M.5 Modeling the Effect of Functional Responses

The functional response is referred to the predation rate as a function of the number of prey per predator.

It is recognized that as the number of prey increases, the rate of prey capture per predator cannot increase indefinitely. Instead, the rate of prey capture is saturated when the population of prey is relatively large. Similar phenomena have been observed in the interactions in chemical reactions and molecular events when one species are abundant. In such cases, the reaction rates are saturated as well. This type of function response can be modeled by the Holling Type II response functions or Michaelis-Menten kinetics, and Type III, and Hill functions. Below are the typical response functions.

Linear response function:

$$f(x) = bx, \qquad b > 0.$$

Holling Type II response function and Michaelis-Menten kinetics (Figure 1):

$$f(x) = \frac{bx}{N + x}, \quad b > 0, N > 0.$$

Type III or Hill function (Figure 2):

$$f(x) = \frac{bx^2}{N^2 + x^2}, \qquad b > 0, N > 0.$$

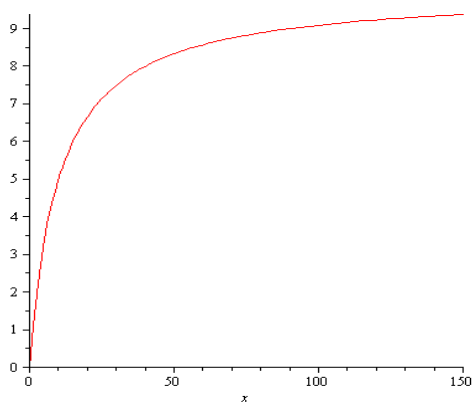

Figure 1

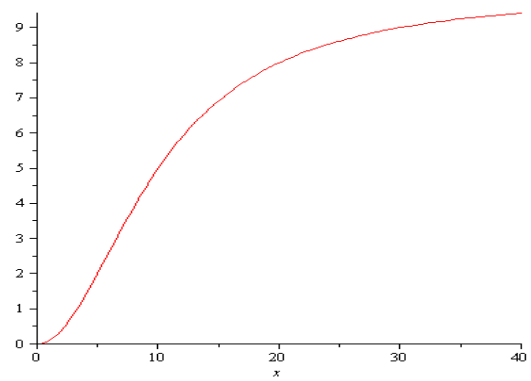

Figure 2

Consider the predator-prey model

$$\begin{cases} x' = rx\left(1 - \dfrac{x}{K}\right) - bxy \\ \\ y' = cxy - dy \end{cases} \tag{1}$$

where parameters $r, K\ b, c, d > 0$. In this model, it is assumed that the predation rate per predator y is linear to the number of prey x. That is, $f(x) = bx$. If there exists a upper limit for the maximum predation rate, the predation rate can be modeled by different response functions. For example, assume that the predation rate increases quickly when the population of the prey is relatively small, and the gets saturated when the population of prey is large. The predation rate can be modeled by Holling type II response function, or also called Michaelis-Menten kinetics in modeling the chemical reactions, pharmacokinetics, and the gene regulations. Therefore the predator prey model with Holling type II response function is given by

$$\begin{cases} x' = rx\left(1 - \dfrac{x}{K}\right) - \dfrac{bxy}{N + x} \\ y' = \dfrac{cxy}{N + x} - dy \end{cases} \tag{2}$$

While the above shows how to formulate and revise mathematical models in the areas of application, following example demonstrates the typical procedures how a model is analyzed and interpreted into the meanings of the area applied.

Ex. Consider the predator-prey model with Holling type II response

$$\begin{cases} x' = x\left(1 - \dfrac{x}{30}\right) - \dfrac{x}{x + 10}y \\ y' = \dfrac{x}{x + 10}y - \dfrac{1}{3}y \end{cases} \tag{3}$$

Analyze the model (3) qualitatively.

Solutions. We will do

1. Find all equilibrium points in the first quadrant and study their stabilities.
2. Perform phase plane analysis
3. Determine the existence of closed orbit
4. Interpret the mathematical results in to biological meanings.

- **Find the Equilibrium Points**

The equilibrium points can be found by solving the system

$$\begin{cases} x\left(1 - \dfrac{x}{30}\right) - \dfrac{x}{x + 10}y = 0 \\ \dfrac{x}{x + 10}y - \dfrac{1}{3}y = 0 \end{cases}$$

They are $E_0 = (0,0), E_1 = (30,0)$ and $E^* = \left(5, \frac{25}{2}\right)$.

- **Study the stability of the equilibrium points**

If the equilibrium points are hyperbolic, their stability can be determined by the linearized system around the equilibrium points.

