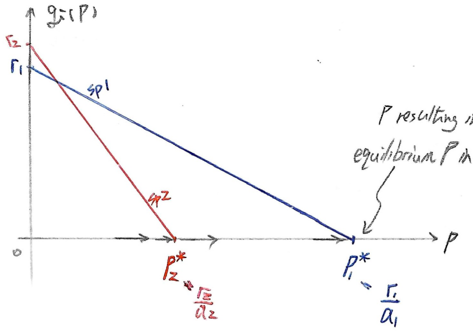
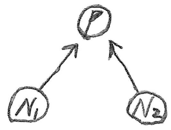
2021.12.21 Apparent Competition (Holt. 1977, Theoretical pop. biol.)

A simple model before Holt (1977)

extension of LV predator-prey

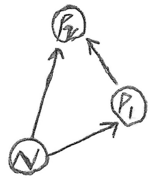
$$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 - a_1 N_1 P = g_1(P) N_1 \\ \frac{dN_2}{dt} = r_2 N_2 - a_2 N_2 P = g_2(P) N_2 \\ \frac{dP}{dt} = e_1 a_1 N_1 P + e_2 a_2 N_2 P - dP = g_P(N_1, N_2) P \end{cases}$$





Apparent competition

Holt (1977) Theo. pop. biol.



Intraguild predation

Holt & Polis (1997) Am. Nat.

Food chain

Rosenzweig (1973) Am. Nat.

a P^* rule : a dominant species under apparent competition would be the one with higher P^* as it withstands and supports higher predator population

Holt (1977) model: Logistically growing prey (competitor) + type I functional response

$$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - a_1 N_1 P = f_1 = N_1 \left[r_1 \left(1 - \frac{N_1}{K_1}\right) - a_1 P \right] \\ \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - a_2 N_2 P = f_2 = N_2 \left[r_2 \left(1 - \frac{N_2}{K_2}\right) - a_2 P \right] \\ \frac{dP}{dt} = e_1 a_1 N_1 P + e_2 a_2 N_2 P - dP = f_P = P \left[e_1 a_1 N_1 + e_2 a_2 N_2 - d \right] \end{cases}$$

Q: conditions allowing the coexistence of competing prey with shared predator?

- Use ZNGIs to find equilibrium

potentially max. 8 of them, but $(0, 0, P^*)$ is impossible and we only care about few

The equilibrium we care about:

$$E_1: \begin{cases} N_1^* = \dfrac{d}{e_1 a_1} \\ N_2^* = 0 \\ P^* = \dfrac{r_1}{a_1}\left(1 - \dfrac{d}{e_1 a_1 K_1}\right) \end{cases}$$

resemble model 2 from predator-prey

feasible & stable when $K_1 > \frac{d}{e_1 a_1}$

Boundary equilibrium

$$E_2: \begin{cases} N_1^* = 0 \\ N_2^* = \dfrac{d}{e_2 a_2} \\ P^* = \dfrac{r_2}{a_2}\left(1 - \dfrac{d}{e_2 a_2 K_2}\right) \end{cases}$$

feasible & stable when $K_2 > \frac{d}{e_2 a_2}$

internal equilibrium

$$E_c: \begin{cases} N_1^* > 0 \\ N_2^* > 0 \\ P^* > 0 \end{cases}$$

from the two prey ZNGIs:

$$P^* = \frac{r_1}{a_1}\left(1 - \frac{N_1^*}{K_1}\right) = \frac{r_2}{a_2}\left(1 - \frac{N_2^*}{K_2}\right)$$

$$\Rightarrow 1 - \frac{N_1^*}{K_1} = \frac{a_1}{r_1}\frac{r_2}{a_2}\left(1 - \frac{N_2^*}{K_2}\right)$$

$$\Rightarrow N_1^* = K_1\left[1 - \frac{a_1}{r_1}\frac{r_2}{a_2}\left(1 - \frac{N_2^*}{K_2}\right)\right]$$

$\Rightarrow$ substitute into predator ZNGIs: $e_1 a_1 N_1^* + e_2 a_2 N_2^* - d = 0$

$$\Rightarrow e_1 a_1\left[K_1 - K_1\frac{a_1}{r_1}\frac{r_2}{a_2} + \frac{a_1}{r_1}\frac{r_2}{a_2}\frac{K_1}{K_2}N_2^*\right] + e_2 a_2 N_2^* = d$$

$$\Rightarrow N_2^* = \frac{d - e_1 a_1 K_1\left(1 - \frac{a_1}{r_1}\cdot\frac{r_2}{a_2}\right)}{e_2 a_2 + e_1 a_1 \frac{K_1}{K_2}\frac{a_1}{r_1}\frac{r_2}{a_2}}$$

