2021.12.7

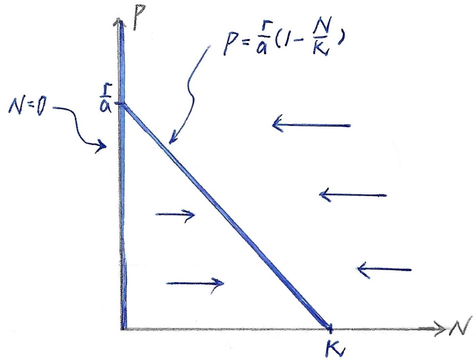
◎ Model 2 : Logistic growth + Type I functional response

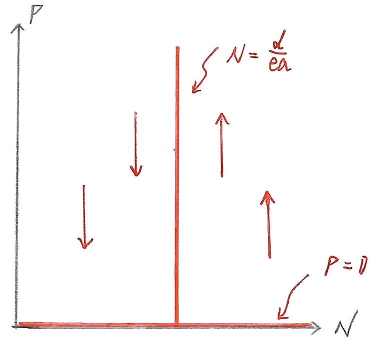
$$\begin{cases} \frac{dN}{dt} = rN\left(1-\frac{N}{K}\right) - aNP = f_N = N\left[r\left(1-\frac{N}{K}\right) - aP\right] \\ \frac{dP}{dt} = eaNP - dP = f_P = P(eaN - d) \end{cases}$$

- Find equilibrium by getting ZNGIs $\Rightarrow \begin{cases} N=0 \ \vee \ P = \frac{r}{a}\left(1-\frac{N}{K}\right) \\ P=0 \ \vee \ N = \frac{d}{ea} \end{cases}$

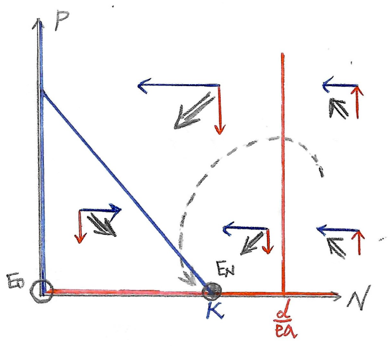
- Get equilibrium : $E_0 \begin{cases} N^*=0 \\ P^*=0 \end{cases}$, $E_N \begin{cases} N^*=K \\ P^*=0 \end{cases}$, $E_{NP} \begin{cases} N^* = \frac{d}{ea} \\ P^* = \underbrace{\frac{r}{a}\left(1-\frac{d}{eaK}\right)}_{\text{feasibility : } eaK > d \ \Rightarrow K > \frac{d}{ea}} \end{cases}$

- Graphical analysis



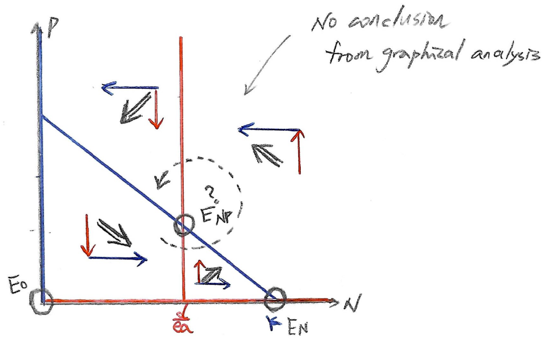


put together, consider two scenarios



« $K < \frac{d}{ea}$ »

only 2 equilibrium, E_{NP} unfeasible



« $K > \frac{d}{ea}$ »

3 equilibrium

• Local stability analysis

$$\begin{cases} \frac{df_N}{dN} = \left[r(1-\frac{N^*}{K}) - aP^* \right] + N^*(-\frac{r}{K}) \\ \frac{df_N}{dP} = -aN^* \\ \frac{df_P}{dN} = eaP^* \\ \frac{df_P}{dP} = eaN^* - d \end{cases}$$

(1) For E_0 ($N^*=0$, $P^*=0$) : $J_0 = \begin{bmatrix} r & 0 \\ 0 & -d \end{bmatrix} \Rightarrow \lambda = r \vee -d$

$\Rightarrow$ E_0 is locally unstable

(2) For E_N ($N^*=K$, $P^*=0$) : $J_N = \begin{bmatrix} -r & -aK \\ 0 & eaK-d \end{bmatrix} \Rightarrow \lambda = -r \vee eaK-d$

