$\boxed{14-2-2012}$

Prey-predator model of Gause

$$\begin{cases} \dfrac{dn}{dt} = g(n) - f(n)p & \text{(prey)} \\[2ex] \dfrac{dp}{dt} = \gamma f(n) p - dp & \text{(pred.)} \end{cases}$$

- The prey-dynamics if predators are absent is given by

$$\boxed{\frac{dn}{dt} = g(n)}$$

For example $\boxed{g(n) = rn\left(1 - \frac{n}{K}\right)}$ gives the logistic growth for the prey if no predators are around

(eg, see page 9 of 26-01-2012 and page 32 of 02-01-2012 for two different individual-based mechanisms for the logistic equation)

• $f(n)$ is the "functional response", i.e., the amount of prey captured per predator per unit of time.

The total amount of prey captured per unit of time is $f(n)p$. A part of this is used by the predator to produce offspring.

That's why the term $\gamma f(n)p$ appears in de predator's equation.

The constant $\gamma > 0$ is the "conversion" constant (conversion of prey into new pred.).

(If the prey is small or has low nutritional value, then γ is small)

Functional responses

Holling-1

Suppose the predation process is fully described by

$$N + P \xrightarrow{\beta} P$$

In the equation for $\frac{dn}{dt}$, this given gives a predation term $\boxed{\beta n p}$, and hence

$$f(n) = \beta n$$

This is called the Holling-1 functional response

Holling-2

Suppose the predation process is described by the reaction network

$$N + X \xrightarrow{\beta} Y \xrightarrow{\frac{1}{\tau}} X$$

where X is a searching predator and Y is a predator busy "handling" the prey in

some sense or another
(like chasing, capturing, eating, digesting, resting)

predation dyn.
$$\begin{cases} \dfrac{dx}{dt} = -\beta n x + \frac{1}{T} y \\[2ex] \dfrac{dy}{dt} = +\beta n x - \frac{1}{T} y \end{cases}$$

($x+y=p$ const) ← fast dyn

i.e, ignoring slow processes as birth and death of predators, and assuming that $n \gg x, y$ so that also changes in n are relatively slow and can be ignored.

Then, at equil. of the predation dynamics we have

$$x = \frac{1}{1+\beta T n} \cdot p$$

where $p = x+y$ is the total pred. pop. dens. (slow variable)

In the equation for $\frac{dn}{dt}$ this gives a predation term

$$\beta n x = \frac{\beta n}{1+\beta T n} \cdot p$$

and so we find

$$f(n) = \frac{\beta n}{1+\beta T n}$$

which is called the Holling-2 functional response

$T > 0$ is the expected time an individual predator stays in the "handling" state Y after having found a prey

(The above predation mechanism

$$N + X \xrightarrow{\beta} Y \xrightarrow{\frac{1}{T}} X$$

is not the only one that leads to the Holling-2 response)

Holling-3

Consider the following predation mechanism:

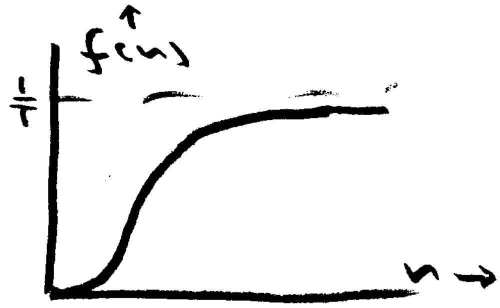
$$\left.\begin{array}{l} N + X_e \xrightarrow{\beta_e} \\ N + X_i \xrightarrow{\beta_i} \end{array}\right\} Y \xrightarrow{\frac{1}{T}} X_e \xrightarrow{\varphi} X_i$$

where X_e is an "experienced" predator and X_i an "inexperienced" predator with capturing rates $\boxed{\beta_e > \beta_i}$ respectively.

A "handling" predator is again denoted by Y.

Experienced predators forget their experience at a rate φ.

Assuming that the predation dynamics are fast compared to everything else, this leads to the Holling-3 response (Exercise) which looks like this $\longrightarrow$ figure:



Some predation mechanisms do not lead to a functional response that fits in the Holling-classification.

Example.

a handling predator (Y) is disturbed by a searching predator (X) who wants to steal the captured prey, which leads to a quarrelling predator pair (Z):

$$N + X \longrightarrow Y \longrightarrow X$$

$$X + Y \rightleftarrows Z$$

(Exercise)

another example

Prey may help captured prey to escape:

$$N + X \longrightarrow Y \longrightarrow Z \longrightarrow X$$

$$N + Y \longrightarrow 2N + X$$

(Exercise) (in Y the prey is still alife; in Z it is killed)

The model of Gause

$$(*)\begin{cases} \dfrac{dn}{dt} = g(n) - f(n)\,p \\[2ex] \dfrac{dp}{dt} = \gamma f(n)\,p - \delta p . \end{cases}$$

<u>with</u>:

- g cont. diff. and $g(0)=0$ and $g(n)>0$ for $n<K$ and $g(n)<0$ for $n>K$ for some given constant K.
- f cont. diff. and $f(0)=0$ and $f(n)>0$ and $f'(n)>0$ for $n>0$, and there exists a $n_0>0$ such that $\gamma f(n_0) - \delta = 0$.

(ie. $n=n_0$ is a zerocline for p)

<u>Then</u>:

<u>Case</u> $\boxed{K \leq n_0}$

There is no equilibrium in the interior of the phaseplane, and all orbits converge to the boundary equil. $(n,p)=(K,0)$.

Case $\boxed{n_0 < K}$

There exists one and only one equilibrium $(n,p) = (n_0, p_0)$ in the interior of the phaseplane

To check (local) stability of (n_0, p_0), evaluate the Jacobi-matrix of ⊛ (previous page) at (n_0, p_0):

$$J = \begin{pmatrix} g'(n_0) - f'(n_0)p_0 & -f(n_0) \\ \gamma f'(n_0)p_0 & \gamma f(n_0) - \delta \end{pmatrix} =$$

$$= \begin{pmatrix} f(n_0)\left(\dfrac{g(n_0)}{f(n_0)}\right)' & -f(n_0) \\ \gamma f'(n_0) p_0 & 0 \end{pmatrix}$$

$$\Rightarrow \begin{cases} \det J = \gamma f(n_0) f'(n_0) p_0 > 0 \\ \operatorname{trace} J = \underbrace{f(n_0)}_{>0} \underbrace{\left(\dfrac{g(n_0)}{f(n_0)}\right)'}_{\uparrow} \end{cases}$$

slope of n zerocline at (n_0, p_0)

So, det J is always positive, and trace J is positive or negative depending whether the n-zerocline is increasing or decreasing at the equilibrium.

$\Rightarrow$ (n_0, p_0) is *stable* if the n-zerocline is *decreasing*, and *unstable* if increasing. (see Appendix A)