Dr. J. Reinhardt Summer semester 2009

Nonlinear Dynamics and Complex Systems

Solutions No. 1

Population Dynamics

1. Predator-Prey Model

a) The development of a population is determined by its net reproduction rate r. Assuming a continuous real-valued population N and continuous-time dynamics the equation of motion is $\dot{N} = r\,N$. A positive constant reproduction rate $r = \text{const}$ leads to exponential growth (population explosion). Realistically r will depend on the population size(s), introducing nonlinearity and interactions. For the rabbit/foxes system we can interpret the terms in (1), (2):

a: reproduction rate of the rabbits
b: rabbits are killed by foxes
c: foxes multiply if food (rabbits) is availabe
d: foxes die off without food (negative reproduction rate)

b) The ansatz $N_1 = c_1 x$, $N_2 = c_2 y$, $t = c_3 \tau$ leads to

$$\frac{dx}{d\tau} = c_3 a x \Big(1 - \frac{b}{a} c_2 y\Big) \quad , \quad \frac{dy}{d\tau} = c_3 d y \Big(\frac{c}{d} c_1 x - 1\Big) .$$

This simplifies to (3), (4) if we choose $c_1 = d/c$, $c_2 = a/b$, and $c_3 = 1/a$, $\alpha = d/a$.

c) The fixed points are $\vec{x}_1^* = (0,0)$ and $\vec{x}_2^* = (1,1)$. The Jacobian reads

$$\underline{M} = \begin{pmatrix} 1-y & -x \\ \alpha y & \alpha(x-1) \end{pmatrix}$$

The first fixed point $(0,0)$ is a *saddle point* (instable):

$$\underline{M}_1 = \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix} \qquad \rightarrow \qquad \text{characteristic values: } \lambda_1 = 1, \lambda_2 = -\alpha \ .$$

The second fixed point $(1,1)$ is a *center* (neutrally stable):

$$\underline{M}_2 = \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix} \qquad \rightarrow \qquad s = 0, d = \alpha \qquad \rightarrow \qquad \text{characteristic values: } \lambda_{1,2} = \pm i\sqrt{\alpha}$$

d) The phase space curves are determined by $\dfrac{dy}{dx} = \dfrac{\dot{y}}{\dot{x}} = \alpha \dfrac{y(x-1)}{x(1-y)}$. Separation of the variables and analytical integration leads to a transcendental equation

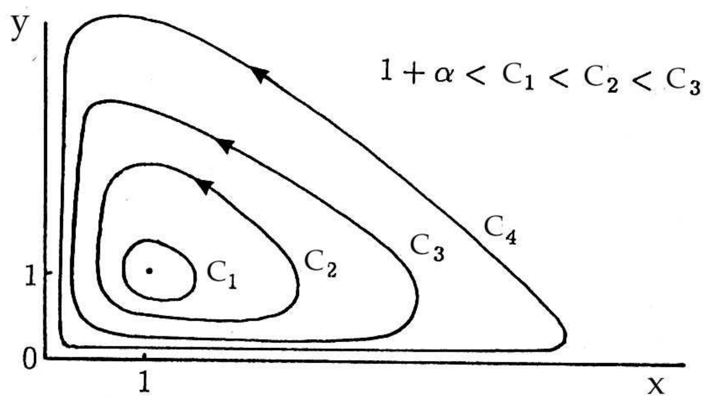
$$\begin{aligned} dx\alpha\left(1-\frac{1}{x}\right) &= dy\left(\frac{1}{y}-1\right) , \\ \alpha(x-\ln x) &= \ln y - y + C \\ \alpha x + y - \ln(x^\alpha y) &= C \ . \end{aligned}$$

The function $g(x, y) = \alpha x + y - \ln(x^\alpha y)$ has an extremum where the partial derivatives vanish:

$$\frac{\partial g}{\partial x} = \alpha - \frac{\alpha}{x} = 0 \qquad \frac{\partial g}{\partial y} = 1 - \frac{1}{y} = 0 \ .$$

Thus the second fixed point $(1, 1)$ corresponds to an extremum (inspection shows: a minimum) of the constant $C = C_0 = 1 + \alpha$

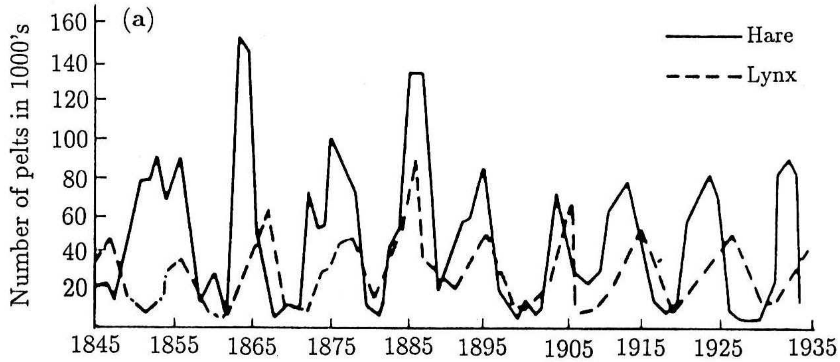
e) Numerical integration of the e.o.m. shows periodically oscillating populations of predators and prey. The (nonlinear) oscillations are phase shifted with the predator population lacking behind. Depending on the initial conditions (i.e., the value of the constant of motion C) the oscillation amplitude can take on arbitrary values (no limit-cycle behaviour).



