

# English support for the course on difference equations (3)

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**For all details, refer to Elaydi S. 2005.**

***An introduction to difference equations***

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# Non linear discrete systems in 2D

$$\begin{cases} x_{n+1} = f(x_n, y_n) \\ y_{n+1} = g(x_n, y_n) \end{cases} \Leftrightarrow \begin{cases} x_{n+1} = x_n \\ y_{n+1} = y_n \end{cases} \Leftrightarrow \begin{cases} x^* = f(x^*, y^*) \\ y^* = g(x^*, y^*) \end{cases}$$

$$\begin{cases} u_{n+1} = x_{n+1} - x^* = f(x_n, y_n) - x^* \\ v_{n+1} = y_{n+1} - y^* = g(x_n, y_n) - y^* \end{cases}$$

$$\begin{cases} f(x_n, y_n) = f(x^*, y^*) + \frac{\partial f}{\partial x_n} \Big|_* \underbrace{(x_n - x^*)}_{u_n} + \frac{\partial f}{\partial y_n} \Big|_* \underbrace{(y_n - y^*)}_{v_n} + \dots \\ g(x_n, y_n) = g(x^*, y^*) + \frac{\partial g}{\partial x_n} \Big|_* u_n + \frac{\partial g}{\partial y_n} \Big|_* v_n + \dots \\ u_{n+1} = \underbrace{f(x^*, y^*) - x^*}_{=0} + \frac{\partial f}{\partial x_n} \Big|_* u_n + \frac{\partial f}{\partial y_n} \Big|_* v_n + \dots \\ v_{n+1} = \underbrace{g(x^*, y^*) - y^*}_{=0} + \frac{\partial g}{\partial x_n} \Big|_* u_n + \frac{\partial g}{\partial y_n} \Big|_* v_n + \dots \\ u_{n+1} \approx \frac{\partial f}{\partial x_n} \Big|_* u_n + \frac{\partial f}{\partial y_n} \Big|_* v_n + \dots \\ v_{n+1} \approx \frac{\partial g}{\partial x_n} \Big|_* u_n + \frac{\partial g}{\partial y_n} \Big|_* v_n + \dots \end{cases}$$

$$\begin{pmatrix} u_{n+1} \\ v_{n+1} \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} u_n \\ v_n \end{pmatrix} \Leftrightarrow \begin{pmatrix} u_{n+1} \\ v_{n+1} \end{pmatrix} = \mathbf{A}^* \begin{pmatrix} u_n \\ v_n \end{pmatrix} \quad \mathbf{A}^* = \begin{pmatrix} \frac{\partial f}{\partial x_n} \Big|_{(x^*, y^*)} & \frac{\partial f}{\partial y_n} \Big|_{(x^*, y^*)} \\ \frac{\partial g}{\partial x_n} \Big|_{(x^*, y^*)} & \frac{\partial g}{\partial y_n} \Big|_{(x^*, y^*)} \end{pmatrix}$$

# Local stability of a fixed point

**Theorem:** A fixed point from the previous system will be locally asymptotically stable if the modulus of all eigenvalues of  $\mathbf{A}^*$  is strictly less than 1.

$$\lambda^2 - \text{tr}\mathbf{A}^* \lambda + \det \mathbf{A}^* = 0$$

$$\Delta = (\text{tr}\mathbf{A}^*)^2 - 4\det\mathbf{A}^*$$

Let suppose that  $\Delta > 0$ .

$$\begin{cases} \lambda_1 = \frac{\text{tr}\mathbf{A}^*}{2} + \frac{1}{2}\sqrt{(\text{tr}\mathbf{A}^*)^2 - 4\det\mathbf{A}^*} \\ \lambda_2 = \frac{\text{tr}\mathbf{A}^*}{2} - \frac{1}{2}\sqrt{(\text{tr}\mathbf{A}^*)^2 - 4\det\mathbf{A}^*} \end{cases}$$

Let  $\text{tr}\mathbf{A}^* = \beta$  and  $\det\mathbf{A}^* = \gamma$

$$\lambda_{1,2} = \frac{\beta}{2} \pm \frac{\sqrt{\Delta}}{2}$$

$$\Delta = \beta^2 - 4\gamma (> 0).$$

# Local stability of a fixed point (*continued*)

$$d_1 = \lambda_1 - \frac{\beta}{2} = \frac{1}{2}\sqrt{\beta^2 - 4\gamma} = \frac{\sqrt{\Delta}}{2}$$

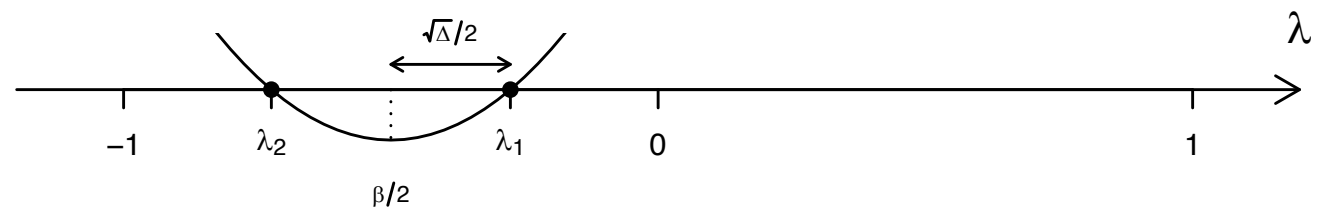
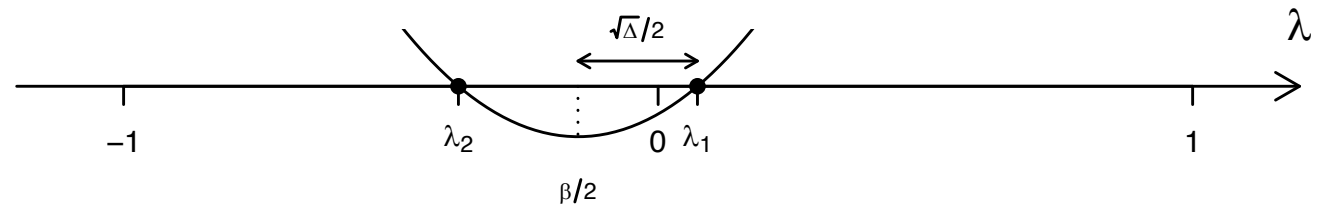
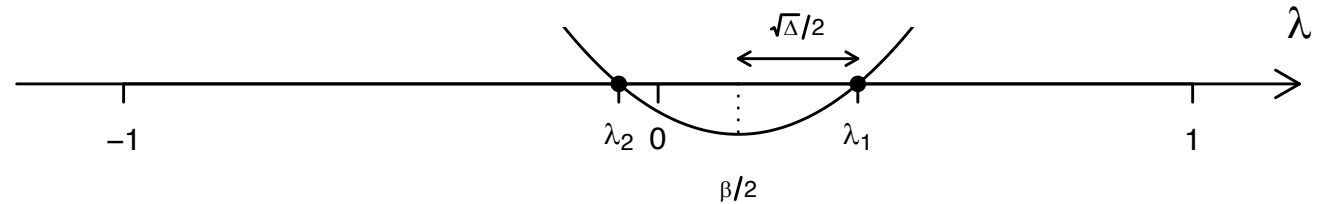
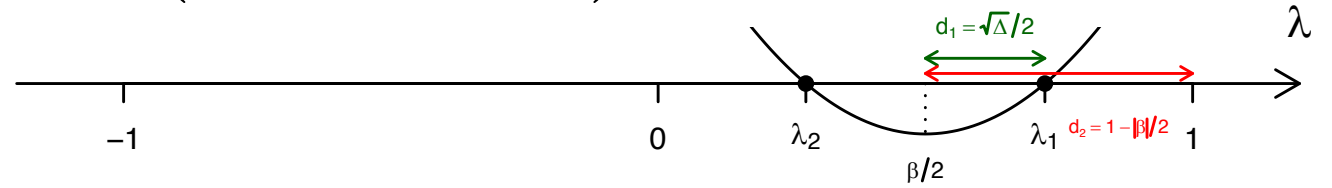
$$d_2 = 1 - \frac{|\beta|}{2}$$

**Stability conditions:**

(i)  $-1 < \frac{\beta}{2} < 1 \Leftrightarrow \left| \frac{\beta}{2} \right| < 1 \Leftrightarrow |\beta| < 2$

(ii)  $d_2 > d_1 \Leftrightarrow 1 - \frac{|\beta|}{2} > \frac{\sqrt{\beta^2 - 4\gamma}}{2}$   
 $\Leftrightarrow \left(1 - \frac{|\beta|}{2}\right)^2 > \left(\frac{\sqrt{\beta^2 - 4\gamma}}{2}\right)^2$   
 $\Leftrightarrow 1 - |\beta| + \frac{\beta^2}{4} > \frac{\beta^2 - 4\gamma}{4}$   
 $\Leftrightarrow 1 + \gamma > |\beta|$