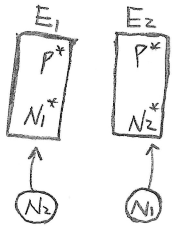
for feasibility numerator should be positive

$$\Rightarrow N_1^* = \frac{d - e_2 a_2 K_2\left(1 - \frac{a_2}{r_2}\frac{r_1}{a_1}\right)}{e_1 a_1 + e_2 a_2 \frac{K_2}{K_1}\frac{a_2}{r_2}\frac{r_1}{a_1}}$$

$$\Rightarrow P^* = \frac{r_1}{a_1}\left(1 - \frac{N_1^*}{K_1}\right)$$

- Graphical analysis: Too difficult for 3D

- Invasion analysis: because it makes senses in this competition sense and because it decrease the dimension



(1) For N_2 to invade E_1:

$$IGR_2 = \lim_{N_2 \to 0} \frac{1}{N_2}\frac{dN_2}{dt}\Big|_{E_1} = r_2\left(1 - \frac{R_2}{K_2}\right) - a_2 P \Big|_{E_1}$$

$$= r_2 - a_2 \cdot \left[\frac{r_1}{a_1}\left(1 - \frac{d}{e_1 a_1 K_1}\right)\right] > 0$$

$$\Rightarrow \frac{r_2}{a_2} > \frac{r_1}{a_1}\left(1 - \underbrace{\frac{d}{e_1 a_1 K_1}}_{N_1^* \text{ scaled by its carrying capacity}}\right)$$

$\frac{r_2}{a_2}$: P^* in exponential model, predation pressure when rare

(2) For N_1 to invade E_2:

$$IGR_1 = \lim_{N_1 \to 0} \frac{1}{N_1}\frac{dN_1}{dt} = r_1 - a_1\left[\frac{r_2}{a_2}\left(1 - \frac{d}{e_2 a_2 K_2}\right)\right] > 0$$

$$\Rightarrow \frac{r_1}{a_1} > \frac{r_2}{a_2}\left(1 - \frac{d}{e_2 a_2 K_2}\right)$$

→ For coexistence, mutual invasability when: $\frac{r_1}{a_1}\left(1 - \frac{d}{e_1 a_1 K_1}\right) < \frac{r_2}{a_2} < \frac{r_1}{a_1}\left(1 - \frac{d}{e_2 a_2 K_2}\right)^{-1}$

If we now go back to the feasibility criterion of the E_c:

- N_1^* feasible when $d - e_2 a_2 K_2\left(1 - \frac{a_2}{r_2}\frac{r_1}{a_1}\right) > 0 \Rightarrow$ when $IGR_1 > 0$
- N_2^* feasible when $d - e_1 a_1 K_1\left(1 - \frac{a_1}{r_1}\frac{r_2}{a_2}\right) > 0 \Rightarrow$ when $IGR_2 > 0$

→ Mutual invasible $\Leftrightarrow$ feasibility of E_c

- Local stability analysis: Now we know coexistence is possible, want to know if stable

$$\frac{\partial f_1}{\partial N_1} = \left[r_1\left(1 - \frac{N_1^*}{K_1}\right) - a_1 P^*\right] + N_1^*\left(\frac{-r_1}{K_1}\right) \;;\; \frac{\partial f_1}{\partial N_2} = 0 \;;\; \frac{\partial f_1}{\partial P} = -a_1 N_1^*$$

$$\frac{\partial f_2}{\partial N_1} = 0 \;;\; \frac{\partial f_2}{\partial N_2} = \left[r_2\left(1 - \frac{N_2^*}{K_2}\right) - a_2 P^*\right] + N_2^*\left(\frac{-r_2}{K_2}\right) \;;\; \frac{\partial f_2}{\partial P} = -a_2 N_2^*$$

$$\frac{\partial f_P}{\partial N_1} = e_1 a_1 P^* \;;\; \frac{\partial f_P}{\partial N_2} = e_2 a_2 P^* \;;\; \frac{\partial f_P}{\partial P} = \left[e_1 a_1 N_1^* + e_2 a_2 N_2^* - d\right]$$