$\Rightarrow$ E_N is stable when $K < \frac{d}{ea}$

matches graphical analysis

E_N is unstable when $K > \frac{d}{ea}$

feasible when $K > \frac{d}{ea}$

(3) For E_{NP} ($N^* = \frac{d}{ea}$, $P^* = \frac{r}{a}(1-\frac{d}{eaK})$) : $J_{NP} = \begin{bmatrix} \frac{-rd}{eaK} & -\frac{d}{e} \\ eaP^* & 0 \end{bmatrix}$

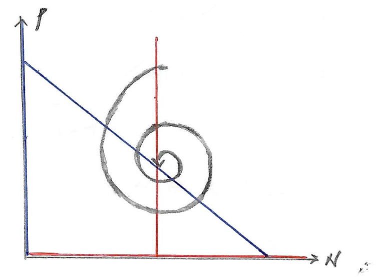
$$\Rightarrow \lambda^2 + \left(\frac{rd}{eaK}\right)\lambda + adP^* = 0$$

$$\Rightarrow \begin{cases} \lambda_1 + \lambda_2 = \frac{-rd}{eaK} < 0 \\ \lambda_1 \cdot \lambda_2 = adP^* > 0 \end{cases}$$

$\Rightarrow Re(\lambda_i) < 0$

E_{NP} is stable when it is feasible ($P^* > 0$)

« Summary » logistic regulation of prey can stabilize predator-prey interactions



◎ Timescale separation

A technique to gain insight into model dynamics, at least in some parameter

Assume the system can be divided into FAST and SLOW process

⇛ The FAST variable views the slow variable as constant and reaches its "Quasi-equilibrium" and adjusts to a new quasi-equilibrium whenever the slow variable changes. For the SLOW variable, the fast variable is always at its quasi-equilibrium

⇛ suitable for, e.g. eco-evo dynamics v across trophic levels

We assume prey dynamics are fast & predator dynamics are slow

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right) - aNP \Longrightarrow r\hat{N}\left(1-\frac{\hat{N}}{K}\right) - a\hat{N}P = 0$$

view as constant

$$\Rightarrow \hat{N} = \frac{K}{r}(r - aP)$$

substitute

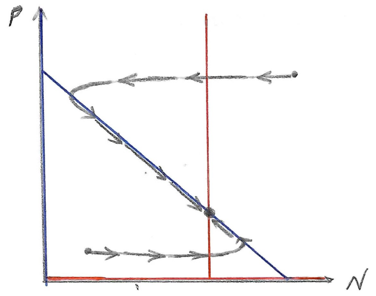
$$\frac{dP}{dt} = eaNP - dP$$

$$= ea\frac{K}{r}(r-aP)P - dP$$

$$= (eaK - d)P - ea^2\frac{K}{r}P^2$$

$$= \underbrace{(eaK-d)}_{\text{predator intrinsic growth rate}}P\left[1 - \frac{P}{\underbrace{\left(\frac{eaK-d}{ea^2\frac{K}{r}}\right)}_{\text{carrying capacity} = \frac{\text{intrinsic growth}}{\text{self-limitation}}}}\right]$$

under some parameters that fulfill timescale separation, predators behave as logistic growth !!



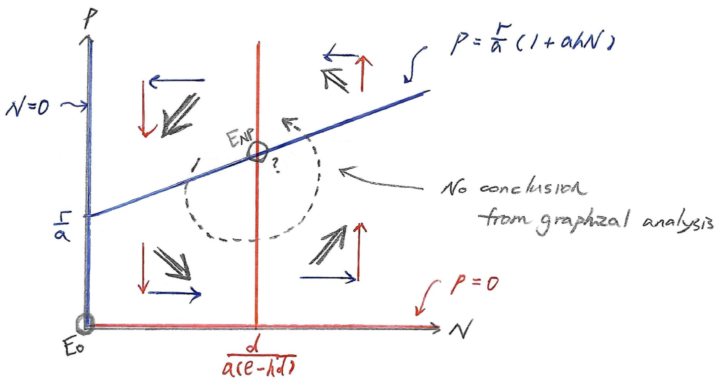
ⓒ Model 3: Exponential growth + Type II functional response

$$\begin{cases} \dfrac{dN}{dt} = rN - \left(\dfrac{aN}{1+ahN}\right)P = f_N = N\left(r - \dfrac{aP}{1+ahN}\right) \\[2ex] \dfrac{dP}{dt} = e\left(\dfrac{aN}{1+ahN}\right)P - dP = f_P = P\left(\dfrac{eaN}{1+ahN} - d\right) \end{cases}$$

