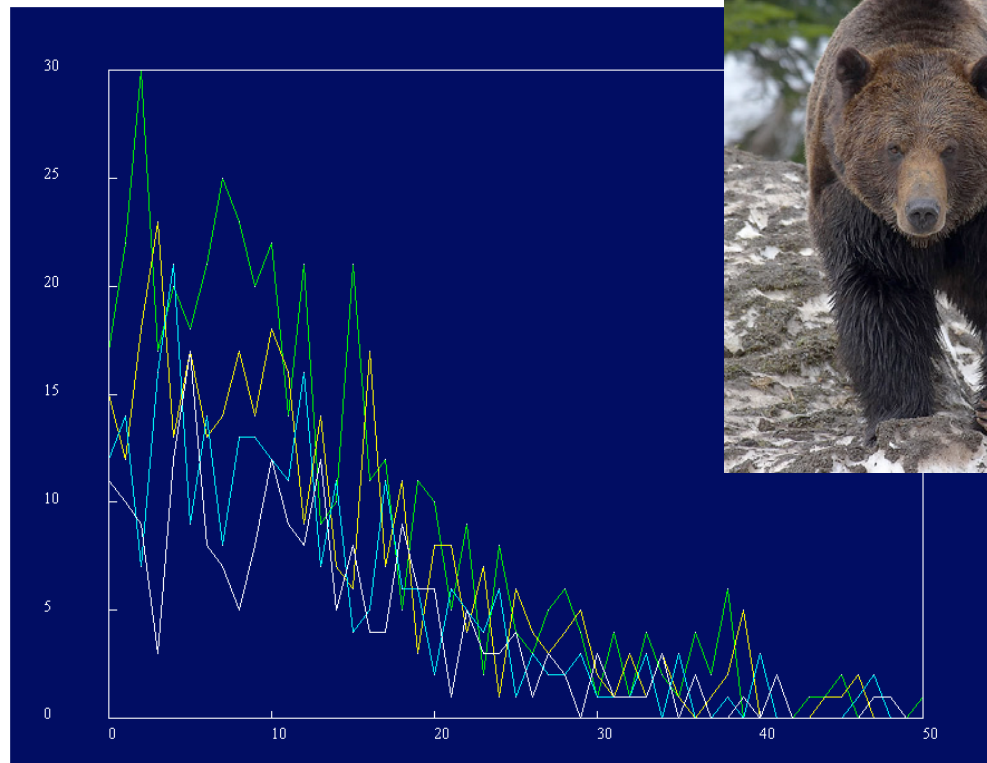


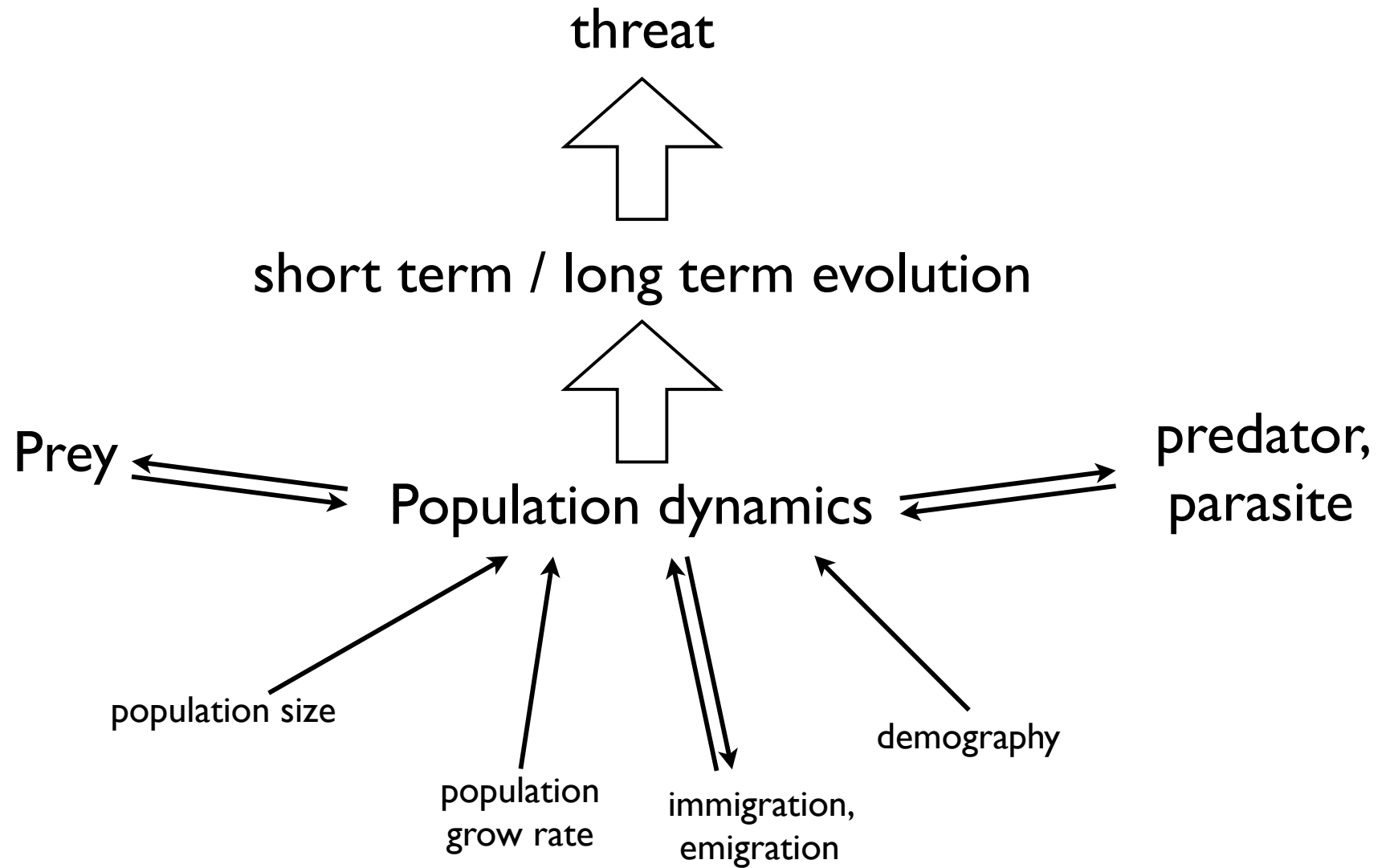
Population dynamics, viability analysis



Sylvain Ursenbacher
NLU, room 36



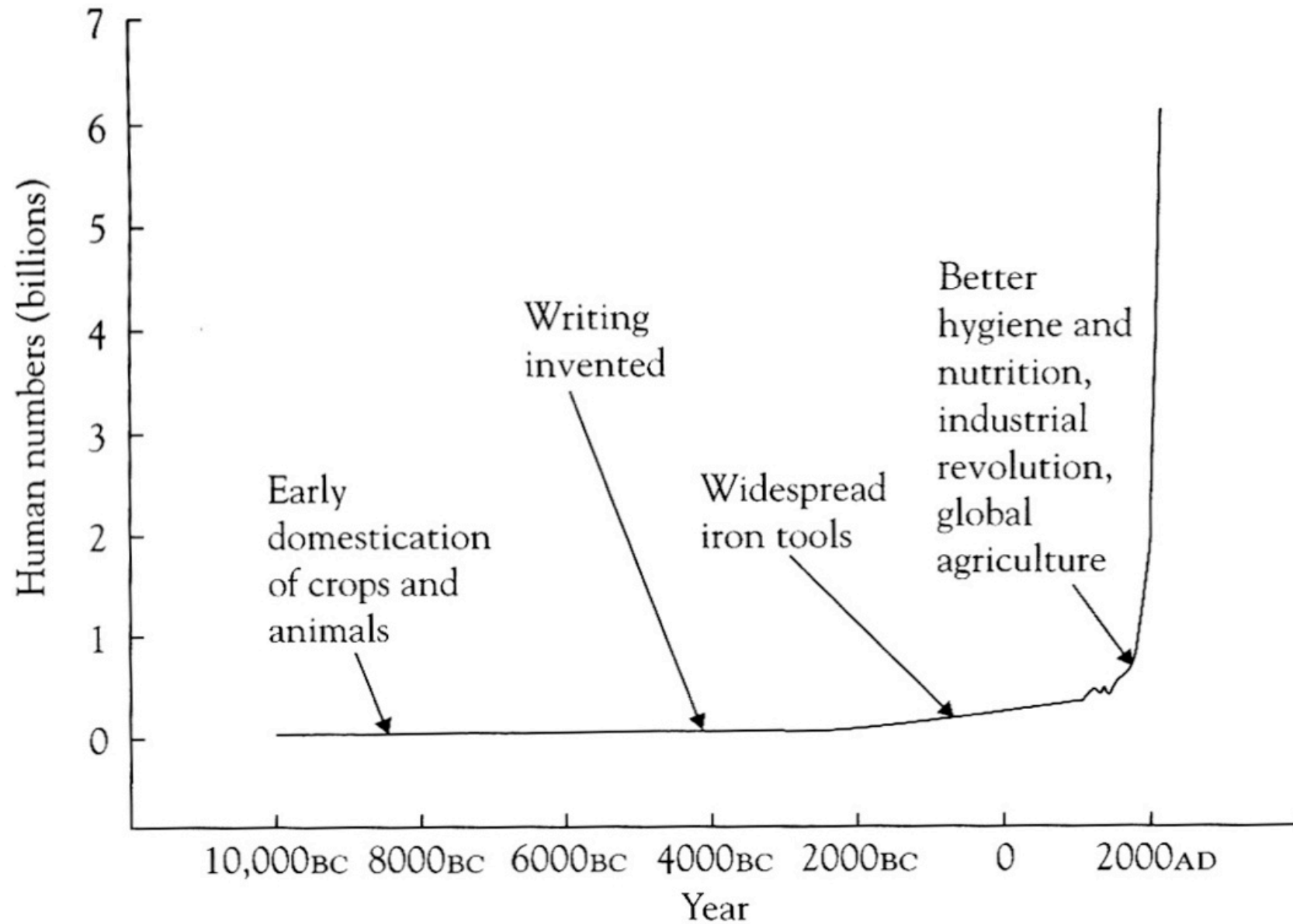
Introduction



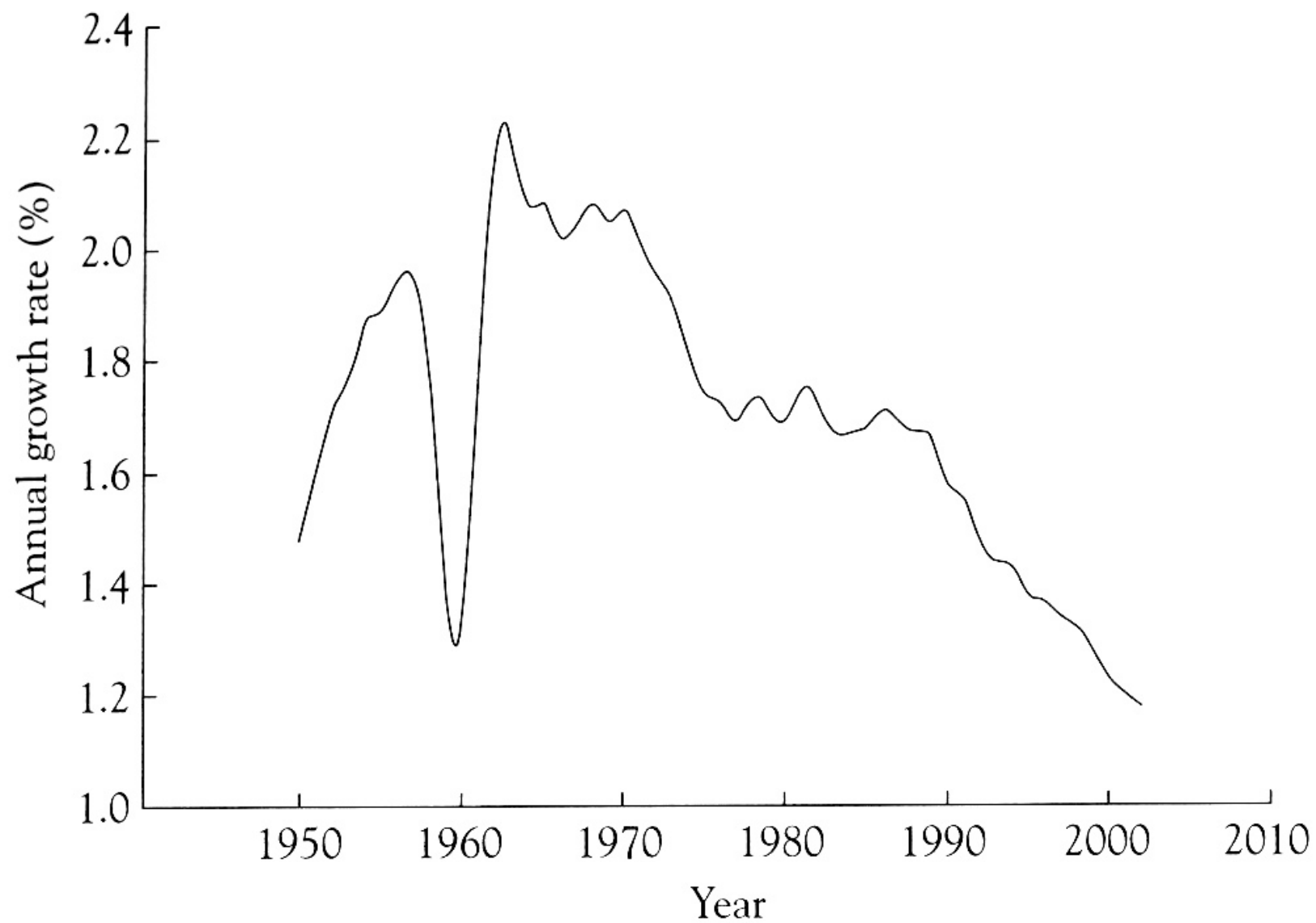
Introduction: *Population dynamics*

- growth rate monitoring
- estimation of demographic parameters
- impact of environment on growth rate
 - ▶ predators / prey / parasites
 - ▶ carrying capacity

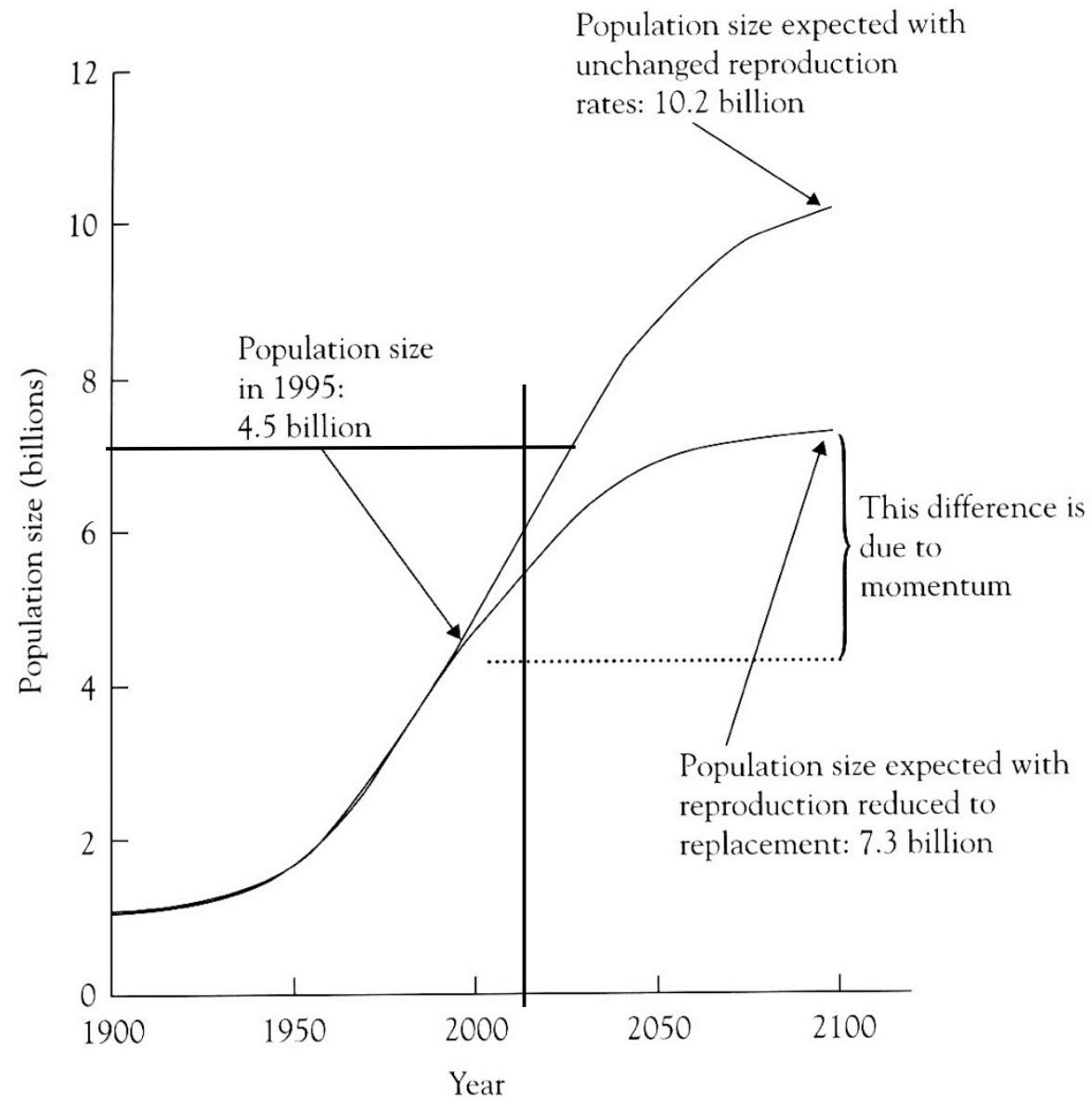
Introduction: *human population*



Introduction: *human population*



Introduction: *human population (conducted in 1995)*



Plan

- Basis information
- requested parameters for the development of simple models
 - ▶ Leslie matrix
- more complex models
 - ▶ geometric or exponential growth
 - ▶ prey-predators (Lotka-Volterra)
 - ▶ density-dependence models
 - ▶ multiple populations
- Population Viability Analyses (PVA)
 - ▶ sensitivity analysis
 - ▶ implications for conservation

Introduction

- Population evolution

$$N_{t+1} = N_t + \underbrace{B + I}_{\text{new individuals}} - \underbrace{D + E}_{\text{individuals that disappeared}}$$

Population size before

intrapopulation variation

interpopulation movements

The diagram shows the equation $N_{t+1} = N_t + B + I - D - E$. An arrow points from the text 'Population size before' to N_t . A bracket under $B + I$ is labeled 'new individuals'. A bracket under $D + E$ is labeled 'individuals that disappeared'. A bracket above $B + I$ is labeled 'intrapopulation variation'. A bracket above $D + E$ is labeled 'interpopulation movements'.

N = abundance at time t

B = birth

I = immigration

D = death

E = emigration

Introduction

- Population evolution

N = abundance at time t

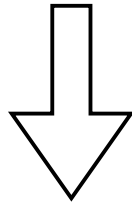
B = birth

I = immigration

D = death

E = emigration

$$N_{t+1} = N_t + B + I - D - E$$



estimation of abundance and density:

e. g. CMR: Capture-Mark-Recapture methods (B. Baur, Monday & Friday)

Introduction

- Population evolution

N = abundance at time t

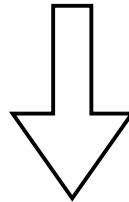
B = birth

I = immigration

D = death

E = emigration

$$N_{t+1} = N_t + B + I - D - E$$



reproduction:

function of fecundity, sex ratio, ...

Introduction

- Population evolution

N = abundance at time t

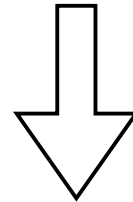