To find the coefficient matrix of the linearized system, we compute the partial derivatives first.

$$\frac{\partial}{\partial x}\left(x\left(1-\frac{x}{30}\right)-\frac{x\,y}{(x+10)}\right) = 1-\frac{1}{15}x-\frac{y}{x+10}+\frac{x\,y}{(x+10)^2}$$
$$\frac{\partial}{\partial y}\left(x\left(1-\frac{x}{30}\right)-\frac{x\,y}{(x+10)}\right) = -\frac{x}{x+10}$$
$$\frac{\partial}{\partial x}\left(\frac{y\cdot x}{x+10}-\frac{1}{3}\cdot y\right) = \frac{y}{x+10}-\frac{x\,y}{(x+10)^2}$$
$$\frac{\partial}{\partial y}\left(\frac{y\cdot x}{x+10}-\frac{1}{3}\cdot y\right) = \frac{x}{x+10}-\frac{1}{3}$$

Find the matrix of the linearized system at E_0:

$$\left(\frac{\partial}{\partial x}\left(x\left(1-\frac{x}{30}\right)-\frac{x\,y}{(x+10)}\right)\right)\Big|_{x=0,\,y=0} = 1$$
$$\left(\frac{\partial}{\partial y}\left(x\left(1-\frac{x}{30}\right)-\frac{x\,y}{(x+10)}\right)\right)\Big|_{x=0,\,y=0} = 0$$
$$\left(\frac{\partial}{\partial x}\left(\frac{y\cdot x}{x+10}-\frac{1}{3}\cdot y\right)\right)\Big|_{x=0,\,y=0} = 0$$
$$\left(\frac{\partial}{\partial y}\left(\frac{y\cdot x}{x+10}-\frac{1}{3}\cdot y\right)\right)\Big|_{x=0,\,y=0} = -\frac{1}{3}$$

So

$$A_0 = \begin{bmatrix} 1 & 0 \\ 0 & -\frac{1}{3} \end{bmatrix}$$

and the eigenvalues are $\lambda_1 = -\frac{1}{3}, \lambda_2 = 1$. So E_0 is a saddle.

Find the matrix of the linearized system at E_1:

$$\left(\frac{\partial}{\partial x}\left(x\left(1-\frac{x}{30}\right)-\frac{x\,y}{(x+10)}\right)\right)\Big|_{x=30,\,y=0} = -1$$
$$\left(\frac{\partial}{\partial y}\left(x\left(1-\frac{x}{30}\right)-\frac{x\,y}{(x+10)}\right)\right)\Big|_{x=30,\,y=0} = -\frac{3}{4}$$
$$\left(\frac{\partial}{\partial x}\left(\frac{y\cdot x}{x+10}-\frac{1}{3}\cdot y\right)\right)\Big|_{x=30,\,y=0} = 0$$

$$\left(\frac{\partial}{\partial y}\left(\frac{y\cdot x}{x+10}-\frac{1}{3}\cdot y\right)\right)\Big|_{x=30,\,y=0} = \frac{5}{12}$$

and thus

$$A_1 = \begin{bmatrix} -1 & -\frac{3}{4} \\ 0 & \frac{5}{12} \end{bmatrix}$$

The eigenvalues are $\lambda_1 = -1, \lambda_2 = \frac{5}{12}$. So E_1 is also a saddle.

At E^*, the matrix of the linearized system

$$\left(\frac{\partial}{\partial x}\left(x\left(1-\frac{x}{30}\right)-\frac{x\,y}{(x+10)}\right)\right)\Big|_{x=5,\,y=\frac{25}{2}} = \frac{1}{9}$$

$$\left(\frac{\partial}{\partial y}\left(x\left(1-\frac{x}{30}\right)-\frac{x\,y}{(x+10)}\right)\right)\Big|_{x=5,\,y=\frac{25}{2}} = -\frac{1}{3}$$

$$\left(\frac{\partial}{\partial x}\left(\frac{y\cdot x}{x+10}-\frac{1}{3}\cdot y\right)\right)\Big|_{x=5,\,y=\frac{25}{2}} = \frac{5}{9}$$

$$\left(\frac{\partial}{\partial y}\left(\frac{y\cdot x}{x+10}-\frac{1}{3}\cdot y\right)\right)\Big|_{x=5,\,y=\frac{25}{2}} = 0$$

$$A^* = \begin{bmatrix} \frac{1}{9} & -\frac{1}{3} \\ \frac{5}{9} & 0 \end{bmatrix}$$

and the eigenvalues are $\lambda_1 = 0.2639 + 0.4023i, \lambda_2 = 0.2639 - 0.4023i$. So E^* is an unstable focus.

