# Handout on
# Theoretical Models for Predator-Prey Population Dynamics

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November 30, 2015

## Contents



## References

[BTH05] M. Begon, C.R. Townsend, J.L. Harper (2005) *Ecology — From Individuals to Ecosystems, 4th Ed.* Blackwell Publishing

[K01] M. Kot (2001) *Elements of Mathematical Ecology* Cambridge University Press

[C00] T.J. Case (2000) *An Illustrated Guide to Theoretical Ecology* Oxford University Press

I will refer to several Figures in Chapter 10 [BTH05]. I do not include these Figures in this handout for several reasons:

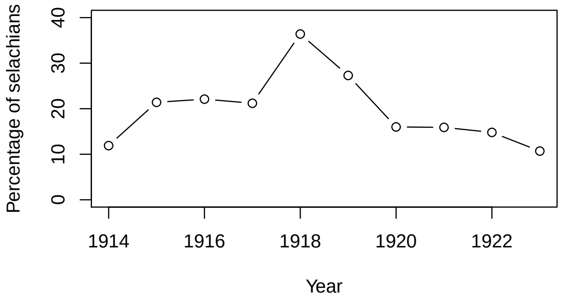
1. to keep the handout small in terms of megabytes and printed pages
2. to avoid copyright issues
3. as it is a good idea to read this and other chapters in the text book
4. as the figures can be downloaded from `http://www.blackwellpublishing.com/begon`

Before we look at theoretical models, remeber:

- *Essentially, all models are wrong, but some are useful.* (George E.P. Box)
- Begon *et al.* (2005, p. 297): "In fact, simple models are most useful when their predictions are *not* supported by real data – as long as the reason for the discrepancy can subsequently be discovered."

## 1 A simple predator-prey model by Volterra

Frequency of selachia (old name for sharks and simlar, mostly predators) on several italian fish markets observed by marine biologist Umberto D'Ancona:




- Almost no fishing from 1914 to 1918 (World War I)
- Why does reduced fishing lead to an increase of predators relative to prey?

D'Ancona's father in law, the mathematician Vito Volterra tried to answer this question with a simple mathematical model:

$N(t)$ prey population size

$P(t)$ predator population size

$$\begin{aligned} \frac{dN}{dt} &= rN - cPN = N \cdot (r - cP) \\ \frac{dP}{dt} &= bNP - mP = P \cdot (bN - m) \end{aligned}$$

- If $P \equiv 0$, $N$ grows exponentially
- If $N \equiv 0$, $P$ shrinks exponentially
- effects of $N$ and $P$ to each other are *mass-action* terms

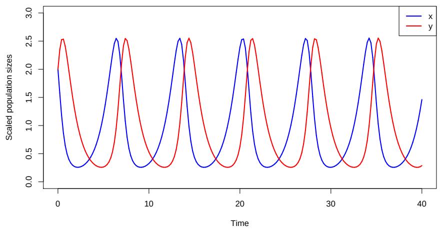
For the analysis, get rid of two parameters by changing variables:

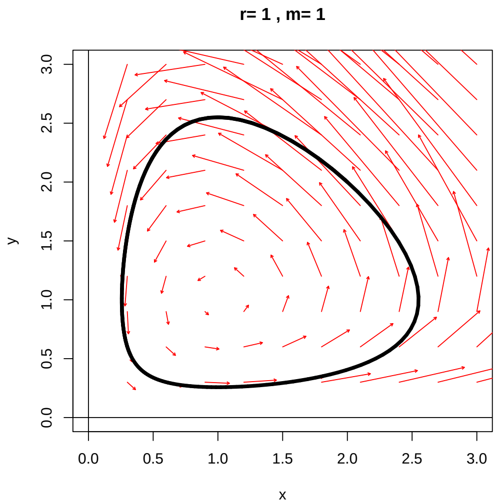
$$\begin{aligned} x &:= \frac{b}{m} N \\ y &:= \frac{c}{r} P \end{aligned}$$