- Get ZNGI $\Rightarrow \begin{cases} N=0 \;\vee\; P = \dfrac{r}{a}(1+ahN) \\ P=0 \;\vee\; N = \dfrac{d}{a(e-hd)} \end{cases}$

- Get equilibrium : $E_0 \begin{cases} N^*=0 \\ P^*=0 \end{cases} \;\vee\; E_{NP} \begin{cases} N^* = \dfrac{d}{a(e-hd)} \\ P^* = \dfrac{r}{a}(1+ahN^*) \end{cases}$ → feasibility : $e > hd$

- Graphical analysis :



- Local stability analysis

$$\begin{cases} \dfrac{\partial f_N}{\partial N} = \left(r - \dfrac{aP^*}{1+ahN^*}\right) + N^* \cdot \dfrac{a^2hP^*}{(1+ahN^*)^2} \\[2ex] \dfrac{\partial f_N}{\partial P} = \dfrac{-aN^*}{1+ahN^*} \\[2ex] \dfrac{\partial f_P}{\partial N} = \dfrac{1}{(1+ahN^*)^2} \times \underbrace{\left[(1+ahN^*)\cdot eaP^* - eaN^*P^* \cdot ah\right]}_{= eaP^*} \\[2ex] \dfrac{\partial f_P}{\partial P} = \dfrac{eaN^*}{(1+ahN^*)} - d \end{cases}$$

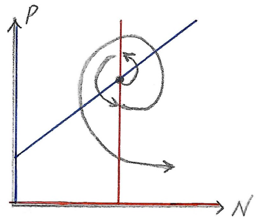
(1) For E_0 : $J_0 = \begin{bmatrix} r & 0 \\ 0 & -d \end{bmatrix} \Rightarrow \lambda = r, -d$

$\Rightarrow$ E_0 is locally unstable

(2) For E_{NP} : $J_{NP} = \begin{bmatrix} \dfrac{a^2 h N^* P^*}{(1+ahN^*)^2} & \dfrac{-aN^*}{(1+ahN^*)} \\ \dfrac{eaP^*}{(1+ahN^*)^2} & 0 \end{bmatrix}$

$$\Rightarrow \lambda^2 - \frac{a^2 h N^* P^*}{(1+ahN^*)^2} + \frac{ea^2 N^* P^*}{(1+ahN^*)^3} = 0$$

$$\Rightarrow \begin{cases} \lambda_1 + \lambda_2 = \dfrac{a^2 h N^* P^*}{(1+ahN^*)^2} > 0 \\ \lambda_1 \cdot \lambda_2 = \dfrac{ea^2 N^* P^*}{(1+ahN^*)^3} > 0 \end{cases}$$



$\Rightarrow$ $Re(\lambda_i) > 0$, E_{NP} is unstable when it is feasible

◎ Model 4 : Logistic growth + Type II functional response

« Rosenzweig – MacArthur model »

$$\begin{cases} \dfrac{dN}{dt} = rN(1-\dfrac{N}{K}) - (\dfrac{aN}{1+ahN})P = f_N = N\left[r(1-\dfrac{N}{K}) - (\dfrac{aP}{1+ahN})\right] \\ \dfrac{dP}{dt} = e(\dfrac{aN}{1+ahN})P - dP = f_P = P\left[(\dfrac{eaN}{1+ahN}) - d\right] \end{cases}$$

• Get ZNGIs : $\begin{cases} N = 0 \vee P = \dfrac{r}{a}(1-\dfrac{N}{K})(1+ahN) \\ P = 0 \vee N = \dfrac{d}{a(e-hd)} \end{cases}$