(1) For E_1 $\begin{cases} N_1^* = \frac{d}{e_1 a_1} \\ N_2^* = 0 \\ P^* = \frac{r_1}{a_1}\left(1 - \frac{d}{e_1 a_1 K_1}\right) \end{cases}$ $\Rightarrow J_1 = \begin{bmatrix} -\frac{r_1}{K_1} \cdot N_1^* & 0 & -a_1 N_1^* \\ 0 & r_2 - a_2 P^* & 0 \\ e_1 a_1 P^* & e_2 a_2 P^* & 0 \end{bmatrix}$

$$\Rightarrow \left(-\frac{r_1}{K_1} N_1^* - \lambda\right)\left(r_2 - a_2 P^* - \lambda\right)(-\lambda) - e_1 a_1 P^* \left(r_2 - a_2 P^* - \lambda\right)\left(-a_1 N_1^*\right) = 0$$

$$\Rightarrow \underline{\left[\left(r_2 - a_2 P^*\right) - \lambda\right]} \underbrace{\left[\lambda^2 + \frac{r_1}{K_1} N_1^* \cdot \lambda + e_1 a_1^2 N_1^* P^*\right]}_{\text{gives two roots with negative real parts when } E_1 \text{ feasible}} = 0$$

$$\lambda = r_2 - a_2 P^*$$
$$= r_2 - a_2 \cdot \left[\frac{r_1}{a_1}\left(1 - \frac{d}{e_1 a_1 K_1}\right)\right] = IGR_2$$

$\Rightarrow$ If $IGR_2 < 0$, N_2 cannot invade, E_1 is stable

If $IGR_2 > 0$, N_2 can invade, E_1 is unstable

(2) For E_2 $\begin{cases} N_1^* = 0 \\ N_2^* = \frac{d}{e_2 a_2} \\ P^* = \frac{r_2}{a_2}\left(1 - \frac{d}{e_2 a_2 K_2}\right) \end{cases}$ $\Rightarrow J_2 = \begin{bmatrix} r_1 - a_1 P^* & 0 & 0 \\ 0 & -\frac{r_2}{K_2} N_2^* & -a_2 N_2^* \\ e_1 a_1 P^* & e_2 a_2 P^* & 0 \end{bmatrix}$

$$\Rightarrow \left(r_1 - a_1 P^* - \lambda\right)\left(-\frac{r_2}{K_2} N_2^* - \lambda\right)(-\lambda) - e_2 a_2 P^* \left(-a_2 N_2^*\right)\left(r_1 - a_1 P^* - \lambda\right) = 0$$

$$\Rightarrow \underline{\left[\left(r_1 - a_1 P^*\right) - \lambda\right]} \underbrace{\left[\lambda^2 + \frac{r_2}{K_2} N_2^* \lambda + e_2 a_2^2 P^* N_2^*\right]}_{\text{gives two negative roots}} = 0$$

$$\lambda = r_1 - a_1 P^*$$
$$= r_1 - a_1 \left[\frac{r_2}{a_2}\left(1 - \frac{d}{e_2 a_2 K_2}\right)\right] = IGR_1$$

$\Rightarrow$ If $IGR_1 < 0$, N_1 cannot invade, E_2 is stable

If $IGR_1 > 0$, N_1 can invade, E_2 is unstable

(3) For E_c $\begin{cases} N_1^* > 0 \\ N_2^* > 0 \\ P^* > 0 \end{cases}$ $\Rightarrow J_c = \begin{bmatrix} -\frac{r_1}{K_1}N_1^* & 0 & -a_1N_1^* \\ 0 & -\frac{r_2}{K_2}N_2^* & -a_2N_2^* \\ e_1a_1P^* & e_2a_2P^* & 0 \end{bmatrix}$

$$\Rightarrow \left(-\frac{r_1}{K_1}N_1^*-\lambda\right)\left(\lambda^2+\frac{r_2}{K_2}N_2^*\lambda\right) - e_1a_1P^*\left(\frac{r_2}{K_2}N_2^*+\lambda\right)a_1N_1^* - e_2a_2P^*\left(\frac{r_1}{K_1}N_1^*+\lambda\right)a_2N_2^* = 0$$

$$\Rightarrow \underbrace{\lambda^3}_{a_3} + \underbrace{\left[\frac{r_1}{K_1}N_1^*+\frac{r_2}{K_2}N_2^*\right]}_{a_2}\lambda^2 + \underbrace{\left[\frac{r_1}{K_1}\frac{r_2}{K_2}N_1^*N_2^* + e_1a_1^2N_1^*P^* + e_2a_2^2N_2^*P^*\right]}_{a_1}\lambda + \underbrace{\left[e_1a_1^2\frac{r_2}{K_2}+e_2a_2^2\frac{r_1}{K_1}\right]N_1^*N_2^*P^*}_{a_0} = 0$$