B = birth

I = immigration

D = death

E = emigration

$$N_{t+1} = N_t + B + I - D - E$$



estimation of survival (ϕ):

$$D = (1 - \phi) * N_t$$

(e.g. extended CMR method: Cormack-Jolly-Seber methods)

Introduction

- Population evolution

N = abundance at time t

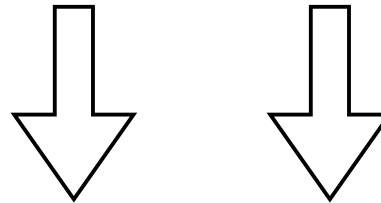
B = birth

I = immigration

D = death

E = emigration

$$N_{t+1} = N_t + B + I - D - E$$



connection(s) with other population(s)

difficult to estimate

(e.g. CMR method: Cormack-Jolly-Seber methods)

requested parameters: survival rate (ϕ)

- 3 groups of survival estimators:
 - ▶ if all animals can be relocated
 - captive populations
 - telemetry
 - ⚠ lost of marks, moving out the study area, etc...
 - ▶ if only survivors are recorded
 - ?? all individuals recaptured at $t+1$?
 - CMR methods, using Cormack-Jolly-Seber methods add probability of detection
 - ▶ if only deaths are recorded
 - band-return approaches (e.g. with hunter / fisherman)



requested parameters: birth rate

- can be related to female only or both sex (depending of the model)
 - ➡ knowledge of sex-ratio important (adults, newborn, etc..)
- field evaluation of embryos / eggs / newborns per female
- mortality rate at the birth/hatching
- mortality rate of newborns (up to sexual maturity)
 - ▶ per time unit
 - ▶ per year
 - ▶ global from birth to sexual maturity

requested parameters: immigration / emigration

- difficult to estimate in wild populations
 - ▶ direct methods
 - ▶ CMR, evaluation with open population models (e.g. Cormack-Jolly-Seber)
 - ▶ indirect estimation
 - ▶ genetic evaluation
- see dynamics of multiple populations

Population evolution

$$N_{t+1} = N_t + B + I - D - E$$

$(f \cdot N_t)$

$([1-\phi] \cdot N_t)$

$$N_{t+1} = (f + \phi)N_t + \text{dispersal}$$

N = abundance at time t

B = birth

I = immigration

D = death

E = emigration

ϕ = survival at time t

f = fecundity

Closed populations

$$N_{t+1} = (f + \phi)N_t + \text{dispersal}$$

- if the population is close: no recruitment

$$N_{t+1} = (f + \phi)N_t$$

⚠ closed population for CMR could also signify no recruitment,
including fecundity and survival

Leslie model

- matrix regrouping survival and fecundity for all age classes
- can be very simple (2 x 2) to very complex ($y \times y$)

from this stage

to this stage...