(iii)  $\gamma = \lambda_1 \lambda_2 < 1$   
 $1 + \gamma < 2$



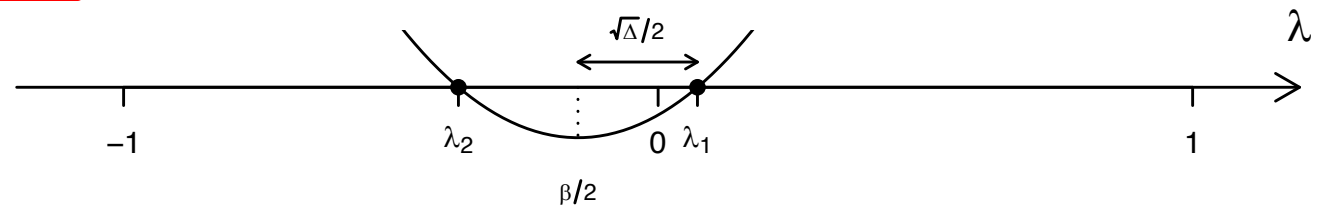
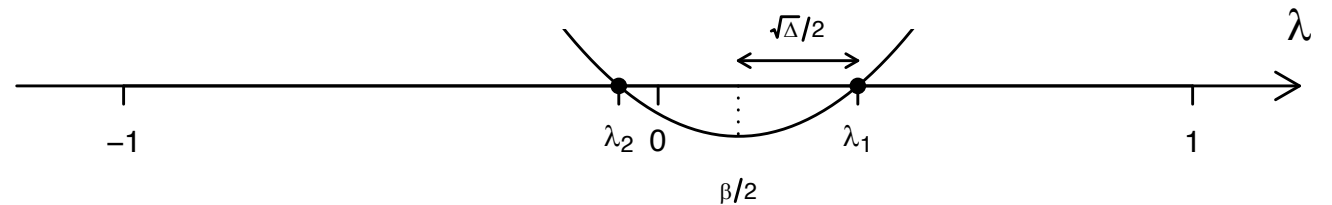
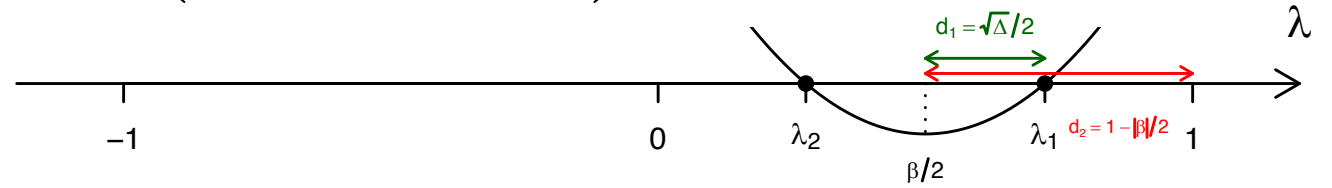
# Local stability of a fixed point (*continued*)

$$d_1 = \lambda_1 - \frac{\beta}{2} = \frac{1}{2}\sqrt{\beta^2 - 4\gamma} = \frac{\sqrt{\Delta}}{2}$$

$$d_2 = 1 - \frac{|\beta|}{2}$$

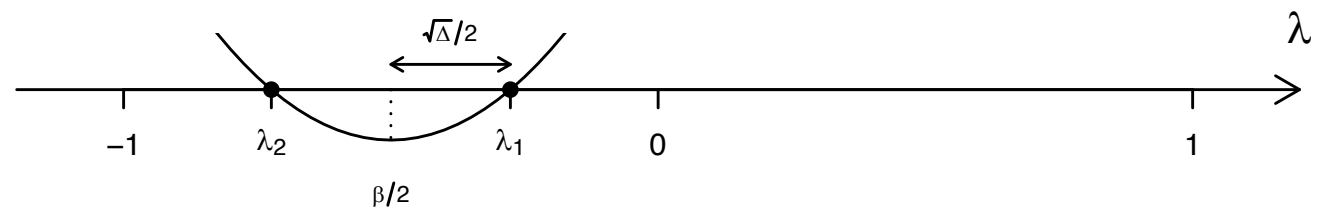
Stability conditions:

$$|\beta| < 1 + \gamma < 2 \Leftrightarrow |\text{tr}A^*| < 1 + \det A^* < 2$$



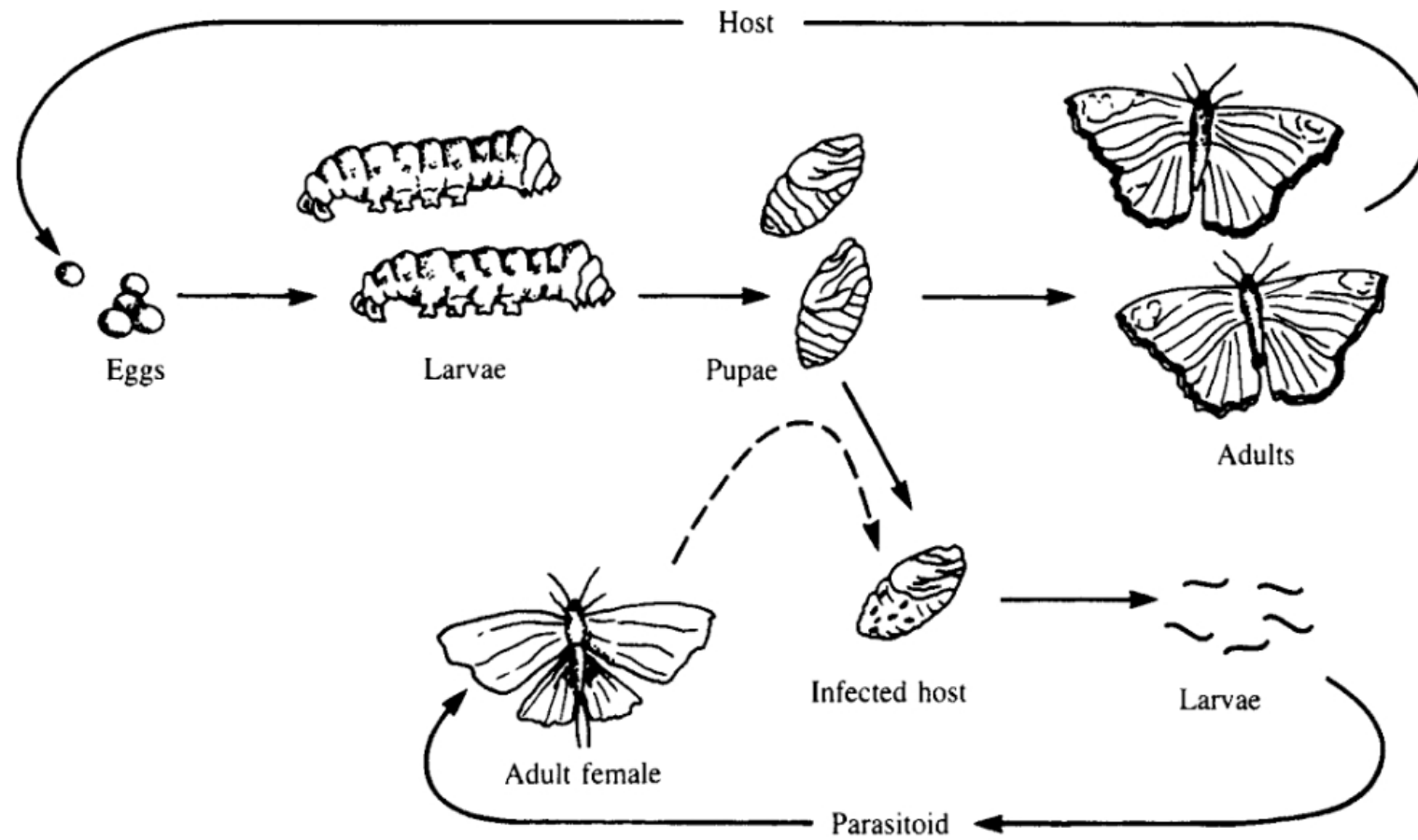
Example

$$x(n+1) = \frac{\alpha x(n)}{1 + \beta x(n)}$$



# Host-parasitoid systems

*Applications of Nonlinear Difference Equations to Population Biology*



**Figure** Schematic representation of a host-parasitoid system. The adult female parasitoid deposits eggs on or in either larvae or pupae of the

host. Infected hosts die, giving rise to parasitoid progeny. Uninfected hosts may develop into adults and give rise to the next generation of hosts.