- **Phase Plain Analysis**

The vertical nullclines are given by

$$P(x,y) = x\left(1-\frac{x}{30}\right)-\frac{x}{x+10}y = 0.$$

and the horizontal nullclines are given by

$$Q(x,y) = \frac{x}{x+10}y - \frac{1}{3}y = 0$$

So the vertical nullclines are

$$x = 0, \;\; y = \frac{1}{30}(x + 10)(30 - x).$$

and the horizontal nullclines are

$$y = 0, \;\; x = 5.$$

Refer to Figure 2 for the nullclines.

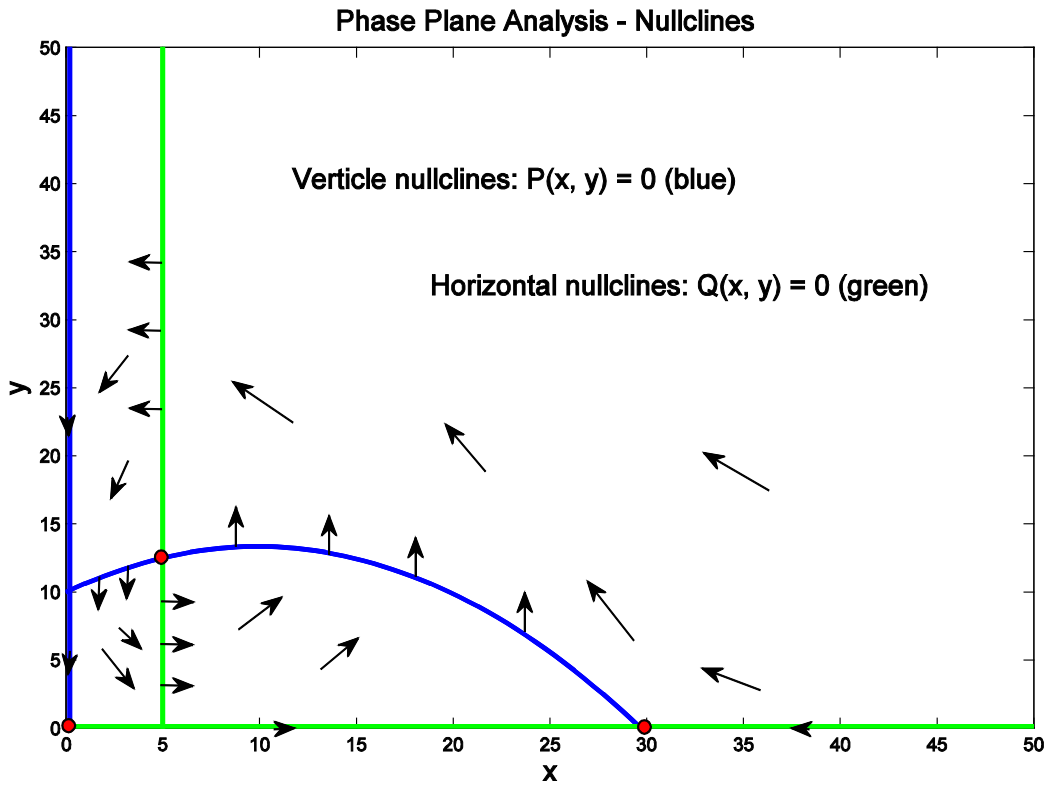

Figure 2

Select test points: $T_1(1,1), T_2(15,5), T_3(30,15)$ and $T_4(1,30)$. Thus the vectors $(P(x,y), Q(x,y))$ at these points are

$$\left(\frac{10}{11}, -\frac{8}{33}\right)^T, \left(12, \frac{4}{3}\right)^T, \left(\frac{75}{4}, \frac{25}{4}\right)^T, \text{ and } \left(-\frac{19}{11}, -\frac{80}{11}\right)^T,$$

respectively. Thus the directions of the vector field can be determined. Refer to Figure 2.

- **Apply Poincare-Bendixson Theorem to show the existence of a closed orbit.**

Let $z = x + y$. Then

$$z' = x' + y' = x\left(1 - \frac{x}{30}\right) - \frac{1}{3}y.$$

Therefore, $z' = x' + y' < 0$ except when $(x, y) \in D = \{(x, y) \mid \frac{1}{3}y \leq x\left(1 - \frac{x}{30}\right)\}$. Refer to Figure 3.