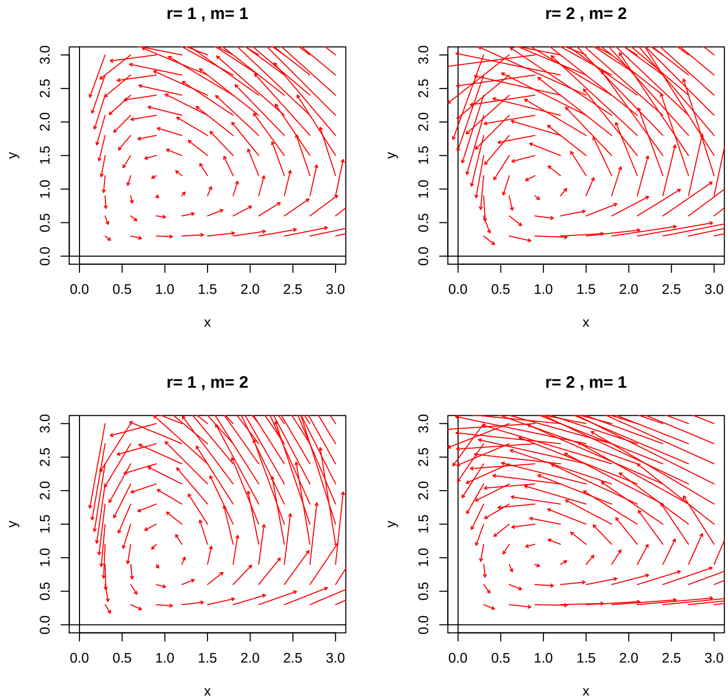
$\Rightarrow$

$$\begin{aligned} \frac{dx}{dt} &= r(1-y)x \\ \frac{dy}{dt} &= m(x-1)y \end{aligned}$$

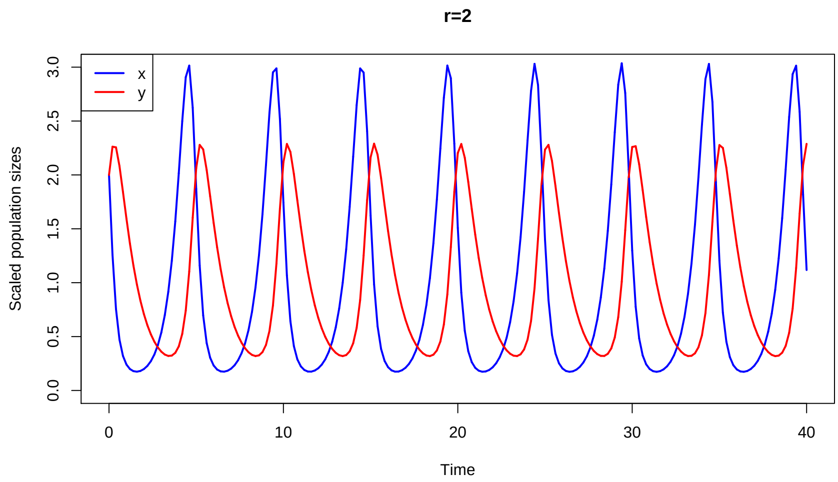
$$\frac{dx}{dt} = r(1-y)x$$
$$\frac{dy}{dt} = m(x-1)y$$

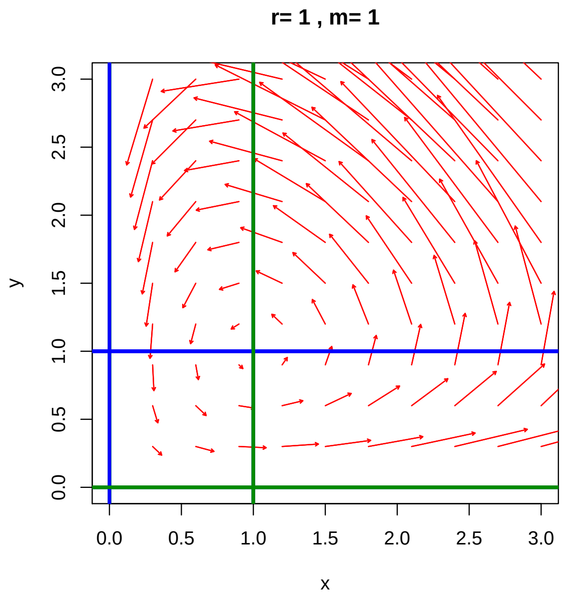



$$\frac{dx}{dt} = r(1-y)x \qquad \frac{dy}{dt} = m(x-1)y$$




Helpful for the anaylsis of the of the system are the

**fixed points:** points $\binom{x}{y}$ with

$$\frac{dx}{dt} = \frac{dy}{dt} = 0,$$

that is, if the system starts there, it will stay there

**isoclines:** lines (or curves) on which either

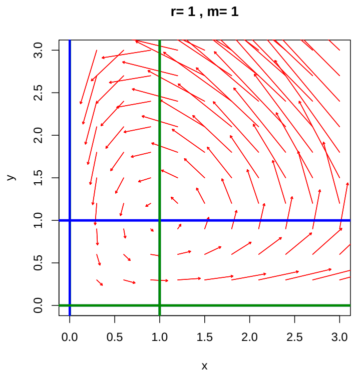
$$\frac{dx}{dt} = 0 \quad \text{or} \quad \frac{dy}{dt} = 0$$