Phase space trajectories for various values of the conserved quantity C.

Note: Roughly periodic oscillations in predator/prey systems have been observed in nature, see the figure. However, the observations are not well described by the Lotka-Volterra model: E.g., in the data the phase space curve is circled in the opposite direction.

For more information on models for population dynamics see J.D. Murray: Mathematical Biology, Spinger 1993, chapter 3.



Annual number of hare and lynx pelts sold by the Hudson Company.

2. Competition Model

a) Interpretation of the model parameters:

K_1: carrying capacity of the rabbit population
K_2: carrying capacity of the sheep population
r_1: unperturbed reproduction rate of rabbits
r_2: unperturbed reproduction rate of sheep
b_1: sheep take away food from rabbits
b_2: rabbits take away food from sheep

b) Rescaling of the parameters $N_1 = c_1 x$, $N_2 = c_2 y$, $t = c_3 \tau$ leads to

$$\frac{dx}{d\tau} = c_3 r_1 x \Big(1 - \frac{c_1}{K_1} x - b_1 c_2 y\Big) \; , \; \frac{dy}{d\tau} = c_3 r_2 y \Big(1 - \frac{c_2}{K_2} y - b_2 c_1 x\Big) \; .$$

This reduces to (5), (6) with the choice $c_1 = K_1$, $c_2 = K_2$, $c_3 = 1/r_1$, leading to $a = b_1 K_2$, $b = b_2 K_1$, $\rho = r_2/r_1$.

c) The nullclines are straight lines:

$$f(x,y) = 0 \qquad \rightarrow \qquad x = 0 \quad \text{or} \quad y = \frac{1}{a}(1-x)$$
$$g(x,y) = 0 \qquad \rightarrow \qquad y = 0 \quad \text{or} \quad y = 1 - bx$$

The fixed points are defined as the intersections of two nullclines. There are four possible solutions:

(1) $\vec{x}_1^* = (0,0)$
(2) $\vec{x}_2^* = (0,1)$
(3) $\vec{x}_3^* = (1,0)$
The intersection of the two "tilted" nullclines occurs at
(4) $\vec{x}_4^* = \Big(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\Big)$
This is a valid fixed point (positive values of x and y) only if either $a < 1$ and $b < 1$ or $a > 1$ and $b > 1$ (see the figure at the end).

Stability analysis: The Jacobian reads

$$\underline{M} = \begin{pmatrix} 1 - 2x - ay & -ax \\ -\rho b y & \rho(1 - 2y - bx) \end{pmatrix}$$

Fixed point (1)

$$\underline{M}_1 = \begin{pmatrix} 1 & 0 \\ 0 & \rho \end{pmatrix} \quad \rightarrow \quad \lambda_1 = 1, \lambda_2 = \rho \quad \rightarrow \quad \text{repeller}$$

Fixed point (2)

$$\underline{M}_2 = \begin{pmatrix} 1-a & 0 \\ -\rho b & -\rho \end{pmatrix} \quad \rightarrow \quad s = \frac{1}{2}(1-a-\rho)\ ,\ d = -\rho(1-a)$$

This leads to the characteristic values

$$\lambda = \frac{1}{2}(1-a-\rho) \pm \frac{1}{2}(1-a+\rho)$$

Thus $\lambda_1 = (1-a)$ and $\lambda_2 = -\rho$: The fixed point is a stable node if $a > 1$ and a saddle point if $a < 1$.

Fixed point (3)

$$\underline{M}_3 = \begin{pmatrix} -1 & -a \\ 0 & \rho(1-b) \end{pmatrix} \quad \rightarrow \quad s = \frac{1}{2}\big(-1+\rho(1-b)\big)\ ,\ d = -\rho(1-b)$$

This leads to the characteristic values

$$\begin{aligned} \lambda &= s \pm \sqrt{s^2-d} = \frac{1}{2}\big(-1+\rho(1-b)\big) \pm \frac{1}{2}\sqrt{\big(-1+\rho(1-b)\big)^2 + 4\rho(1-b)} \\ &= \frac{1}{2}\big(-1+\rho(1-b)\big) \pm \frac{1}{2}\big(1+\rho(1-b)\big) \end{aligned}$$

Thus $\lambda_1 = \rho(1-b)$ and $\lambda_2 = -1$: The fixed point is a stable node if $b > 1$ and a saddle point if $b < 1$.