# Utida (1957): *Heteropsilus prosopilus* vs *Callosobruchus chinensis*

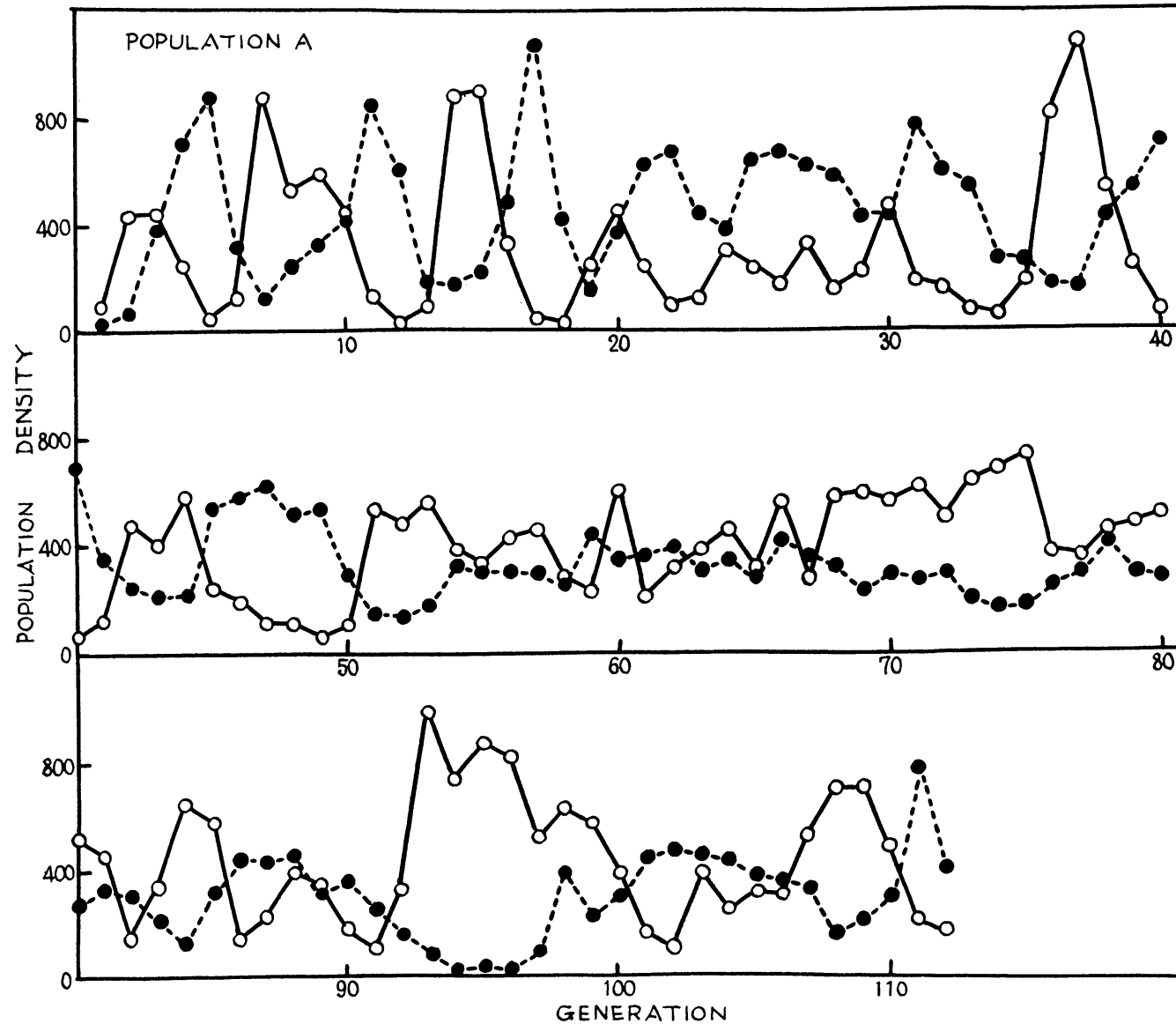


FIG. 1. Fluctuation of population density from generation to generation in population A. Host population:—○—, Parasite population: ----●----

# Host-parasitoid models

$$H_{t+1} = RH_t f(H_t, P_t)$$

$$P_{t+1} = cH_t [1 - f(H_t, P_t)]$$

- $H_t$  is the female density of hosts at time  $t$ ;
- $P_t$  is the female density of parasitoids at time  $t$ ;
- $R$  is the net fecundity of host females (x sex-ratio) ;
- $c$  is the net fecundity of parasitoids, i.e., the mean number of parasitoid females that emerge from a unique host female and that survive until the next time step (x sex-ratio);
- $f(H_t, P_t)$  is the fraction of non-parasitized host females which depends on the encounter probability between hosts and parasitoids.



# The Nicholson-Bailey's model (1935)

- Developed before Utida's data who tried to check the model.
- Hypotheses:
  - Exponential growth for hosts (parameter  $R$ );
  - The functional response, *i.e.* the nbr of attacks per parasitoid is proportional to the host density with coefficient  $a =$  search efficiency of host per parasitoid that leads to infection (supposed to be constant).
- Parameter  $a$  is supposed to be constant:
  - Independent from host nbr (exponential growth, parameter  $R$ );
  - Independent from parasitoid nbr (no competition, no avoidance of host already parasitized).

# The Nicholson-Bailey's model (*continued*)

- Be  $X$  the random variable of the number of attacks per host.
- The total number of attacks within a population is  $aH_tP_t$ , with  $aH_t$  the number of attacks per parasitoid.
- $X$  can be described by a binomial distribution:

$$X \sim \mathcal{B}\left(aH_tP_t, \frac{1}{H_t}\right)$$

- If the spatial distribution of attacks on the  $H_t$  host is random, then  $1/H_t$  is the probability of attack per host.
- We can reasonably consider that  $H_t$  and  $P_t$  are high numbers, so that  $aH_tP_t$  is high and  $1/H_t$  is small.
- Then we can approximate the binomial law by a Poisson's law with parameter  $\mu = aH_tP_t \times \frac{1}{H_t} = aP_t$  :

$$X \sim \mathcal{P}(aP_t)$$

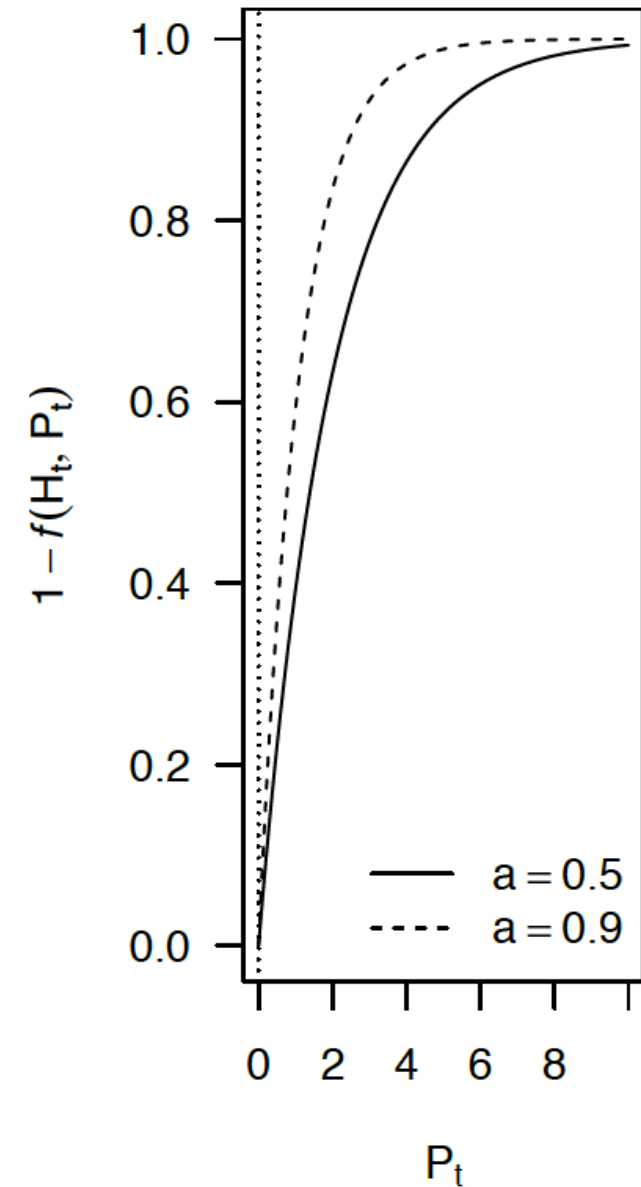
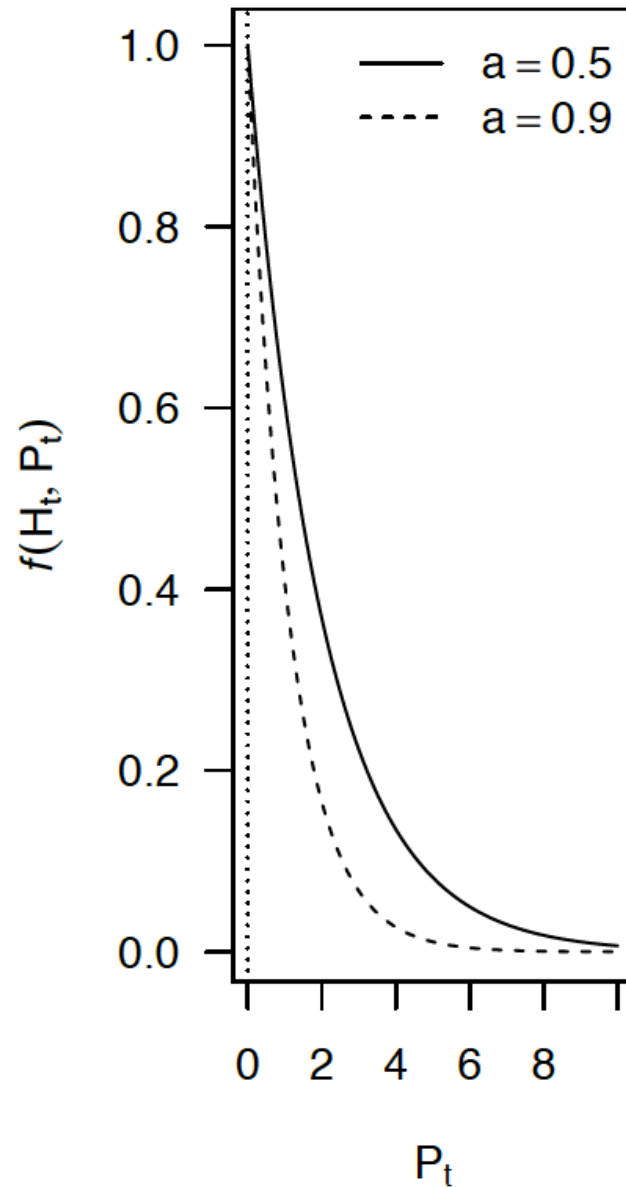
# The Nicholson-Bailey's model (*continued*)