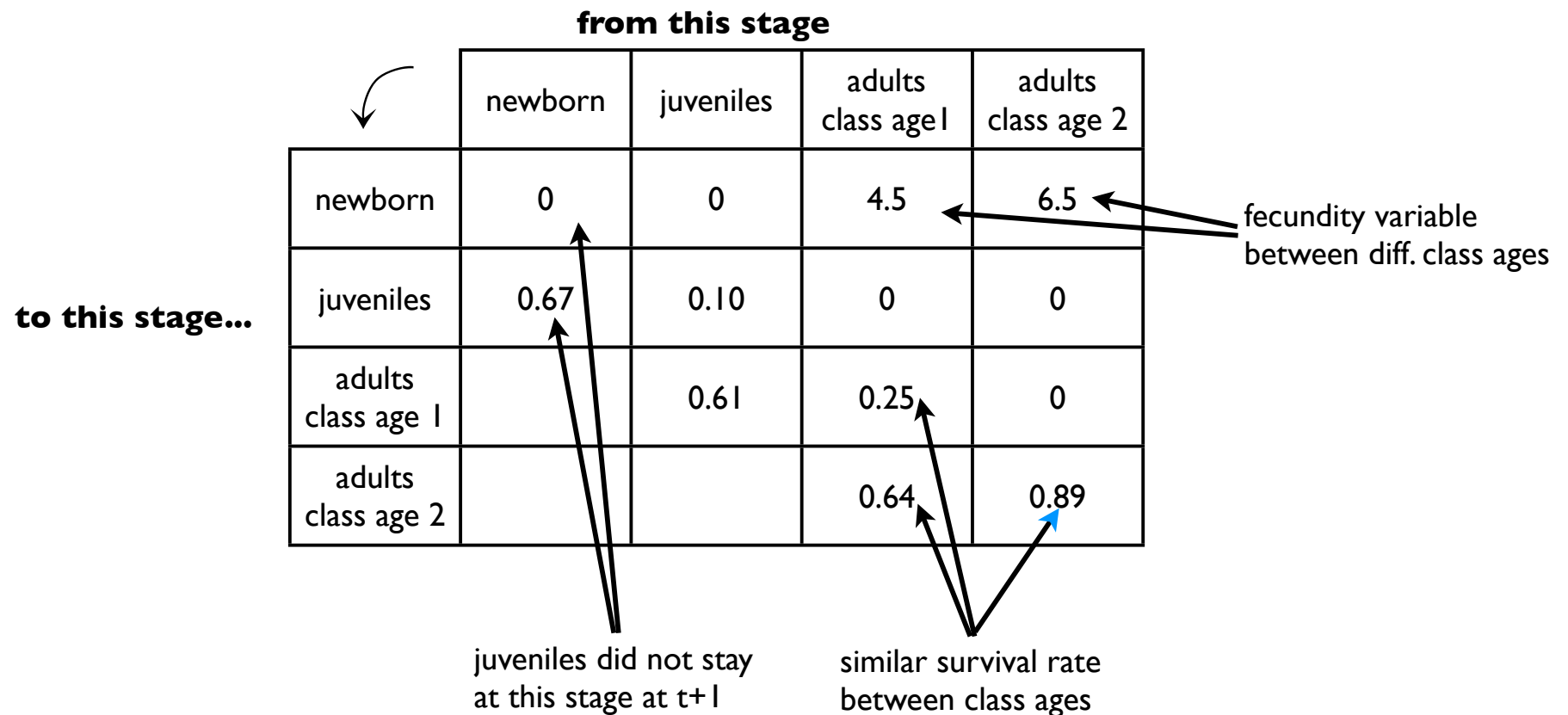
	newborn	adults
newborn	0	15.4
adults	0.43	0.65

fecundity

survival
(move to an other group)

Leslie model

- matrix regrouping survival and fecundity for all age classes
- can be very simple (2 x 2) to very complex (y x y)



More complex methods...

- geometric or exponential growth
- density-dependence models
- stochasticity
- prey-predators relationship (Lotka-Volterra equations)
- multiple populations

geometric and exponential growth

- closed populations

$$N_{t+1} = (f + \phi)N_t$$

$$N_{t+1} = \lambda N_t$$

λ = geometric growth rate

if $\lambda = 1$, population size stable

if $\lambda < 1$, reduction of the population size

if $\lambda > 1$, growth of the population size

geometric = discrete growth rate

geometric and exponential growth

$$N_{t+1} = \lambda N_t$$

- for long t time steps

$$N_t = N_0 * \lambda_1 * \lambda_2 * \lambda_3 * ... \lambda_t$$

- to estimate constant annual growth

$$N_t = N_0 * \lambda^t$$

- for annual growth rate over t time steps

$$\lambda = \sqrt[t]{N_t / N_0}$$

geometric and exponential growth

- exponential (continuous) growth rate

- ▶ not focused on one year (or a time unit)

- when Δt tend to 0

- ▶ tiny change in population size (dN) over a tiny interval of time (dt)

$$dN / dt = rN$$

- ▶ r = instantaneous growth rate per capita (per individual)

- dN / dt = derivative; rN = slope of the tangent of the curve of N plotted against time

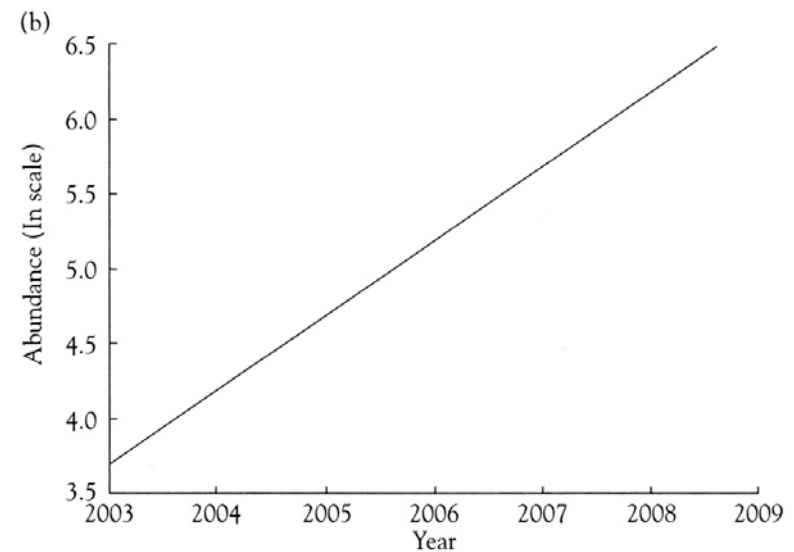
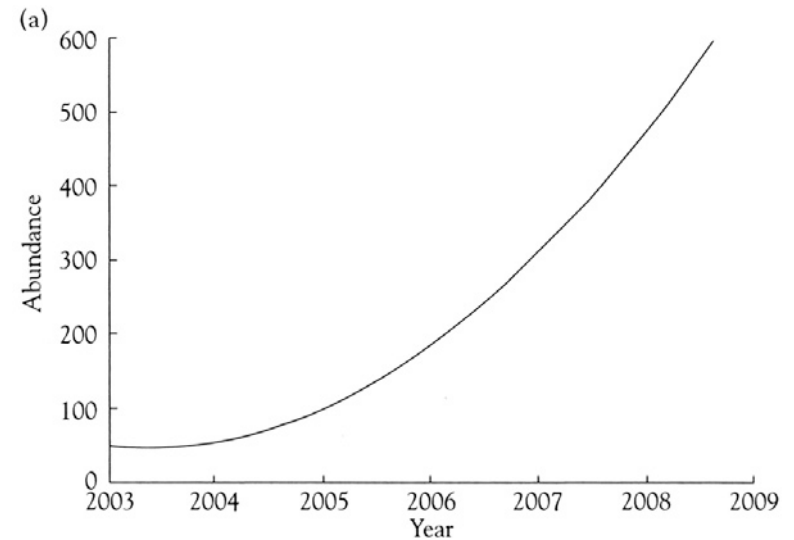
geometric and exponential growth