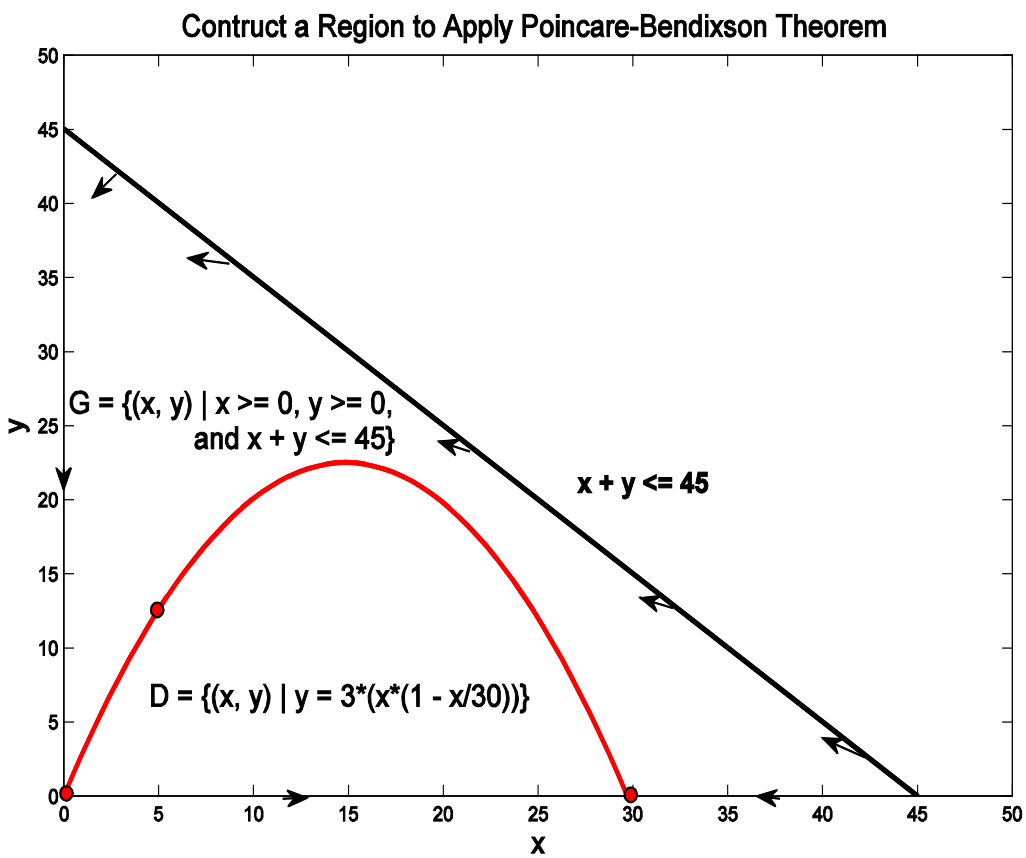

Figure 3

Choose $C > 0$ large enough so that the line $x + y = C$ does not intersect with D. Thus the direction of any trajectory starting at the line segment of $x + y = C$ in the first quadrant is pointing down-ward. We choose $C = 45$. In addition, the trajectory starting at a point on the x-axis will stay in the x-axis and approach to $E_1(30, 0)$. Meanwhile, any trajectory starting at a point on the y-axis will stay on the y-axis and approaches to $E_0(0, 0)$. Consider the region

$$G = \{(x, y) | x \geq 0, y \geq 0, and\ x + y \leq 45\}.$$

Above analysis shows that G is an **invariant** set, that is, any trajectory starting at a point in G will stay in G. Refer to Figure 3.

Notice that G is closed and bounded. Let γ^+be a positive semitrajectory starting a point $x_0 \in G$ and x_0 is not E_0, E_1 or E^*. By Poincare-Bendixson Theorem, the $\omega(\gamma^+)$ must be an equilibrium point, a separatrix cycle, or a closed orbit.

Since all E_0, E_1 and E^* are unstable, and the stable manifold of E_0 and E_1 are on the y-axis and x-axis, respectively, $\omega(\gamma^+)$ cannot be an equilibrium point. Since the stable manifold of E_0 is the positive y-axis, by the phase plane analysis above, it cannot be the unstable manifold of E_1 since the unstable manifold of E_1 cannot intersect with the y-axis. Thus, there is no separatrix cycle contained in G, $\omega(\gamma^+)$ cannot be a separatrix cycle. Therefore, $\omega(\gamma^+)$ must be a closed orbit, denoted by γ_1. Refer to Figure 4.