$$p(X = k) = \frac{e^{-\mu} \mu^k}{k!}$$

$$f(H_t, P_t) = p(X = 0)$$

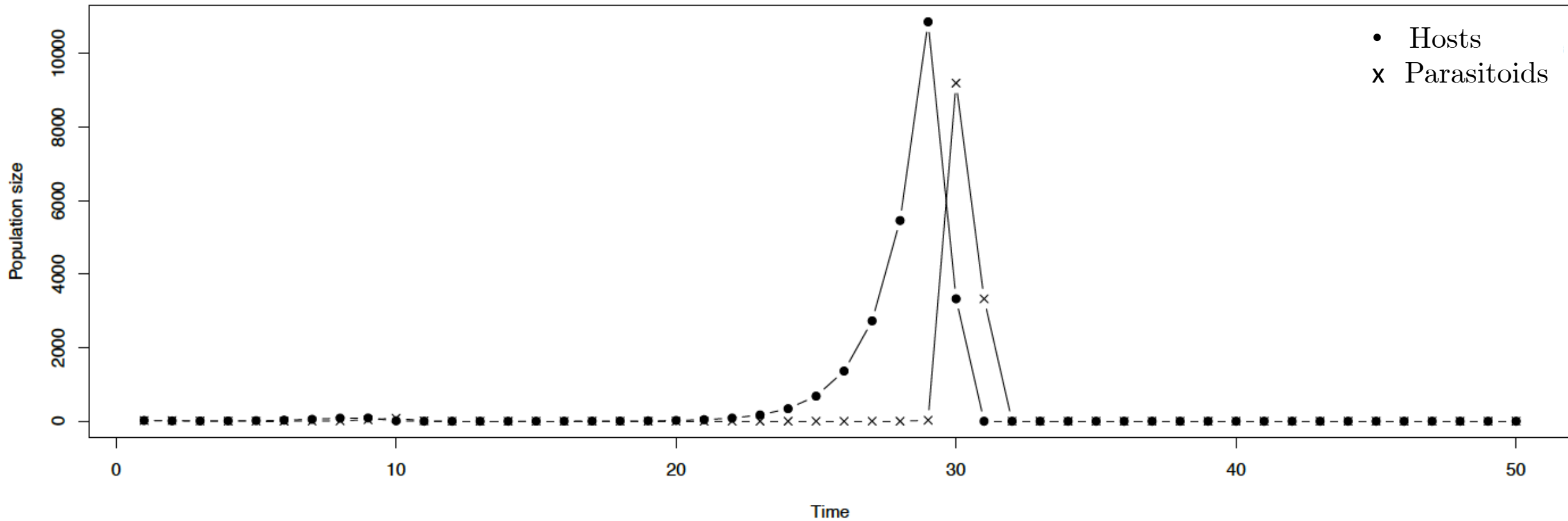
$$f(H_t, P_t) = e^{-\mu} = e^{-aP_t}$$

$$\begin{cases} H_{t+1} = RH_t e^{-aP_t} \\ P_{t+1} = cH_t (1 - e^{-aP_t}) \end{cases}$$



# The Nicholson-Bailey's model (*continued*)

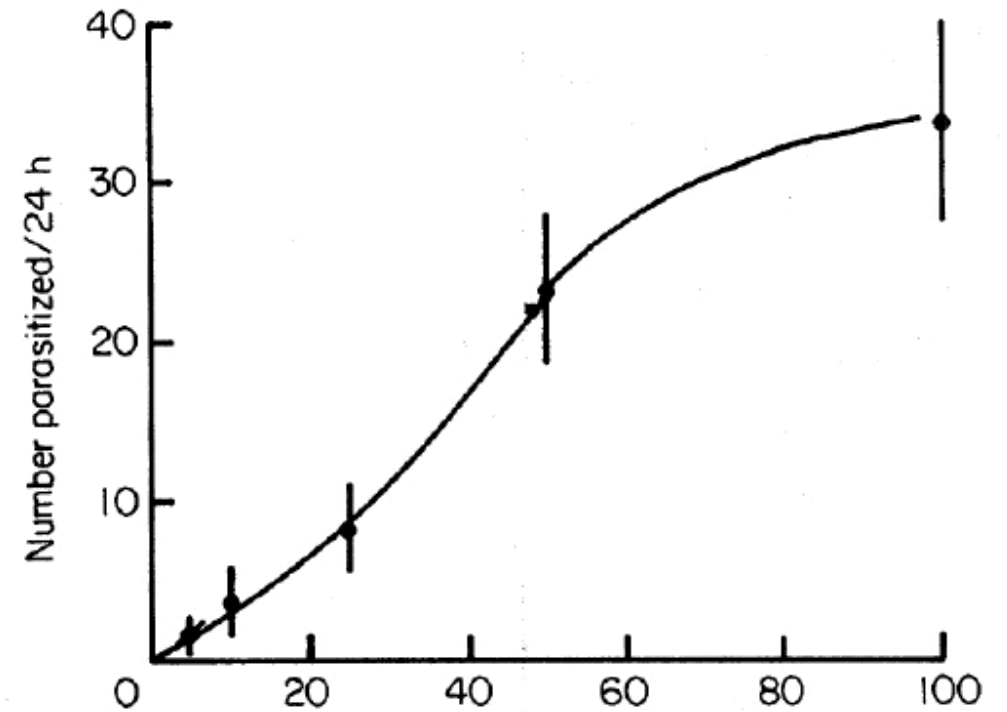
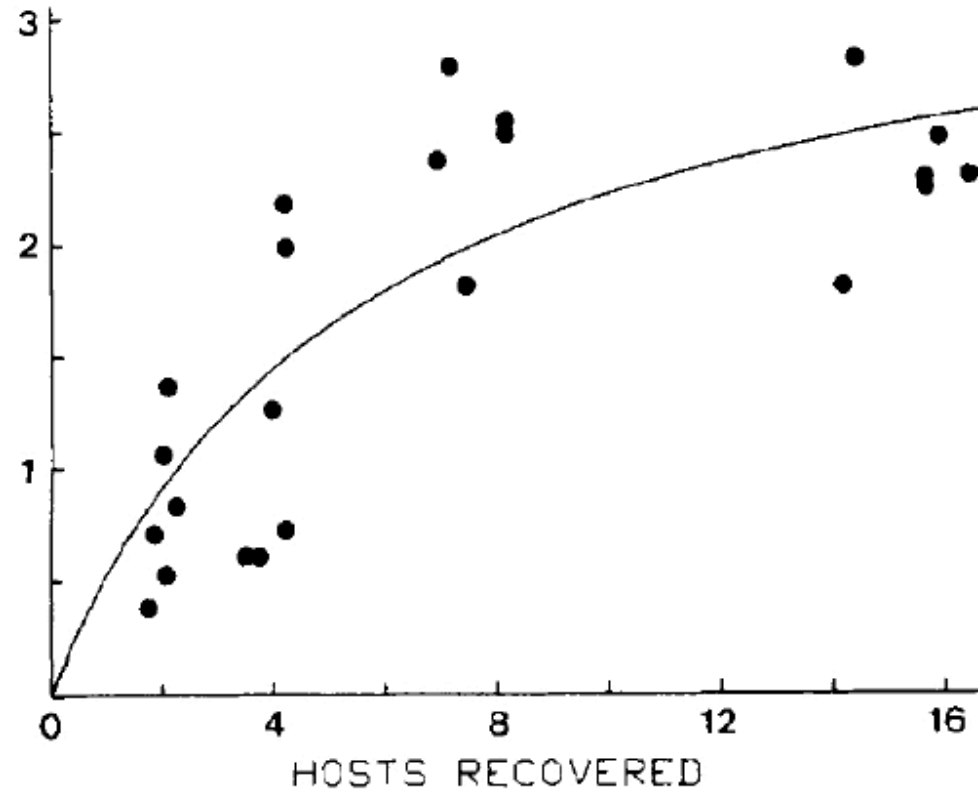
- Fixed points
- Stability