- Example of a exponential growth

- ▶ $\lambda = 1.65$

- or plotted against the natural logarithm (ln) of abundance

- ▶ slope in (b): r



density dependance: *introduction*

- previous models: unaffected by its own density
- but population cannot grow exponentially for long periods...
 - ➡ “limitation” of growth due to numerous reasons
 - e.g. food limits, territoriality, ...
- Density dependance: refer to the profound influence that a population's density has on the vital rates of individuals in the population
changes in vital rates lead to changes in population growth rate

density dependance

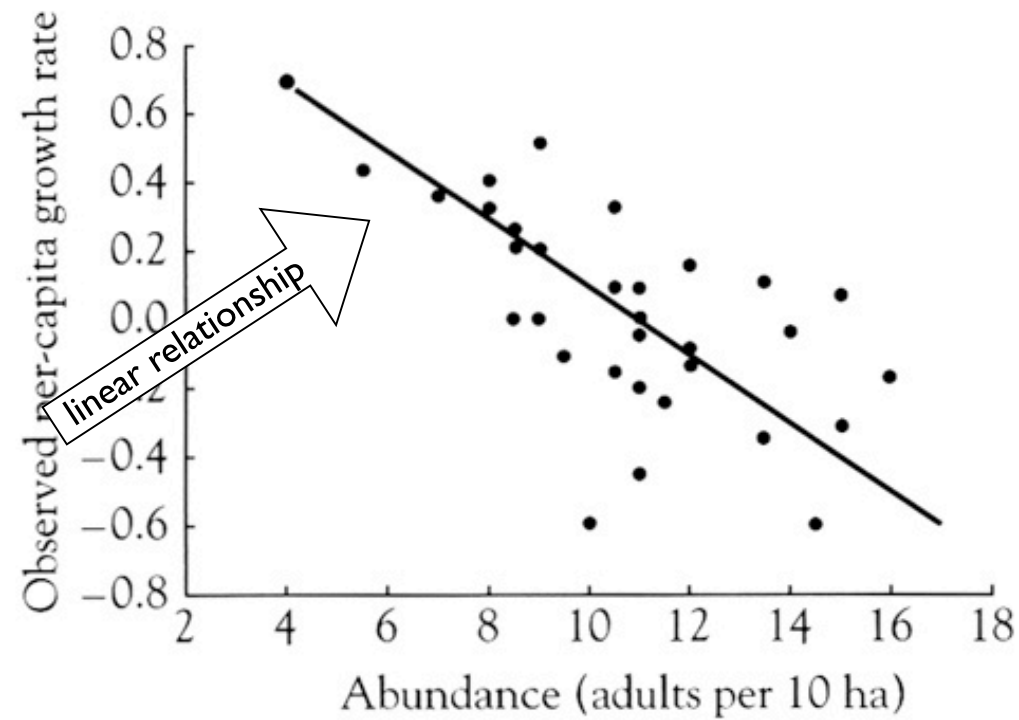
- high density → negative impact: competition between individuals
 - ▶ direct competition: interference or contests (fights)
 - for food, mates, territories
 - ★ winners can reproduce, losers not
 - ▶ predators, parasites or contagious diseases
 - ★ regulates populations
 - ▶ others....
- high density → positive impact: avoiding Allee effect
 - ▶ difficulties to find a mate in very small populations
 - ▶ confusion to avoid predation (e.g. mormont crickets)
 - ▶ co-operation for founding food, to defend food
 - ▶ ...



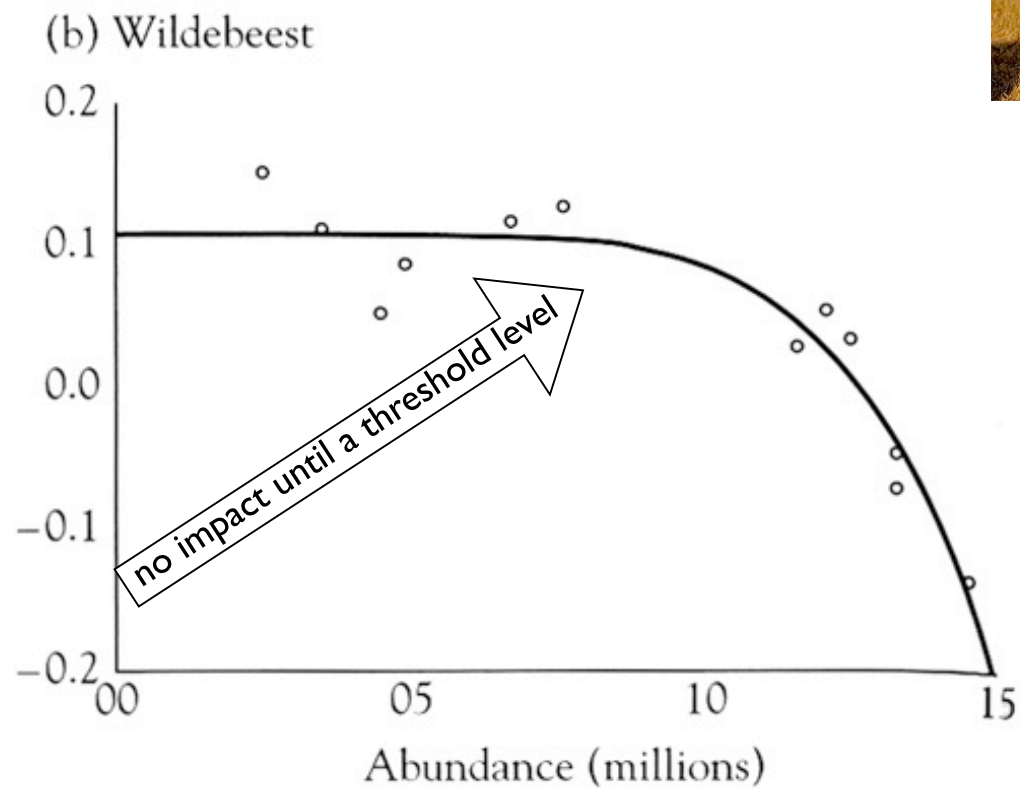
density dependance: some *examples of negative density dependance*



(a) Black-throated blue warbler



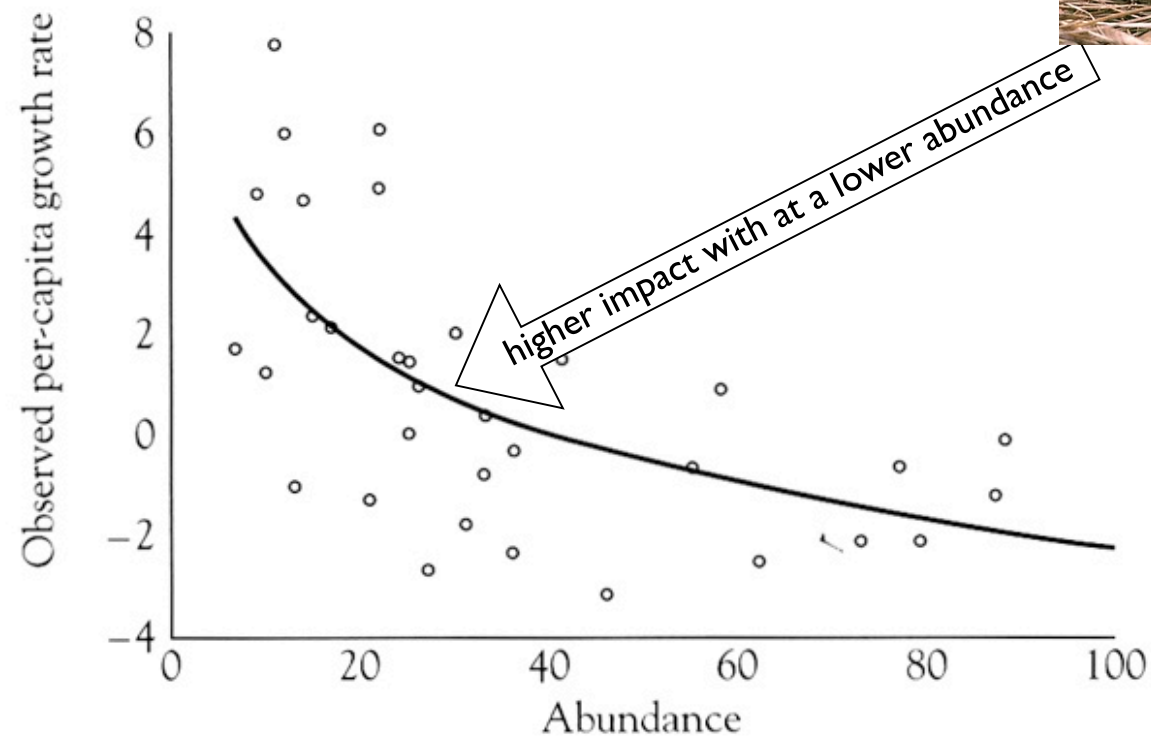
density dependance: some *examples of negative density dependance*