For any point (x_0, y_0) in the Quadrant I, if $x_0 + y_0 = C_0$ is large enough so that $x + y = C_0$ does not intersect with the curve D, then the trajectory $\gamma^+(x_0, y_0)$ must move downward along $x + y = C$ till $x + y = C$ intersects with the curve D. This is because $z' = x' + y' < 0$ as shown above, and thus the level curve $z = x + y = C$ shrink to the origin as $C > 0$ decreases. Therefore, $\omega(\gamma^+(x_0, y_0)) = \gamma_1$, that is, the closed orbit γ_1 is exterior globally stable.

For any trajectory starting at a point (x_0, y_0) near to E^*whose α-limit set isE^*, its ω-limit set must be a closed orbit γ_2. The closed orbit γ_2 is interior stable. γ_2 could coincide with γ_1, that is, $\gamma_2 = \gamma_1$. If $\gamma_1$and γ_2 do not coincide, the area between $\gamma_1$and γ_2 are filled with cycles. (We don't require you know this in very much details.)

In either case, any orbit starting at a point $(x_0, y_0), x_0, y_0 > 0$, is attracted to a closed orbit. (Remember, the ω-limit set of a closed orbit is itself.)

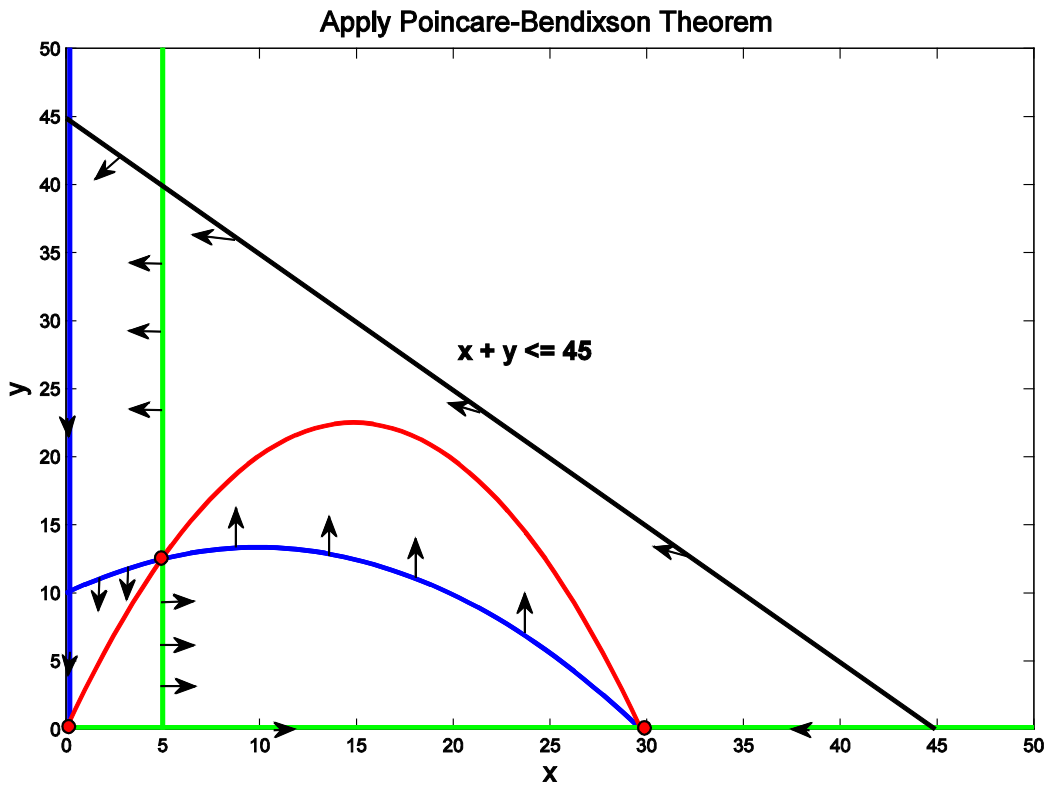

Figure 4

- **Interpretations in Biology**

The closed orbit is equivalent to a periodic solution of the model. Both species will coexist in the environment under given conditions if the initial numbers of the species are both not equal to zero. (The given conditions refer to the assumptions based on the considered biological background, and thus the parameter values.)

If the predator is absent initially, it will never invade into the environment and the prey follows the logistic growth.

If the prey is absent initially, it will never join and the predator will extinct eventually.

In the predator prey model (1), we found that the interior equilibrium point is globally asymptotically stable. In biological meaning, both species will coexist over the time and the population sizes of the species will approach to a certain number, respectively.