrated by plotting the two members of the equation $\lambda = be^{-d_j\tau}p(1)e^{-\lambda\tau} - d$ in relation to lambda, and using that $be^{-d_j\tau}p(1) - d$ is positive.

If, instead, $be^{-d_j\tau}p(1) - d \leq 0$, then we can show that no root has positive real part.

The coexistence equilibrium exists if and only if H1 holds, and hence the existence of a coexistence equilibrium makes E_1 unstable.

References

- 1- TIAN, X et al. Global dynamics of a predator-prey system with Holling type II functional response. Nonlinear Analysis: modeling and control, v.16, n.2, p.242- 253, 2011.
- 2- FORDE, J.E. Delay differential equation models in mathematical biology 2005.104p. Dissertation (Doctor of Philosophy) - The University of Michigan, Michigan, 2005.
- 3- The Telegraph, 12 Oct 2009. Image by Jason Heller.