density dependance: some *examples of negative density dependance*

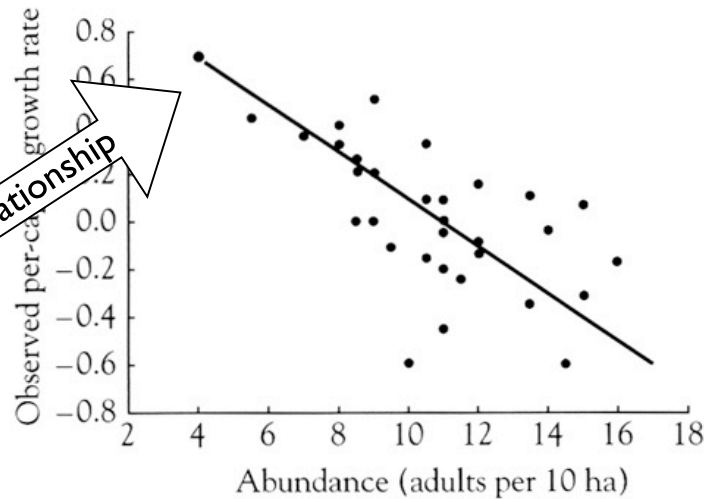


(c) Meadow vole

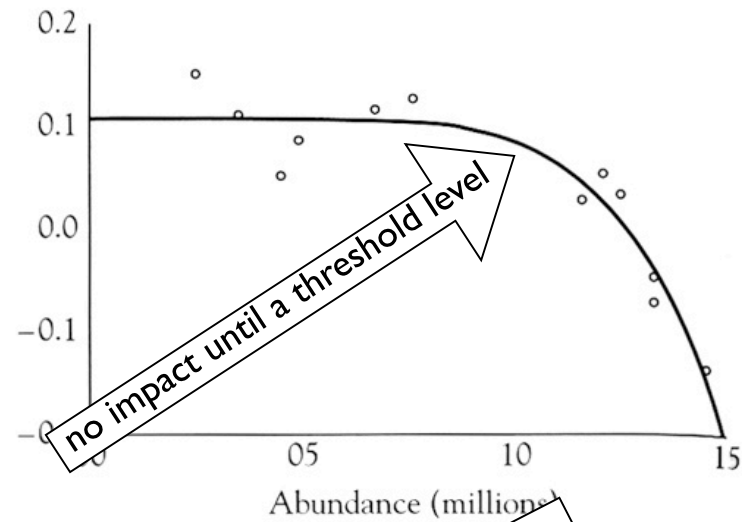


density dependance: some *examples of negative density dependance*

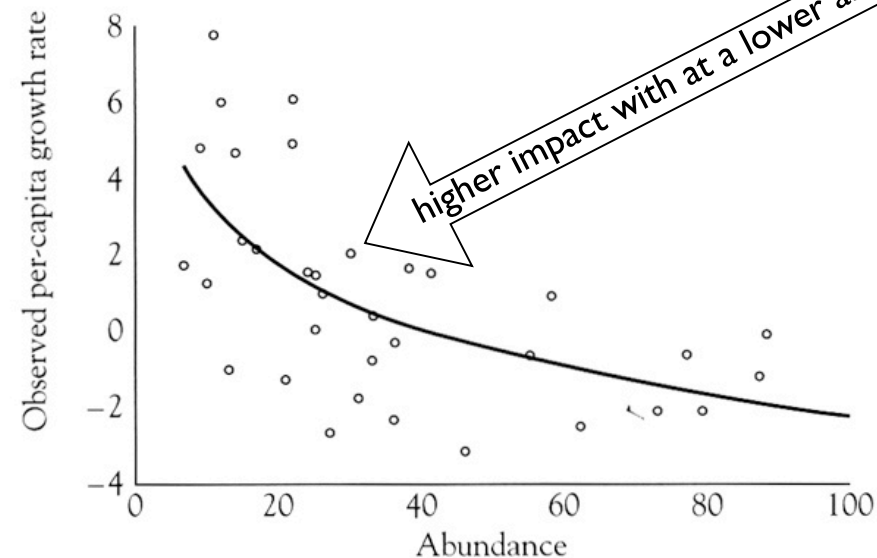
(a) Black-throated blue warbler



(b) Wildebeest

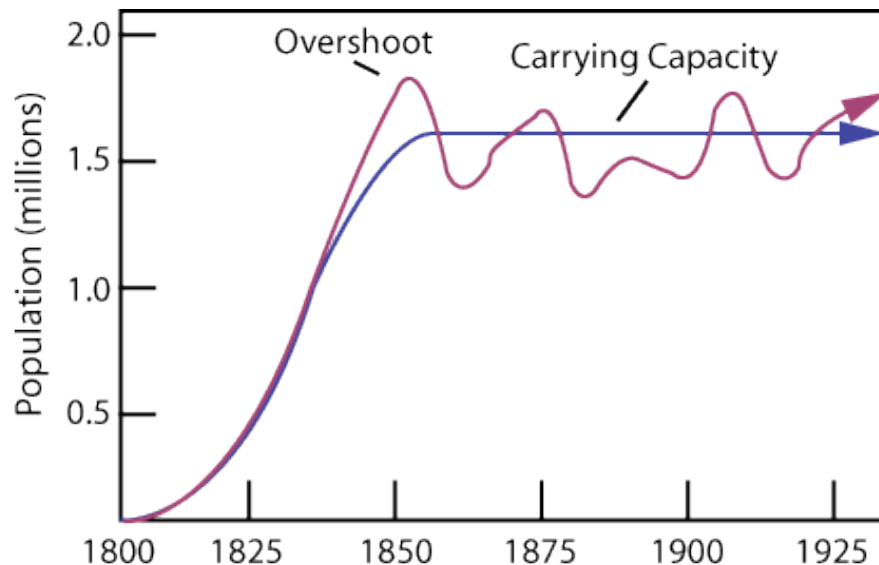


(c) Meadow vole



density dependance: *carrying capacity*

- Carrying capacity: K
- the point at which per-capita mortality (1-survival) and reproduction are equal, so that the population just replaces itself
 $\lambda = 1$ ($r = 0$)
- carrying capacity = equilibrium
if density is greater than K : mortality > reproduction
if density is lower than K : reproduction > mortality

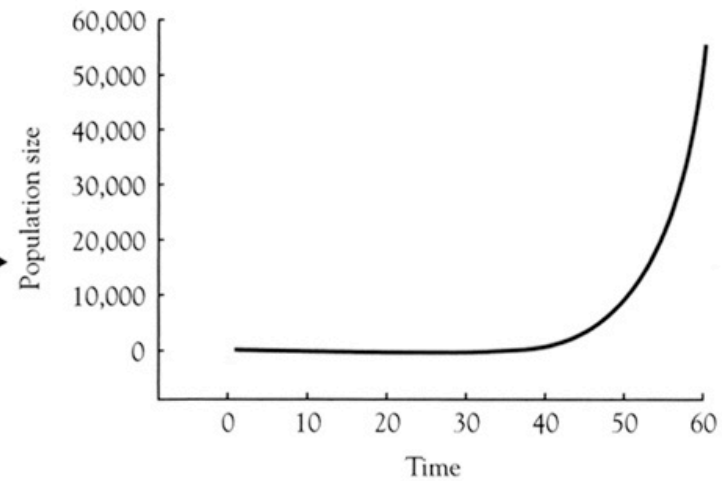
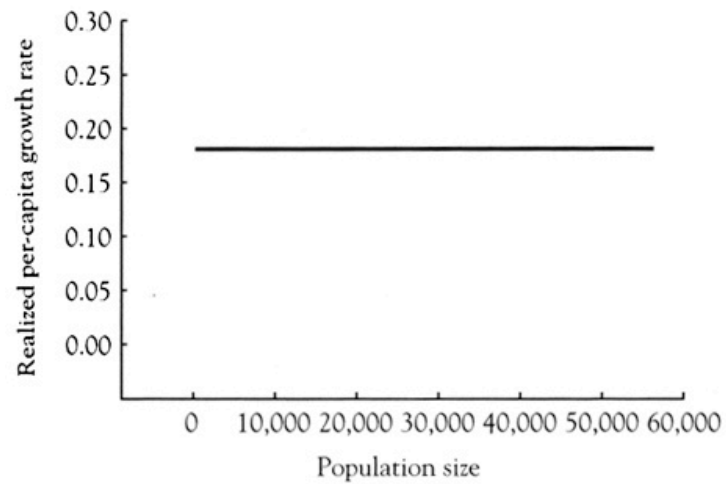


density dependence: *logistic growth model*

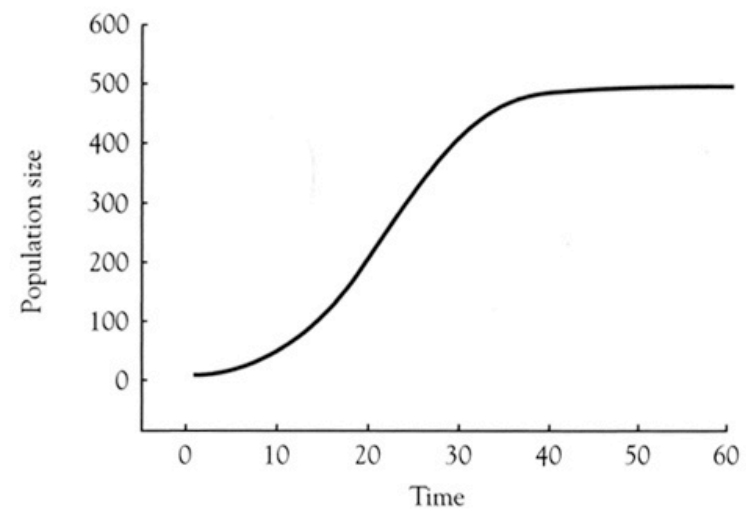
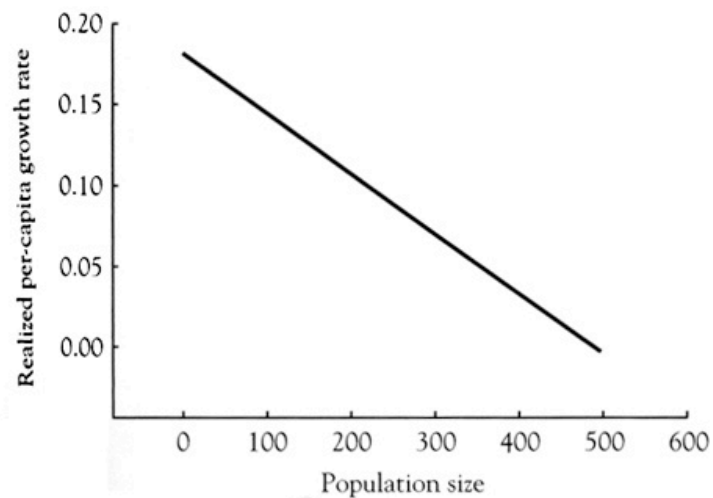
- exponential growth:
 - ▶ $r = \text{constant}$
- logistic growth:
 - ▶ r change $f(\text{population size})$
 - ▶ $r \propto [\ln(N_{t+1}/N_t)] = \text{intrinsic growth rate}$