# Modifications of the Nicholson-Baileys model (1)

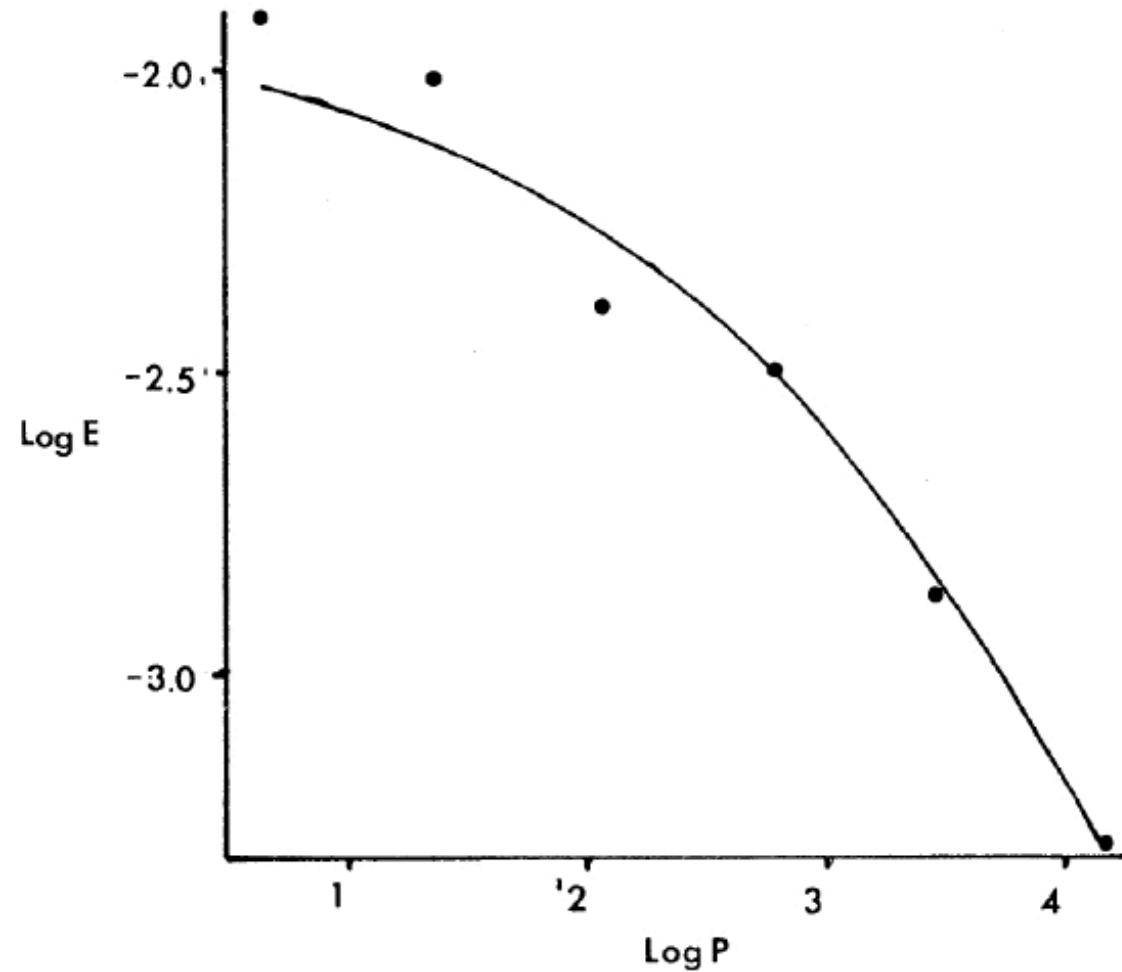
- Change in the functional response

EGGS LAID PER OBSERVATION



# Modifications of the Nicholson-Baileys model (2)

- Change in parameter  $a$ : dependent on  $P_t$



# Modifications of the Nicholson-Baileys model (3)

- Change in the spatial distribution of hosts: not random, not homogeneous
- Change in the growth model for hosts

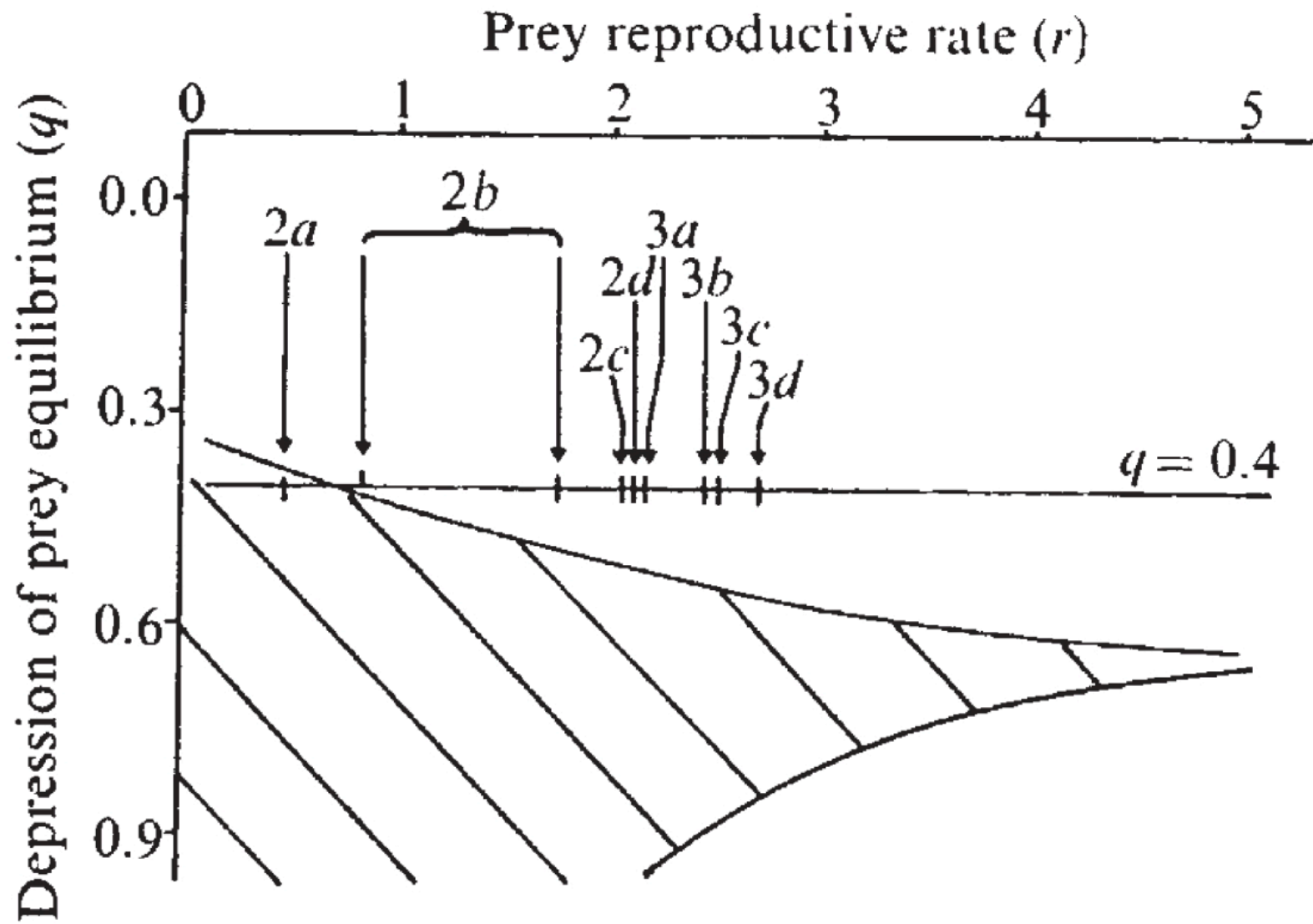
→ Beddington et al. (1975)

$$\begin{cases} H_{t+1} = e^{r(1-H_t/K)} H_t e^{-aP_t} = H_t e^{r(1-H_t/K)-aP_t} \\ P_{t+1} = cH_t (1 - e^{-aP_t}) \end{cases}$$

Link with the Nicholson-Bailey's model:  $r = \ln R$ .