feasible when $e > hd$

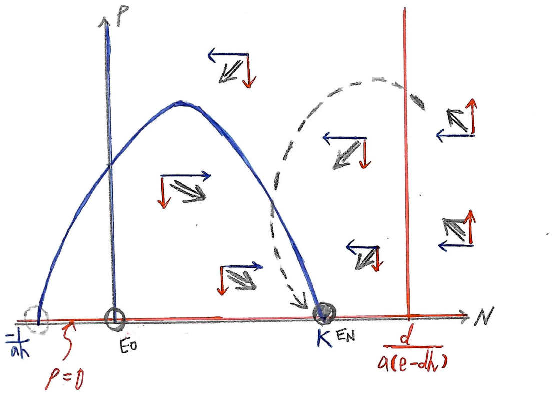
• Get equilibrium : $E_0 \begin{cases} N^* = 0 \\ P^* = 0 \end{cases} \vee E_N \begin{cases} N^* = K \\ P^* = 0 \end{cases} \vee E_{NP} \begin{cases} N^* = \dfrac{d}{a(e-hd)} \\ P^* = \dfrac{r}{a}(1-\dfrac{N^*}{K})(1+ahN^*) \end{cases}$

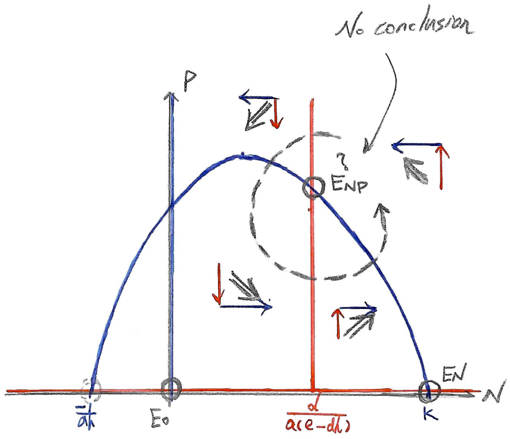
do not consider $N^* = \dfrac{1}{-ah}$

feasible when $\dfrac{d}{a(e-hd)} < K$

i.e., large e & a, small d & h

- Graphical analysis :





« $K < \frac{d}{a(e-hd)}$ »

2 equilibrium , E_{NP} unfeasible

« $K > \frac{d}{a(e-dh)}$ »

3 equilibrium

- Local stability analysis :

$$\frac{\partial f_N}{\partial N} = \left[r\left(1-\frac{N^*}{K}\right) - \left(\frac{aP^*}{1+ahN^*}\right) \right] + N^* \left[\frac{-r}{K} + \frac{a^2hP^*}{(1+ahN^*)^2} \right]$$

$$\frac{\partial f_N}{\partial P} = \frac{-aN^*}{1+ahN^*}$$

$$\frac{\partial f_P}{\partial N} = \frac{1}{(1+ahN^*)^2} \underbrace{\left[(1+ahN^*)\, eaP^* - eaN^*P^*\, ah \right]}_{= eaP^*}$$

$$\frac{\partial f_P}{\partial P} = \frac{eaN^*}{1+ahN^*} - d$$

(1) For E_0 : $J_0 = \begin{bmatrix} r & 0 \\ 0 & -d \end{bmatrix} \Rightarrow \lambda = r \, , \, -d$

$\Rightarrow$ E_0 is locally unstable

(2) For E_N : $J_N = \begin{bmatrix} -r & \frac{-aK}{1+ahK} \\ 0 & \frac{eaK}{1+ahK} - d \end{bmatrix} \Rightarrow \lambda = -r \, , \, \frac{eaK}{1+ahK} - d$

$\Rightarrow$ E_N is stable if $\frac{eaK}{1+ahK} < d$

$\Rightarrow$ E_N is stable if $K < \frac{d}{a(e-dh)}$

E_N is unstable if the opposite

matches graphical analysis

(3) For E_{NP} : $J_{NP} = \begin{bmatrix} N^*\left[\frac{-r}{K} + \frac{a^2 h P^*}{(1+ahN^*)^2}\right] & \frac{-aN^*}{1+ahN^*} \\ \frac{eaP^*}{(1+ahN^*)^2} & 0 \end{bmatrix}$

$$\Rightarrow \lambda^2 - N^*\left[\frac{-r}{K} + \frac{a^2 h P^*}{(1+ahN^*)^2}\right]\lambda + \frac{ea^2 N^* P^*}{(1+ahN^*)^3} = 0$$

$$\Rightarrow \begin{cases} \lambda_1 + \lambda_2 = N^*\left[\frac{-r}{K} + \frac{a^2 h P^*}{(1+ahN^*)^2}\right] \text{ must be negative} \\ \lambda_1 \cdot \lambda_2 = \frac{ea^2 N^* P^*}{(1+ahN^*)^3} > 0 \end{cases}$$