density dependance: *logistic growth model*

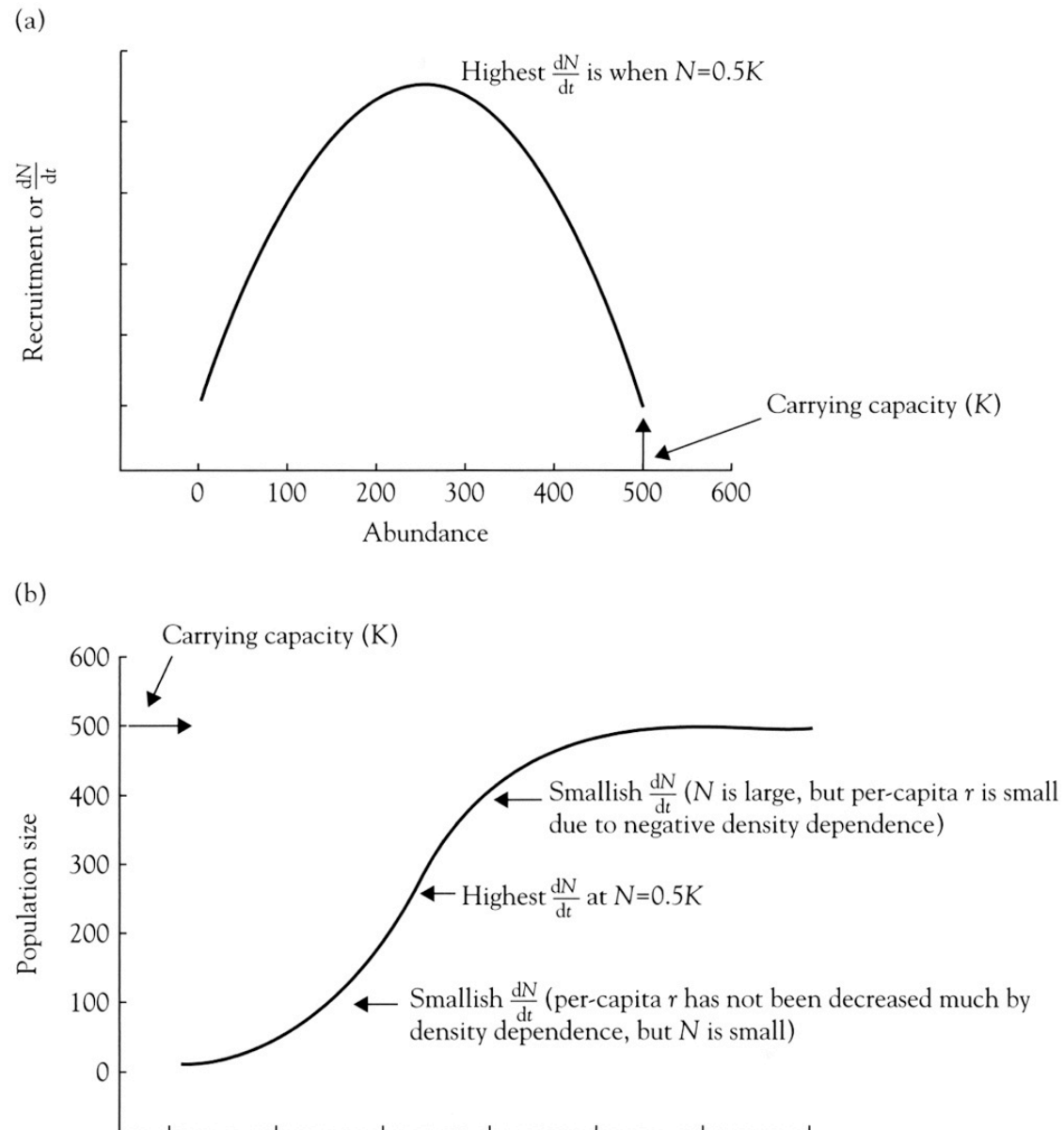
(a) Exponential growth with $r=0.18$



(b) Logistic growth with $r=0.18$, $K=500$



density dependance: *ratio of recruitment and abundance*



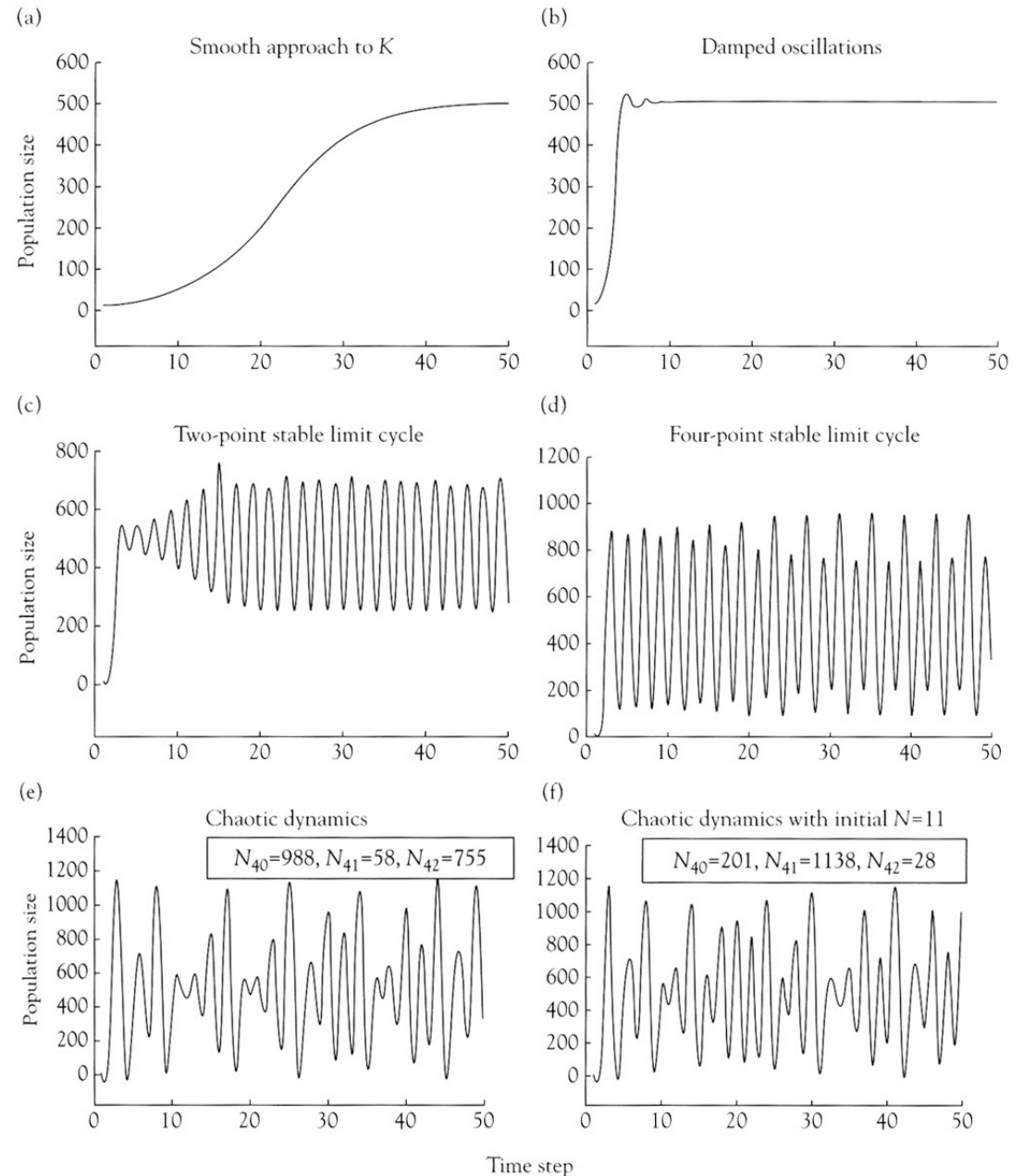
density dependance: some *conterintuitive dynamics*

- with the discrete logistic growth equation:

$$N_{t+1} = N_t e^{\left(r \left[1 - \left(\frac{N_t}{K} \right) \right] \right)}$$

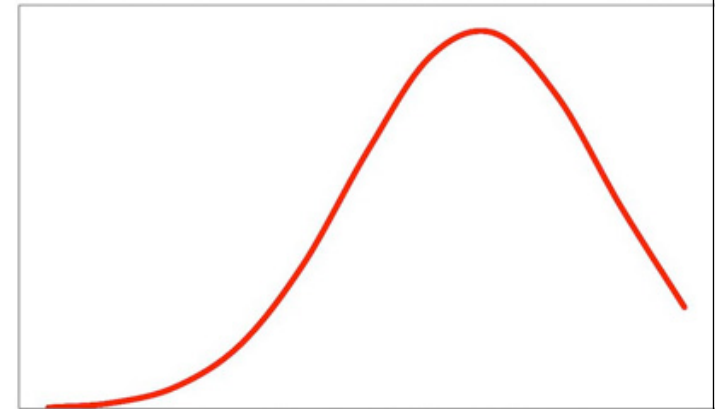
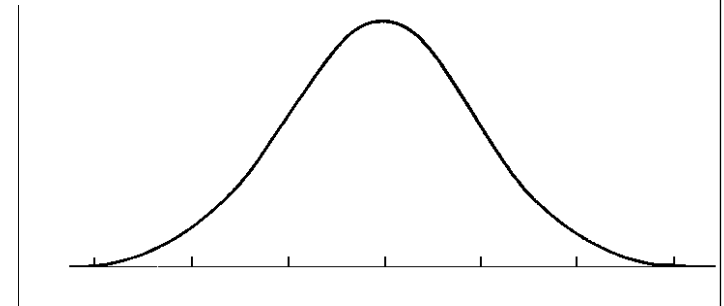
without stochasticity

- can become:
 - ▶ cycles
 - ▶ unpredictable
- for $r < 1.0$: s-shape curve
- for $2.0 < r < 2.69$: predictable cycles
- for $r > 2.69$: chaos

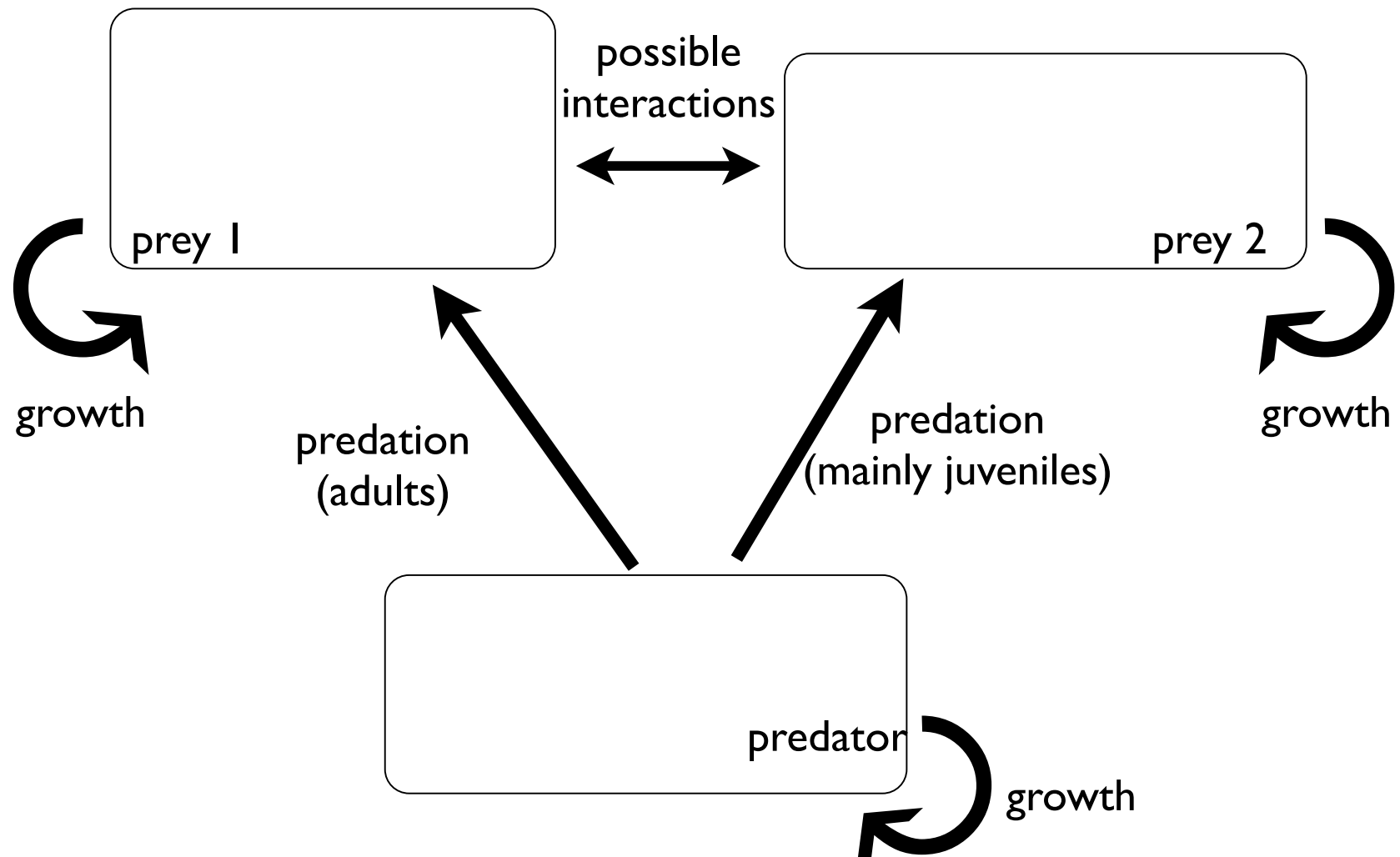


Stochasticity in models

- all presented model: no variation in the different parameters
- add some “variability” in different parameters
- distribution of I parameter:
 - ▶ uniform distribution between min and max
 - ▶ central tendency (e.g. lognormal, normal, ...)
 - ▶ pick up several values measured in the field