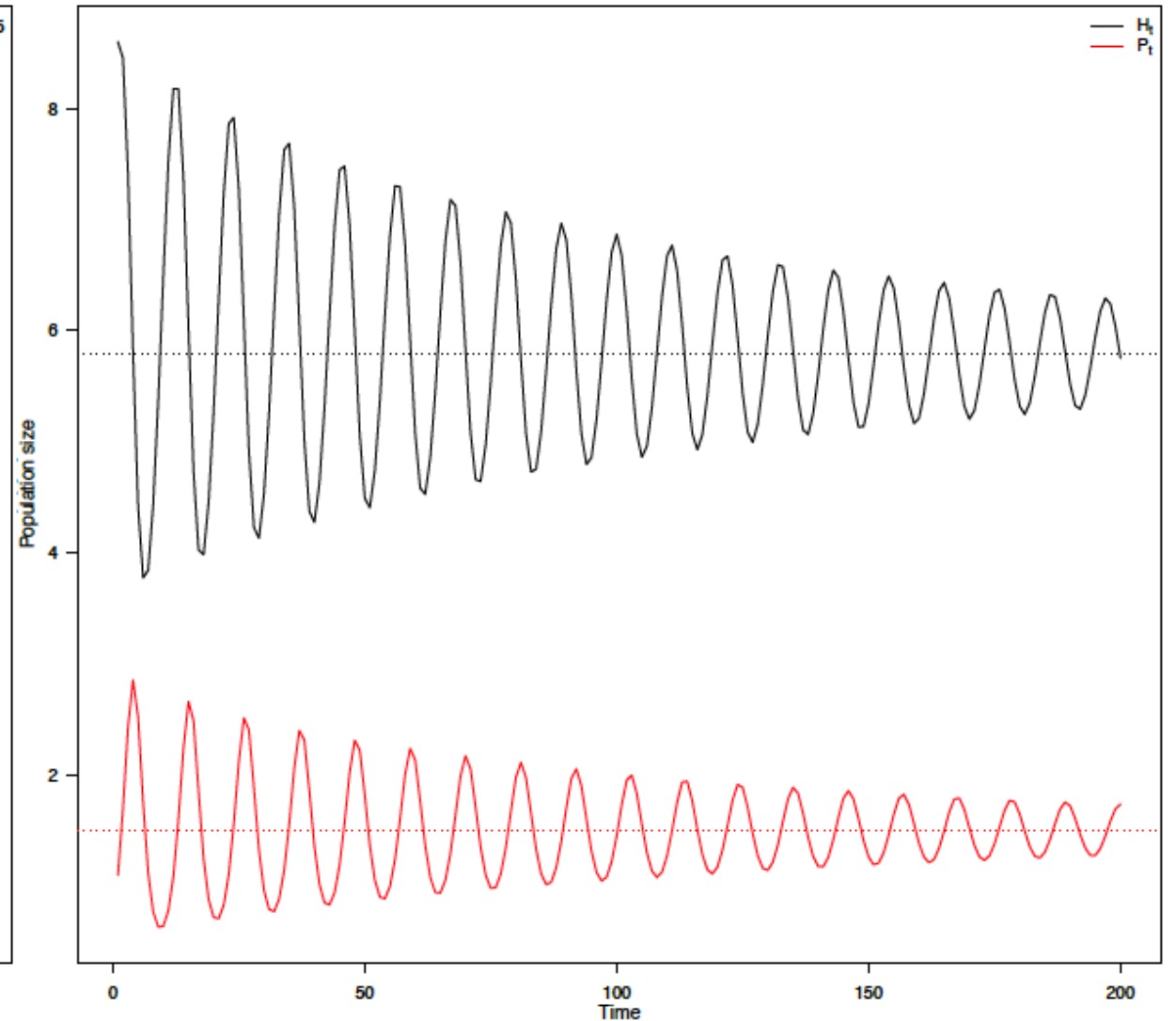
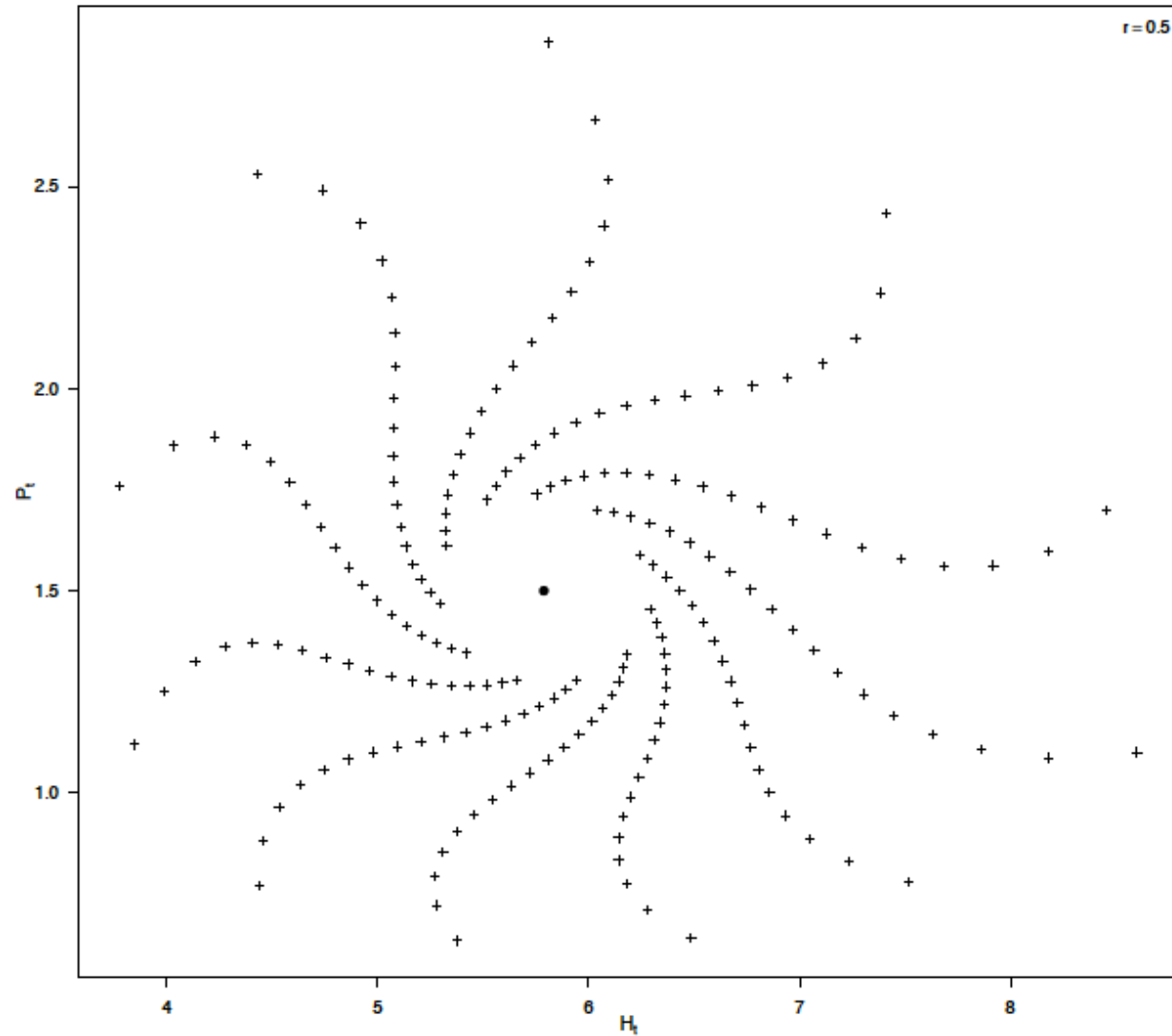
# The Beddington's model

$$q = H^*/K$$

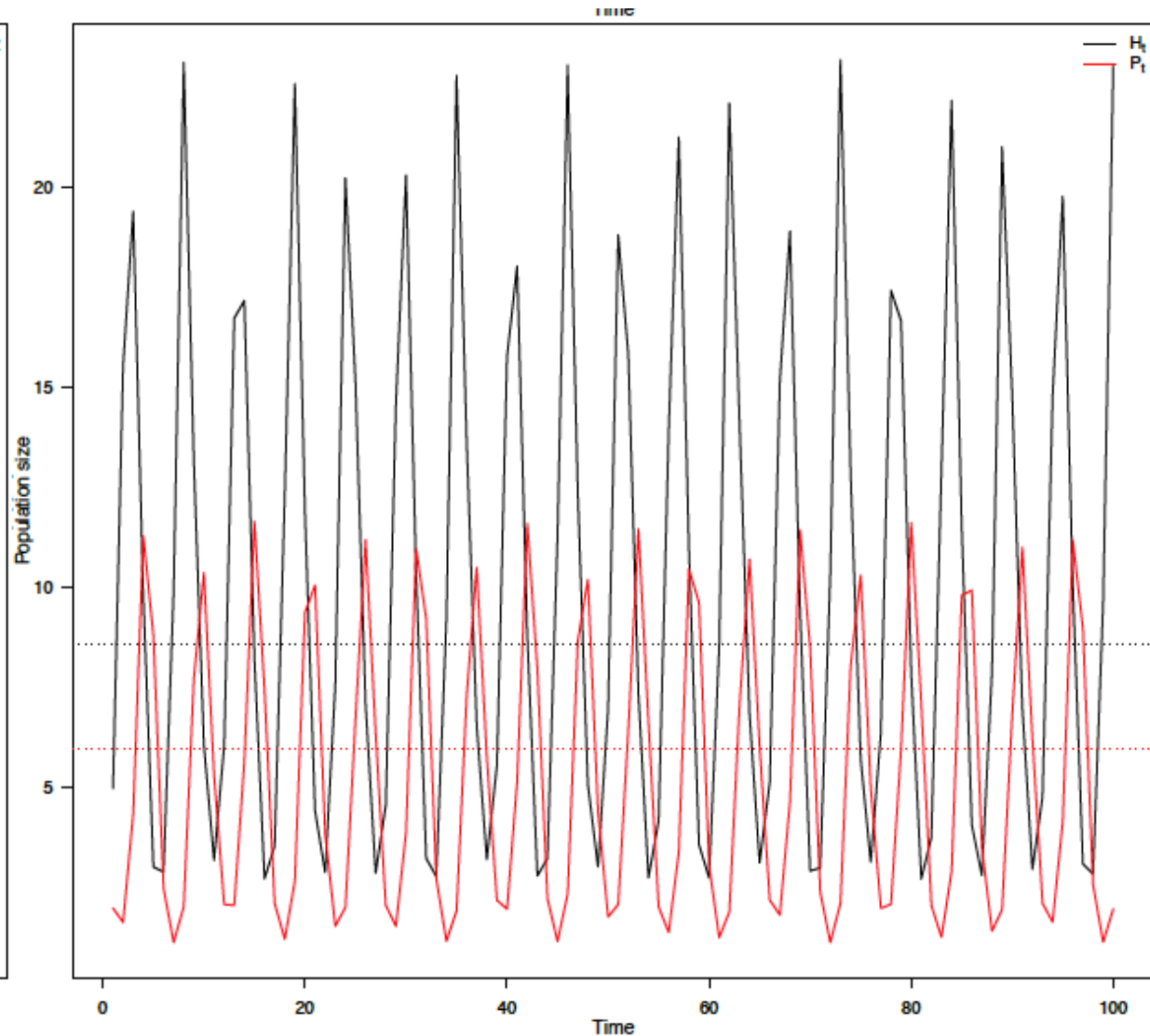
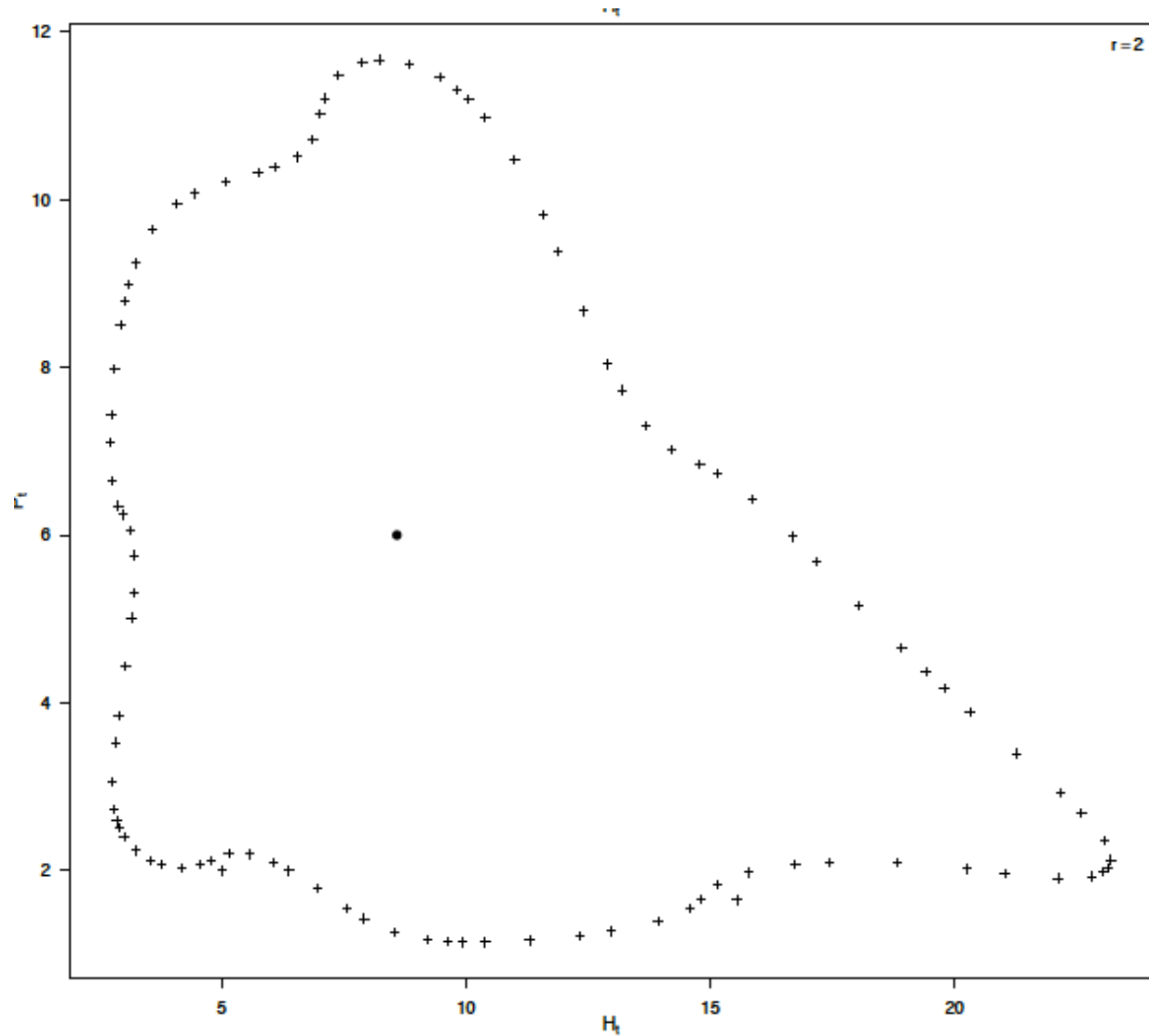