or both

**finding isoclines and fixed points**

$$0 = \frac{dx}{dt} = r(1-y)x \quad \Rightarrow x = 0 \text{ or } y = 1$$

$$0 = \frac{dy}{dt} = m(x-1)y \quad \Rightarrow x = 1 \text{ or } y = 0$$




Fixed points:

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

and

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

**Stability of these two fixed points**

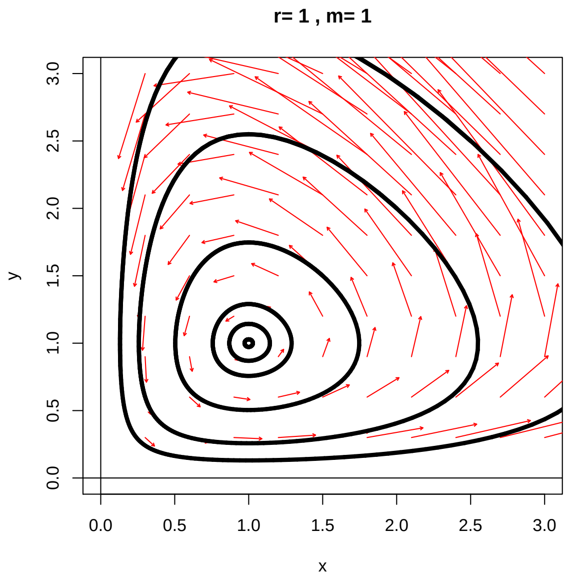
Remeber that *local stability* means that if the system starts very close to the fixed point it will move to it.

Is $\binom{0}{0}$ locally stable?

$$\left.\frac{dx}{dt}\right|_{\binom{0}{0}} \approx rx \qquad \left.\frac{dy}{dt}\right|_{\binom{0}{0}} \approx -my$$

It is not stable as it will be left into direction of $x$ (leading to exponential growth of host population).

The mathematical analysis of $\binom{1}{1}$ is a bit more subtle, see [K01]. In fact, if the system starts close to this fixed point, it will stay on an orbit around it.




Note that on each orbit, movement is faster for higher values of $x$ and $y$. Volterra could show that on each orbit, when averaged over time:

$$\text{average}(x) = 1 \quad \text{and} \quad \text{average}(y) = 1$$

Thus, for the average abundance of predator or prey over a longer time period, the starting point is irrelevant.

Average frequency in original scaling (fixed point):

$$\begin{aligned}\frac{dN}{dt} &= N\cdot(r-cP)\\ \frac{dP}{dt} &= P\cdot(bN-m)\end{aligned}$$

$$\text{average}(N)=\frac{m}{b},\qquad \text{average}(P)=\frac{r}{c}$$

Model effect of fishing by additional death rate:

$$\begin{aligned}\frac{dN}{dt} &= N\cdot(r-cP-d)\\ \frac{dP}{dt} &= P\cdot(bN-m-d)\end{aligned}$$

$$\text{average}(N)=\frac{m+d}{b},\qquad \text{average}(P)=\frac{r-d}{c}$$

Thus, Volterra's simple model even predicts, that fishing increases the abundance of prey fish!

Maybe, this model can explain why the usage of pesticides sometimes lead to an increase in the abundance of the pest.

# 2 Should we believe in these oscillations?

Three questions:

1. Do we observe long-term oscillations in nature? See Figure 10.1 in [BTH05]
2. Does the model fit these data? E.g. in the hare-lynx system the hare is also prey of other predators and predator of its plant food. This makes thorough statistical ananlysis very complex. Time-series analysis of Lynx abundance given hare data fits well to predator-prey model. *GENERAL PROBLEM:* Data can never confirm that a model is valid! All models are wrong!
3. Are these osciallations still predicted if we make the model a bit more realistic?