Prey-predation relationships

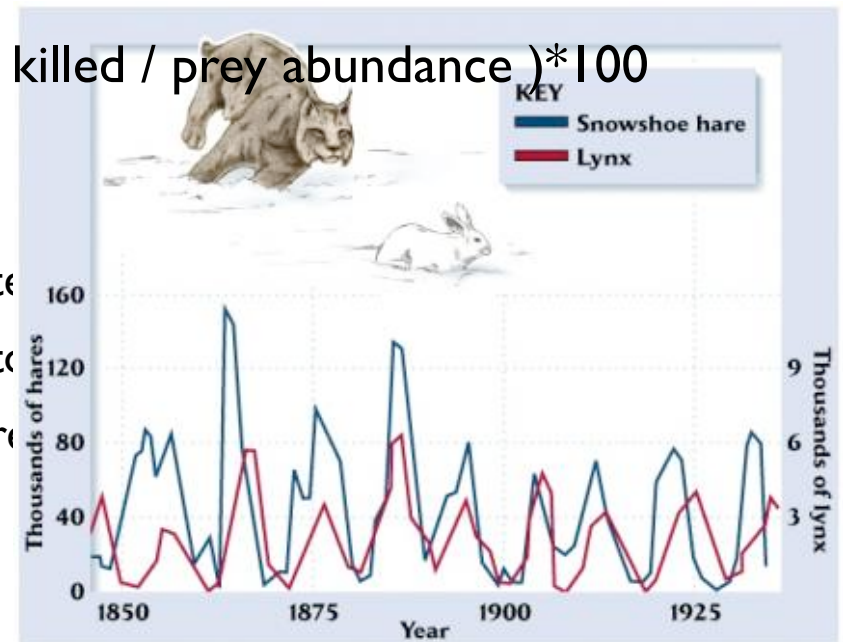


Prey-predation relationships: *introduction*

- predators (or parasites) can have an impact on population abundance
- close relationship between prey and predator densities
- predation rate:

$$\text{Predation rate} = (\text{number of prey killed} / \text{prey abundance}) * 100$$

- numerous possible responses:
 - ▶ high level of prey → higher survival rate
 - ▶ high level of prey → increase of predation
 - ▶ generally not only one prey and one predator



from Purves et al., 1992

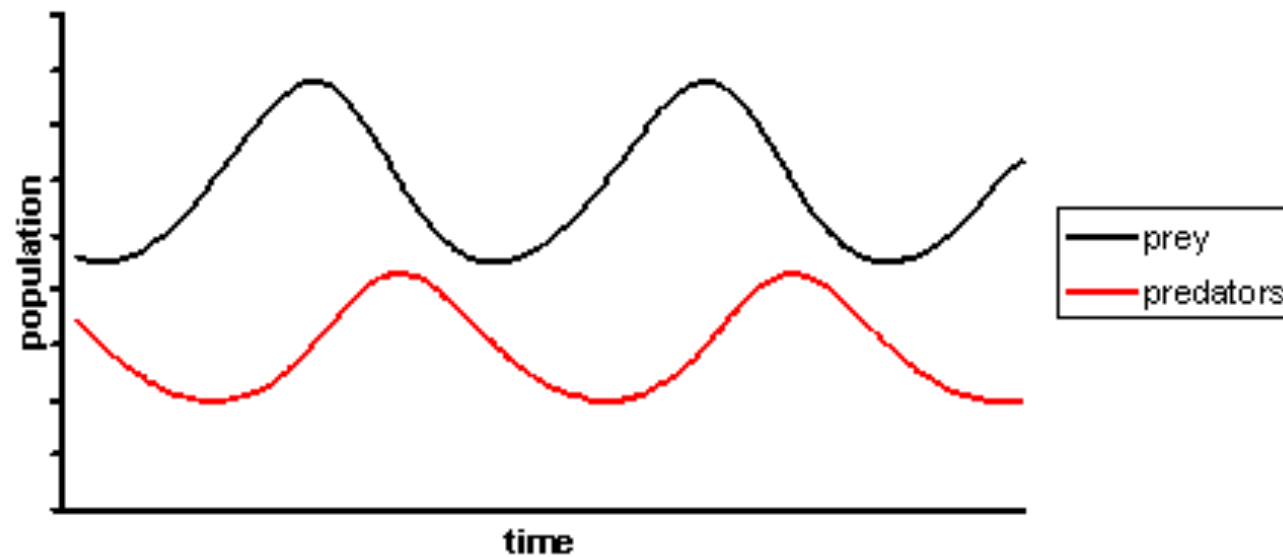
Prey-predation relationships: *Lotka-Volterra equations*

$$\frac{dx}{dt} = x(\alpha - \beta y)$$

$$\frac{dy}{dt} = -y(\gamma - \delta x)$$

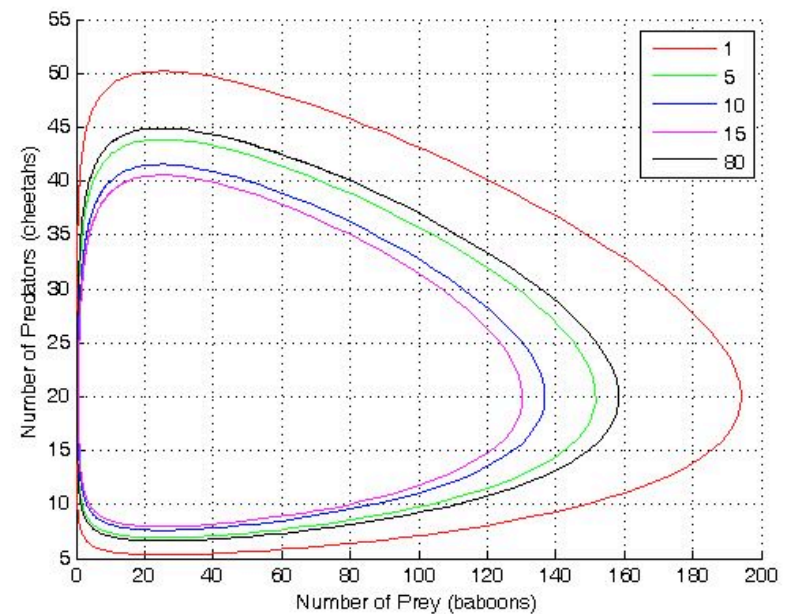
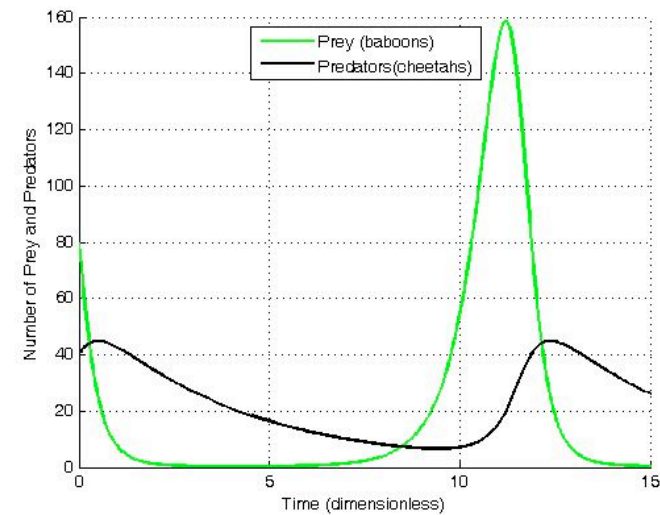
- y = predator abundance
 - x = prey abundance
 - dy/dt and dx/dt = growth of the two populations against time
 - α , β , γ and δ = parameters representing the interaction between the two species
- prey: unlimited food supply; exponential reproduction (αx); rate of predation (βxy), function of meeting frequency between predator and prey
 - predator: growth rate of the predator (δxy); γ natural death of the predator

Prey-predation relationships: *Lotka-Volterra solutions*



Prey-predation relationships: *Lotka-Volterra solutions*

- Example: baboons and cheetahs
- oscillations
- relationship between prey and predator abundance



Multiple populations

- Until now: no emigration / immigration
- “closed population”