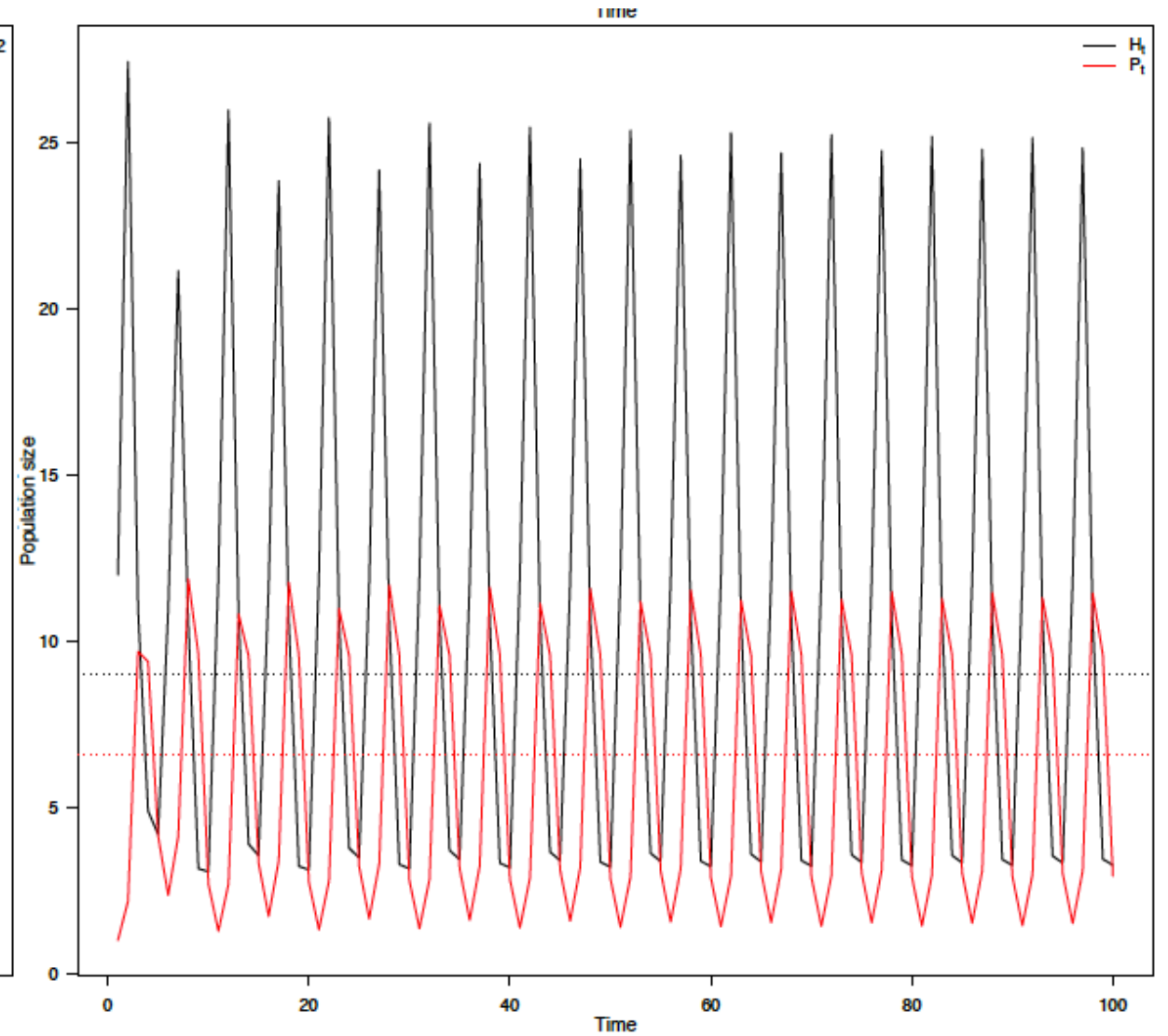
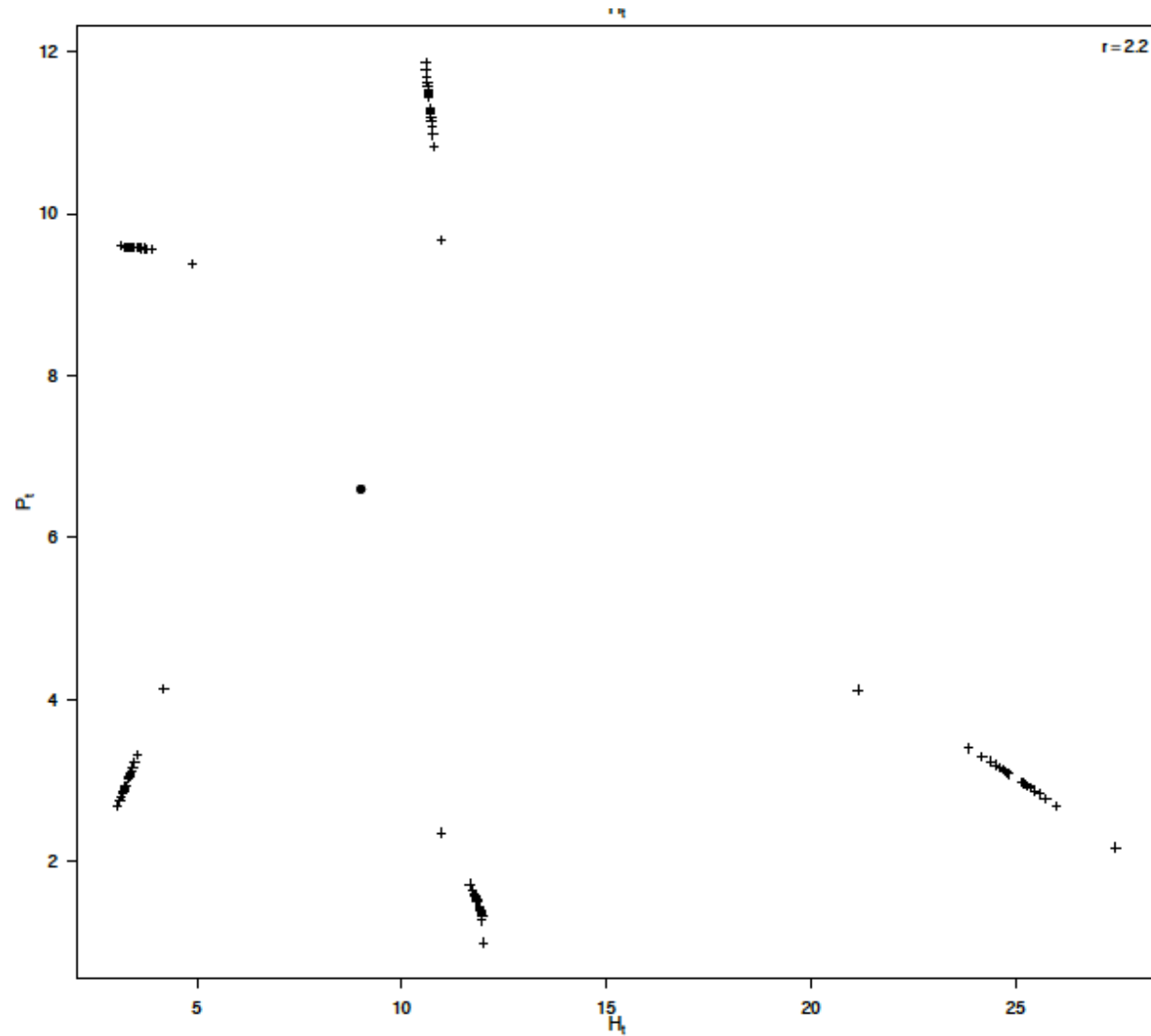
# The Beddington's model: (1) $r = 0.5$