$\Rightarrow$ Given a feasible E_{NP} $\left(K > \frac{d}{a(e-dh)}\right)$, it will be stable when

$$\left(\frac{-r}{K}\right) + \frac{a^2 h}{(1+ahN^*)^2} \cdot \left[\frac{r}{a}\left(1-\frac{N^*}{K}\right)(1+ahN^*)\right] < 0$$

$$\Rightarrow -\frac{r}{K}(1+ahN^*) + ahr - ahr\frac{N^*}{K} < 0$$

$$\Rightarrow -r - 2ahrN^* + ahrK < 0$$

midpoint of the parabola ZNGI of prey

$$\Rightarrow N^* > \frac{-1+ahK}{2ah} = \frac{\left(\frac{-1}{ah}\right) + K}{2}$$

$$\Rightarrow \frac{d}{a(e-dh)} > \frac{\left(\frac{-1}{ah}\right) + K}{2}$$

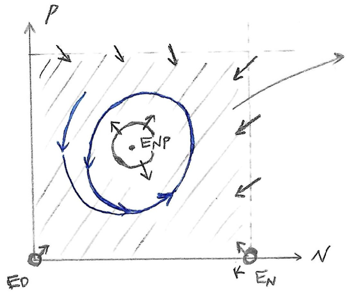
$$\Rightarrow K < \frac{dh+e}{ah(e-dh)}$$

$\Rightarrow$ If feasible $\left(K > \frac{d}{a(e-hd)}\right)$, the E_{NP} will be stable if N^* is located at the right hand side of the parabola $\left(K < \frac{dh+e}{ah(e-dh)}\right)$, but unstable if N^* is at the left hand side $\left(K > \frac{dh+e}{ah(e-dh)}\right)$.

Q. what happens when E_{NP} is also unstable?

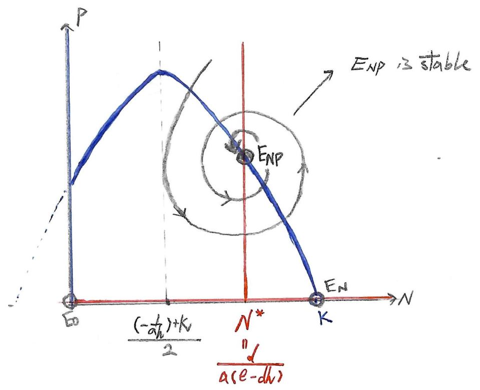
「In 2-D state space, if the region is bounded (a trajectory never leaves the region and doesn't blow up) and does not include an equilibrium, then trajectories inside must exhibit sustained periodic behavior」

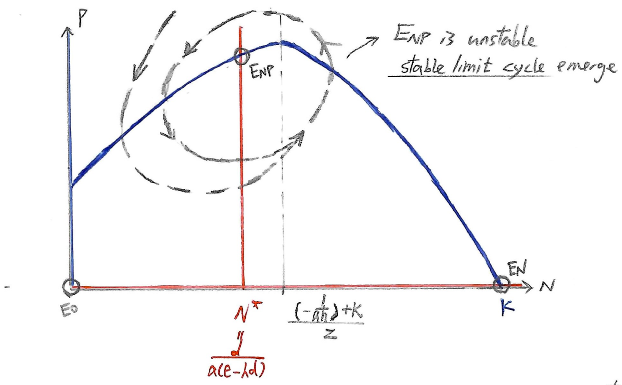
« Poincaré - Bendixon theorm »



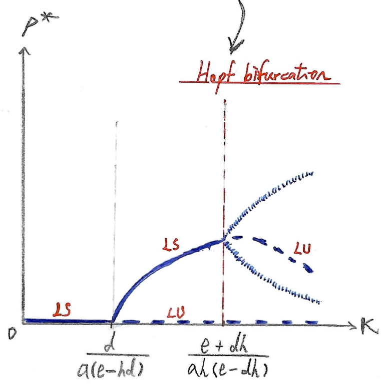
a trapping region for Poincaré - Bendixon theorm

a cycle will emerge when E_{NP} is unstable





« paradox of enrichment »



« Bifurcation diagram »

bifurcation: change in parameter result in qualitative change in system stability

e.g. increase K will destabilize the system (stable → unstable)