※ Routh-Hurwitz stability criterion (1876)

↘ a criteria to determine whether all roots of the characteristic equation of a dynamic system has negative real parts

1. for 2^{nd} order: $a_2\lambda^2 + a_1\lambda + a_0 = 0 \longrightarrow$ all $a_i > 0$ (根与係数)
2. for 3^{rd} order: $a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0 \longrightarrow \begin{cases} \text{all } a_i > 0 \\ a_2a_1 > a_3a_0 \end{cases}$
3. for 4^{th} order: $a_4\lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0 \longrightarrow \begin{cases} \text{all } a_i > 0 \\ a_3a_2 > a_4a_1 \\ a_3a_2a_1 > a_4a_1^2 + a_3^2a_0 \end{cases}$

$\Rightarrow$ when E_c is feasible, $a_i > 0$

$a_2a_1 - a_3a_0$

$$= \left[\frac{r_1}{K_1}N_1^*+\frac{r_2}{K_2}N_2^*\right]\left[\frac{r_1}{K_1}\frac{r_2}{K_2}N_1^*N_2^* + e_1a_1^2N_1^*P^* + e_2a_2^2N_2^*P^*\right] - \left[e_1a_1^2\frac{r_2}{K_2}N_1^*N_2^*P^* + e_2a_2^2\frac{r_1}{K_1}N_1^*N_2^*P^*\right]$$

will be greater than zero if E_c is feasible, therefore if E_c is feasible, it is stable

$\Rightarrow$ Mutual invasible $\Leftrightarrow$ feasibility of E_c $\Leftrightarrow$ E_c locally stable

or

N_i cannot invade E_j $\Leftrightarrow$ E_c not feasible $\Leftrightarrow$ E_j locally stable

$N_1 \to \boxed{N_2^* \ P^*}$ E_2

$N_2 \to \boxed{N_1^* \ P^*}$ E_1

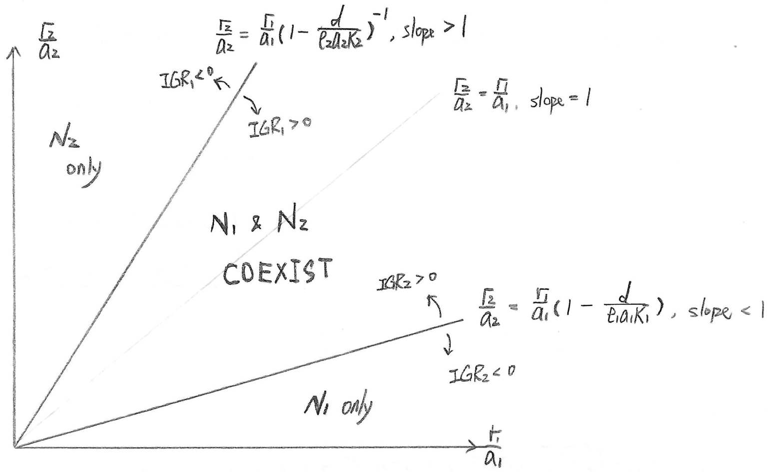
	✓	X
✓	Coexist E_c	N_2 only E_2
X	N_1 only E_1	NA

NA → cannot $\frac{r_2}{a_2} < \frac{r_1}{a_1}\left(1-\frac{d}{e_1 a_1 K_1}\right)$

and $\frac{r_1}{a_1} < \frac{r_2}{a_2}\left(1-\frac{d}{e_2 a_2 K_2}\right)$

at the same time

« A parameter space »



carrying capacity limits predator density, thereby less indirect negative effect on each other, allowing coexistence. As K_1 & $K_2 \to \infty$, the two invasion boundary lines collaspe to the diagonal and we're back to the P^* rule with no coexistence