## 2.1 Intraspecific competition

Lotka-Volterra model for predator-prey with intraspecific competition:

$$\begin{aligned}\frac{dN}{dt} &= N\cdot(r-cP-kN)\\ \frac{dP}{dt} &= P\cdot(bN-m-gP)\end{aligned}$$

non-trivial isoclines are given by

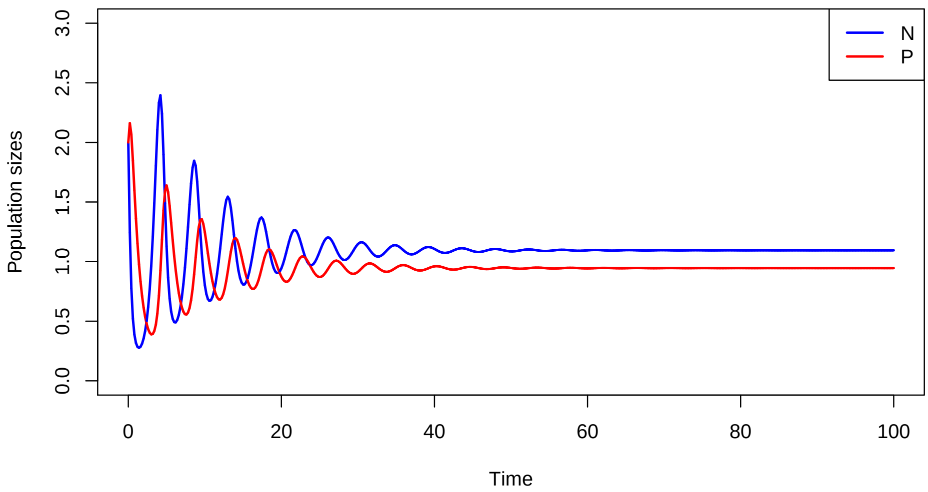
$$\begin{aligned}P &= \frac{r-kN}{c}\\ P &= \frac{bN-m}{g}\end{aligned}$$

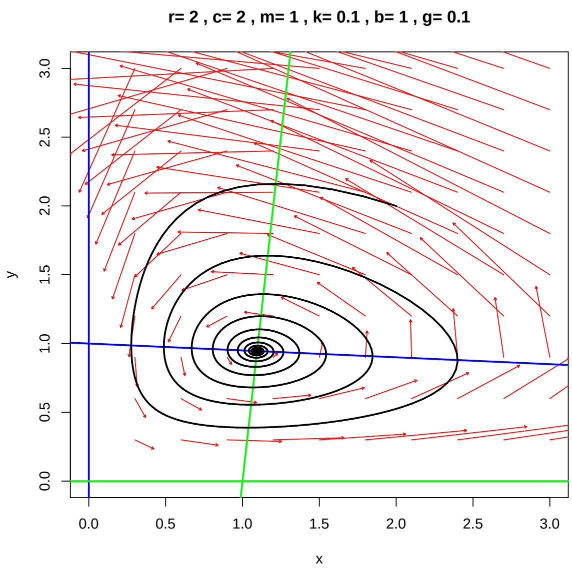
If non-trivial equilibrium exists, it must be

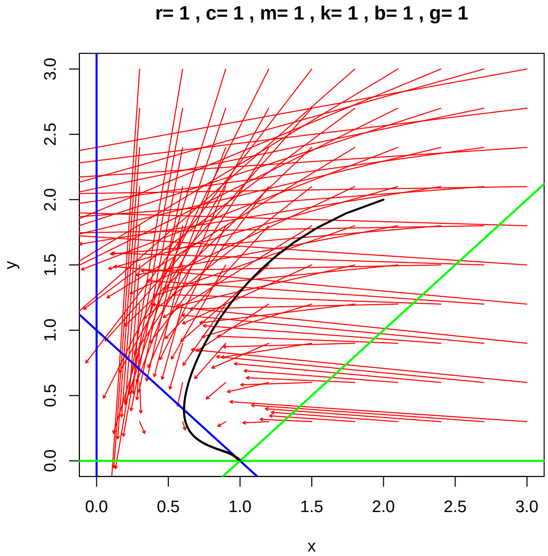
$$(N,P)=\left(\frac{gr+cm}{cb+gk},\frac{br-mk}{cb+gk}\right)$$

Thus, coexistence is only possible if $br > mk$ or, equivalently,

$$\frac{b}{m} > \frac{k}{r}$$






## 2.2 When predators eat only as much as they can

Model for type II functional response:

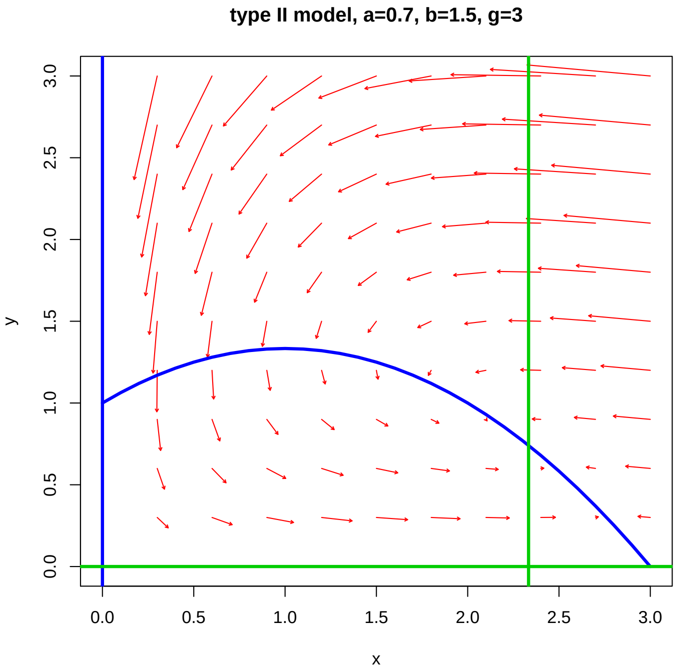
$$\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \frac{cNP}{a+N}$$
$$\frac{dP}{dT} = \frac{bNP}{a+N} - mP$$

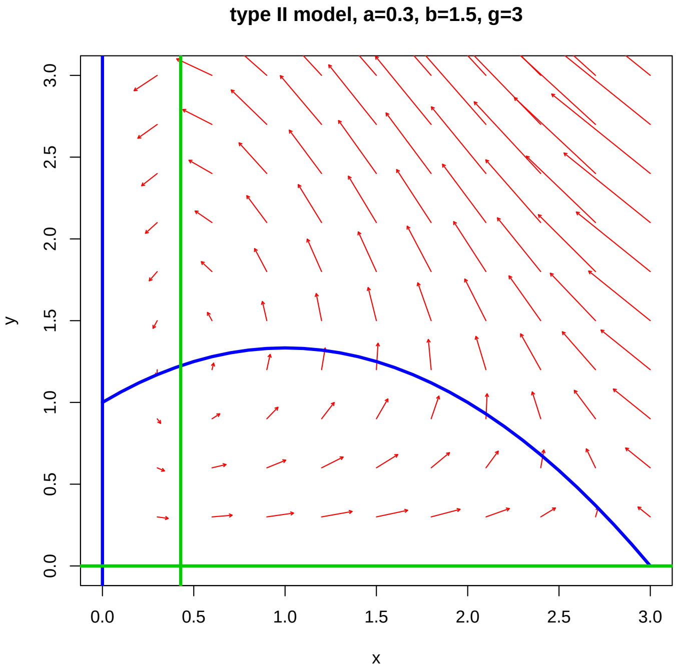
rescaling the variables and setting

$$N = ax \quad P = r\frac{a}{c}y \quad T = \frac{1}{r}t \quad \alpha = \frac{m}{b} \quad \beta = \frac{b}{r} \quad \gamma = \frac{K}{a}$$

leads to

$$\frac{dx}{dt} = x \cdot \left(1 - \frac{x}{\gamma} - \frac{y}{1+x}\right)$$
$$\frac{dy}{dt} = \beta \cdot \left(\frac{x}{1+x} - \alpha\right) \cdot y$$




Watch the simulation in the R script!
isocline $\frac{dx}{dt} = 0$:

$$x = 0 \qquad y = (1+x)\left(1 + \frac{x}{\gamma}\right)$$

isocline $\frac{dy}{dt} = 0$:

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

non-trivial fixed point is stable if and only if

$$\frac{\alpha}{1-\alpha} > \arg\max_x (1+x)\left(1+\frac{x}{\gamma}\right)$$

See Figures 10.6 to 10.12 in [BTH05]
Other reasons why oscillations can be damped:

- spatial structure: local oscillation are averaged
- role of stochasticity?

## 2.3 Conclusions

Our aims:

- understand ecological mechanisms theoretically/mathematically
- but also intuitively/biologically
- how intuitive and theoretical predictions correspond to each other
- how robust these predictions are against violations of basic assumptions