# The Beddington's model: (1) $r = 2$

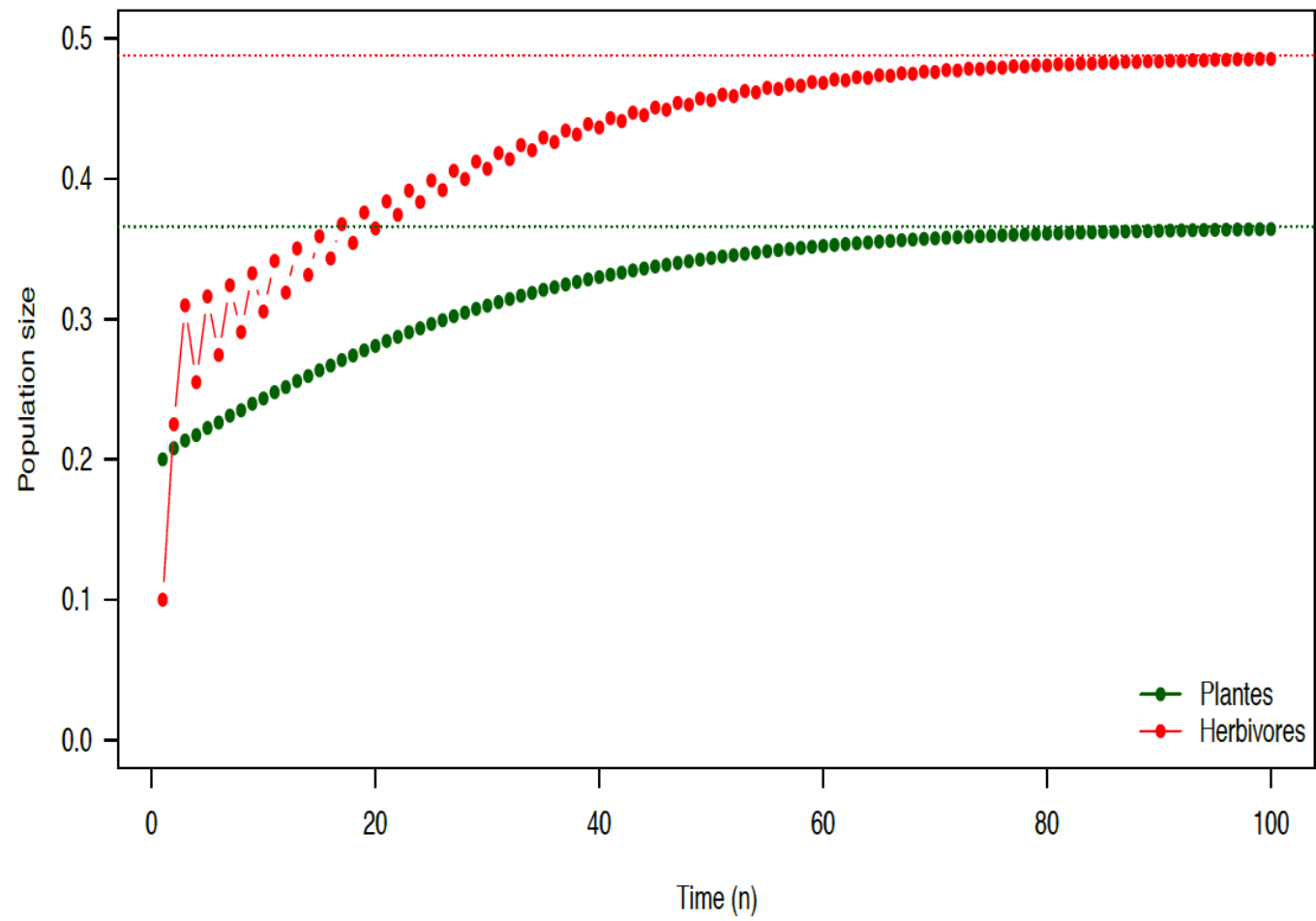
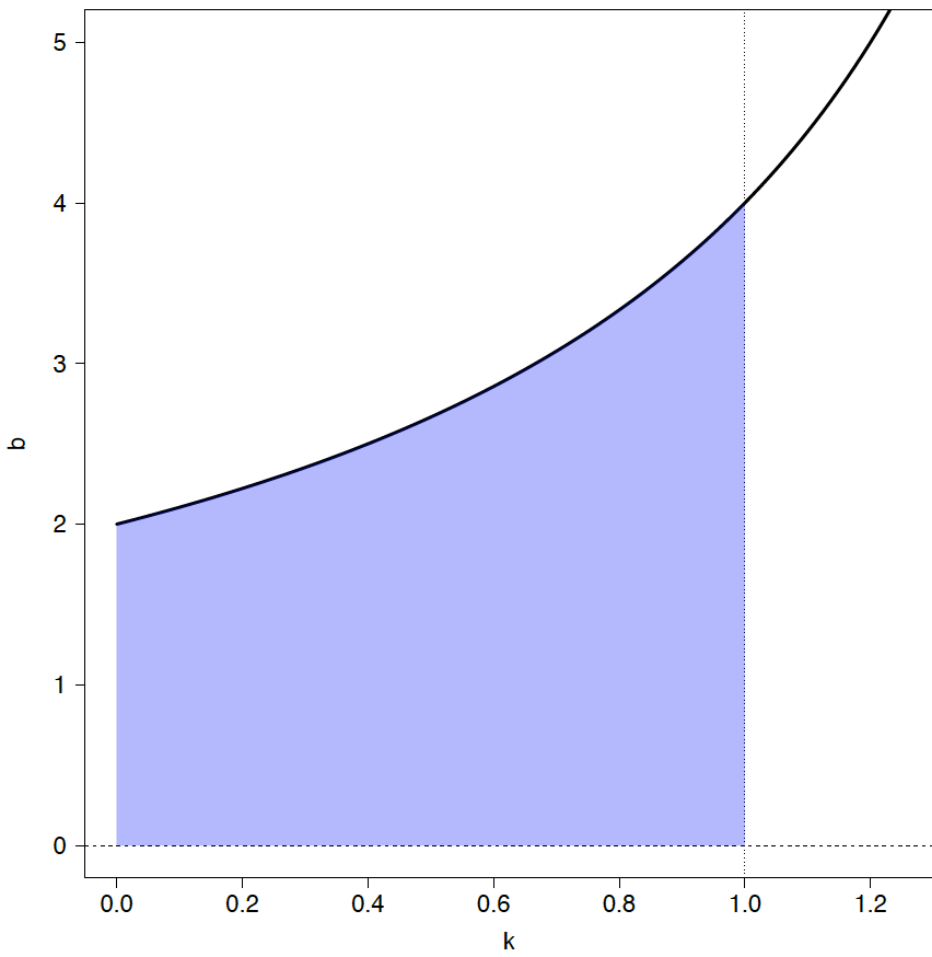


# The Beddington's model: (1) $r = 2.2$



# Plants-herbivores interaction

$$\begin{cases} v_{n+1} = f v_n e^{-a h_n} \\ h_{n+1} = r h_n \left( \delta - \frac{h_n}{v_n} \right) \end{cases}$$



# Hardy-Weinberg's law

		Pères				
		Génotypes	<i>AA</i>	<i>Aa</i>	<i>aa</i>	
		Génotypes	Fréquence	<i>u</i>	<i>v</i>	<i>w</i>
Mères	<i>AA</i>	<i>u</i>	$u^2$	$uv$	$uw$	
	<i>Aa</i>	<i>v</i>	...	$v^2$	...	
	<i>aa</i>	<i>w</i>	...	...	...	

# Hardy-Weinberg's law

		Fréquence des génotypes des descendants		
Type des parents	Fréquence	$AA$	$aA$	$aa$
$AA \times AA$	$u^2$	$u^2$	...	...
$AA \times Aa$	$2uv$	$uv$	$uv$	...
$AA \times aa$	...	0	...	...
$Aa \times Aa$	$v^2$	$v^2/4$	$v^2/2$	$v^2/4$
$Aa \times aa$	...	0	...	...
$aa \times aa$	...	0	...	...
	<b>TOTAL</b>	$u^2 + uv + v^2/4$	...	...