Fixed point (4)

After inserting x_4^* and y_4^*:

$$\underline{M}_4 = \frac{1}{1-ab} \begin{pmatrix} a-1 & a(a-1) \\ \rho b(b-1) & \rho(b-1) \end{pmatrix}$$

leading to the trace and determinant

$$s = \frac{1}{2}\frac{a-1+\rho(b-1)}{1-ab} \quad , \quad d = \frac{\rho(a-1)(b-1)}{1-ab}\ .$$

This has to be inserted into $\lambda = s \pm \sqrt{s^2-d}$ and the formula does not simplify.

d) For the special case $a = 4/3$, $b = 3/2$, $\rho = 2/3$ both $(1,0)$ and $(0,1)$ are stable nodes. Fixed point number (4) exists and has the coordinates $x_4^* = 1/3$, $y_4^* = 1/2$. The parameters s and d are $s = -1/3$ and $d = -1/9$, thus

$$\lambda = -\frac{1}{3} \pm \sqrt{\frac{1}{9} + \frac{1}{9}} = \frac{1}{3}\big(-1 \pm \sqrt{2}\big)\ .$$

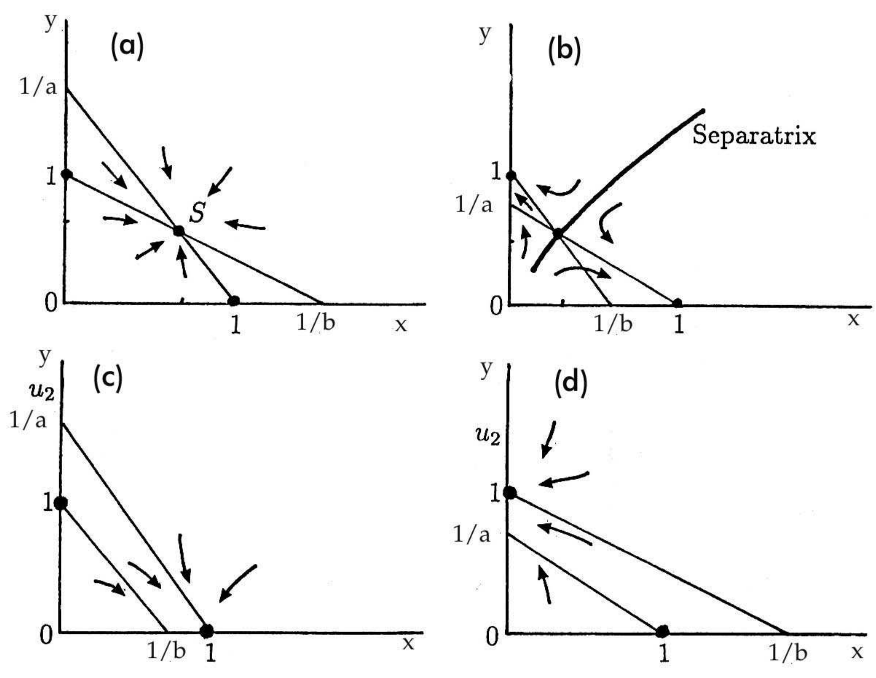
Thus $\vec{x}_4^*$ is a *saddle point*. Only the fixed points $\vec{x}_2^*$ and $\vec{x}_3^*$ are stable. There is no stable coexistence solution.
To have $\vec{x}_4^*$ as a stable fixed point the conditions $s < 0$ and $0 < d < s^2$ have to be fulfilled. The first condition requires $a < 1$ and $b < 1$. To check whether the second condition can be met we may, as an example, look at a symmetric system with $b = a$ and $\rho = 1$:

$$s = \frac{1}{2}\frac{1}{1-a^2}(2a-2) = -\frac{1}{1+a} \quad , \quad d = \frac{(a-1)^2}{1-a^2} = \frac{1-a}{1+a} \, .$$

This fulfills the stability condition $d < s^2$ since $s^2 - d = \frac{1}{(1+a)^2} - \frac{1-a}{1+a} = \frac{a^2}{(1+a)^2} > 0$.
Interpretation: If the competition rates are small so that $a < 1$, $b < 1$, the rabbits and sheep will coexist, each with a somewhat reduced population compared to the undisturbed carrying capacity. In the symmetric case $a = b$ we find $x^* = y^* = 1/(1+a) < 1$ or

$$N_1^* = \frac{K_1}{1+b_2K_1} \quad , \quad N_2^* = \frac{K_2}{1+b_1K_2} \, .$$

However, if the competition is stronger ($a > 1$ or $b > 1$ or both) one species will be driven to extinction. The biologist have called this phenomenon the "*Principle of Competitive Exclusion*". If $a > 1$ and $b < 1$ the sheep will survive, if $b > 1$ and $a < 1$ the rabbits will survive. If both species show strong competition $a > 1$ and $b > 1$ there are two attractors which divide the phase space into two (simply shaped) basins of attraction. Which species survives in this case depends on the initial condition.



Schematic phase space trajectories for the cases (a) $a < 1$ and $b < 1$: stable coexistence point, (b) $a > 1$, $b > 1$: two basins of attraction, (c) $a < 1$, $b > 1$: only rabbits survive, (d) $a > 1$, $b < 1$: only sheep survive.