$$N_{t+1} = N_t + B + I - D - E$$

N = abundance at time t

B = birth

I = immigration

D = death

E = emigration


$$N_{t+1} = (f + \phi)N_t + \text{migration}$$

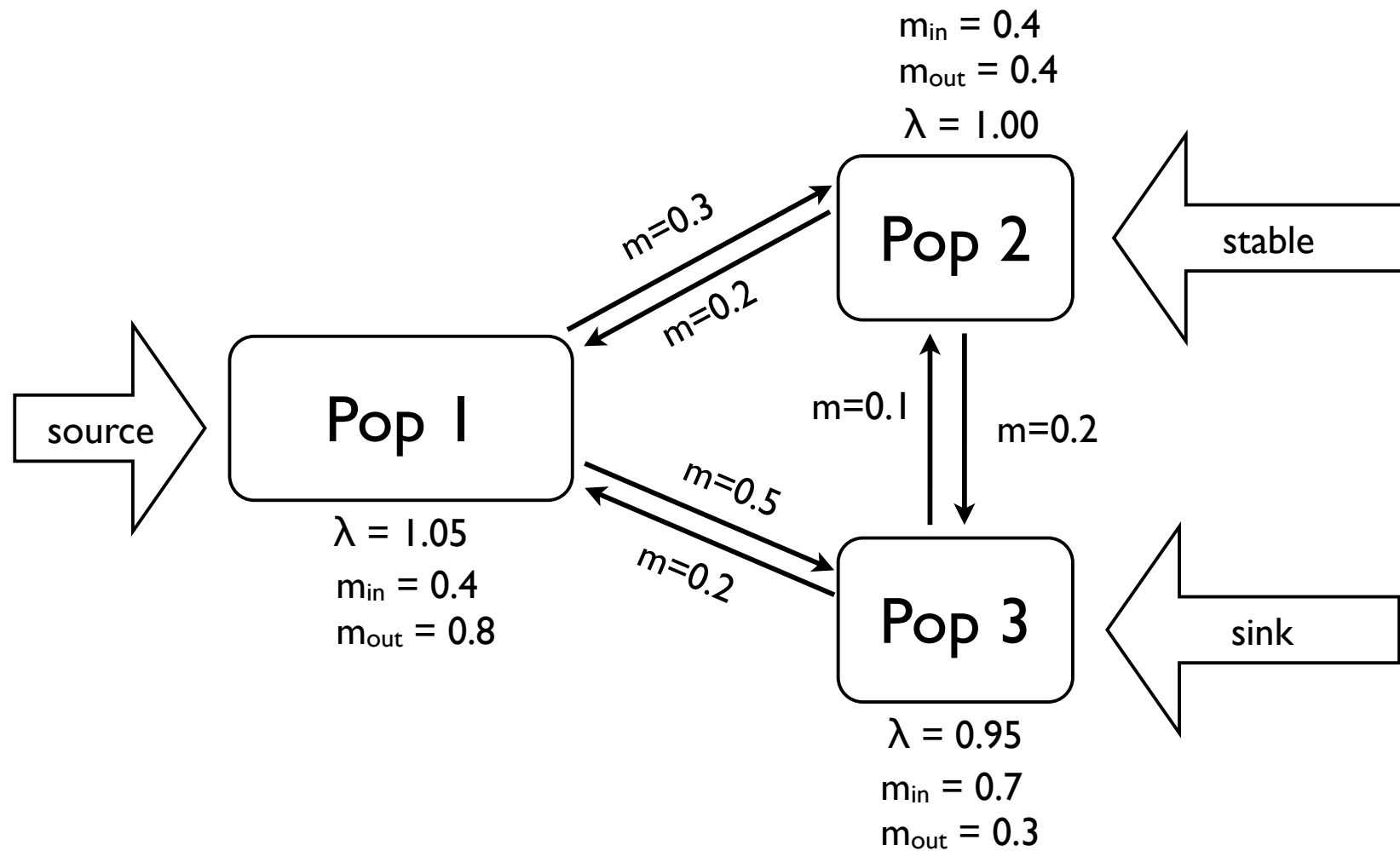
ϕ = survival at time t

f = fecundity

Multiple populations

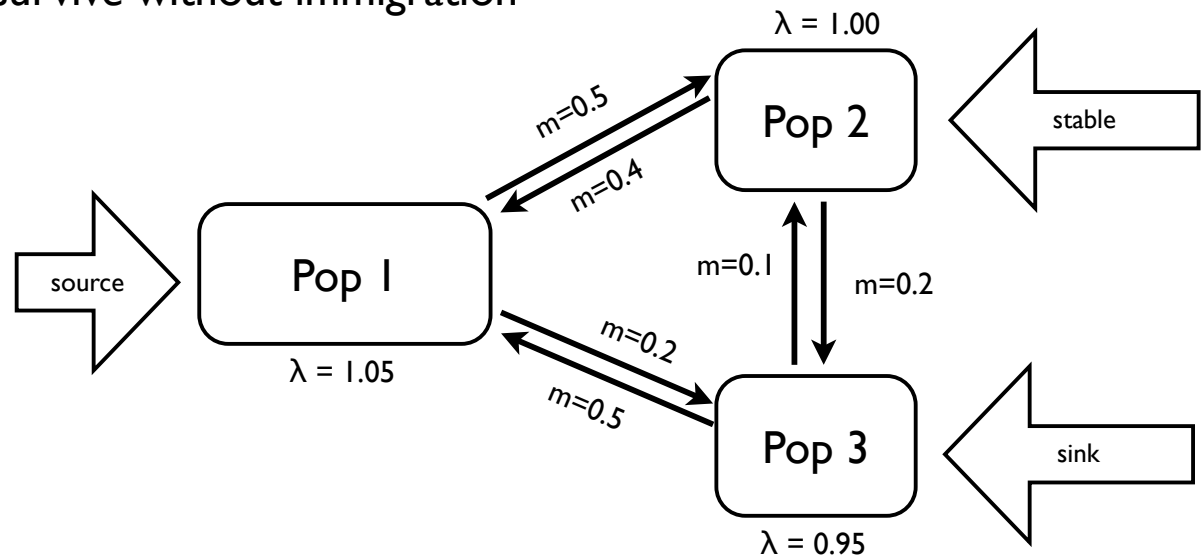
- immigration /emigration: difficult to estimate
 - ▶ radio-tracking / Capture-Mark-Recapture
 - ▶ ...
- Complex model, implying population dynamic for each deme

Multiple populations: *source/sink populations*



Multiple populations: *source/sink populations*

- source population: population that is strong contributor
 - ▶ more emigration than immigration
 - ▶ often: $\lambda > 1.0$
- sink population: population that drains on the system (metapopulation)
 - ▶ more immigration than emigration
 - ▶ population cannot survive without immigration

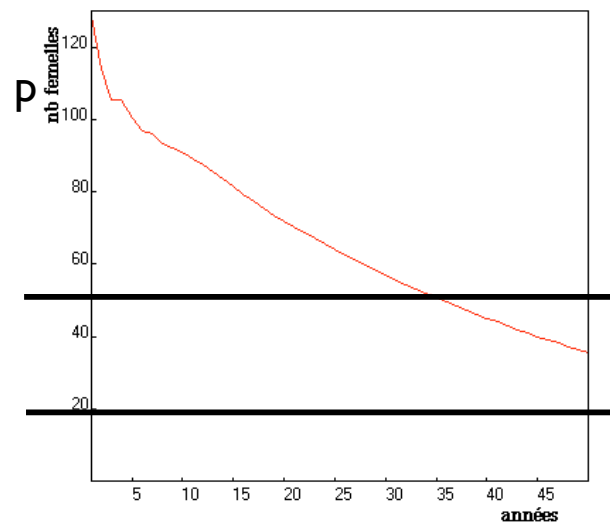


Population dynamic: summary

- important tools to estimate if population has a positive or negative growth rate.
- can be used for testing impact of treatments on experimental populations (e.g. test of parameters on the fitness, using the complete life cycle)
- can be use with natural populations
- ⚠ difficulties to evaluate all parameters (survival, fecundity), with the complete variance
- ⚠ complexity of some models...
- allow to evaluate the future of populations:
PVA (Population Viability Analysis)

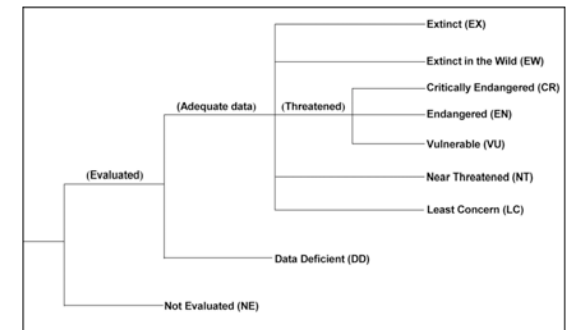
Population Viability Analysis: *estimate the future evolution...*

- PVA: application of data and models to estimate probabilities that a population will persist for a specific time into the future (and to give insights into factors that constitute the biggest threats)
- include:
 - ▶ survival rate, fecundity of different class ages
 - ▶ stochasticity
(on different variables, following specific models)
try to ground it on the field observation
 - ▶ density dependence models
(not necessary for small, low density - threaten - p
 - ▶ (predator / parasites interaction)
- Minimum Viable Population (MVP)
 - ▶ difficulty do define



Population Viability Analysis: *estimate the future evolution...*

- implication for conservation aspect
 - ▶ prediction of risks in small populations (risk of extinction, quasi-extinction, ...)
- IUCN Red List: Categories and Criteria (Version 3.1)
 - ▶ some criteria related to the probability of extinction:
E. Quantitative analysis of extinction risk



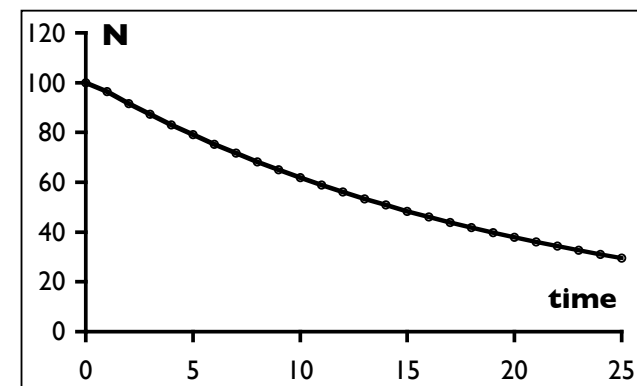
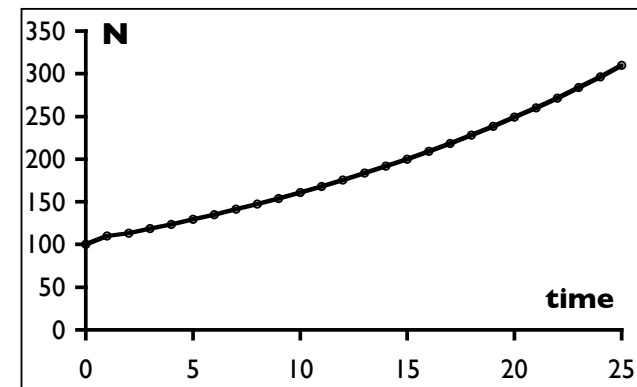
Use any of the criteria A-E	Critically Endangered	Endangered	Vulnerable
E. Indicating the probability of extinction	50% in 10 years or 3 generations (100 year max)	20% in 20 years or 5 generations (100 years max)	10% in 100 years

Population Viability Analysis: *simple model*

- based on a 2x2 Leslie Matrix

N=100	class age 0	class age 1
class age 0	0	1.2
class age 1	0.3	0.7

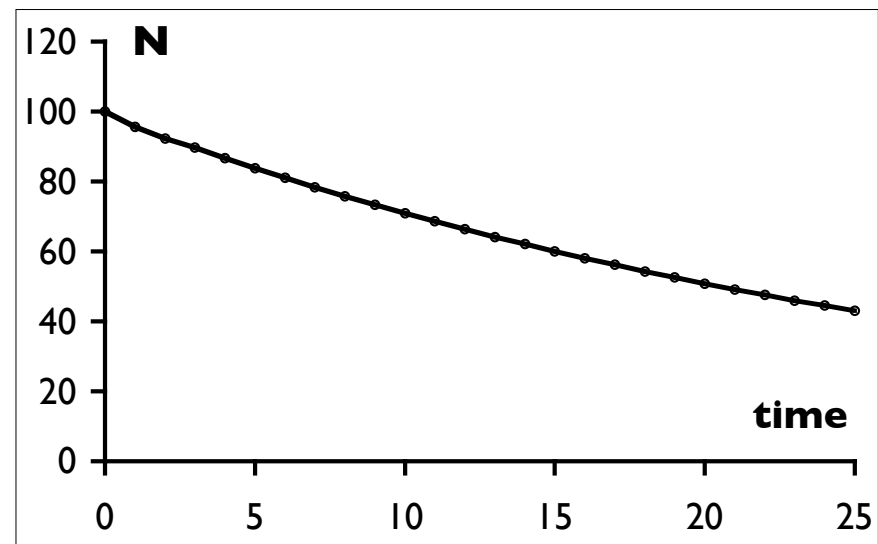
N=100	class age 0	class age 1
class age 0		1.2
class age 1	0.2	0.7



Population Viability Analysis: *simple model*

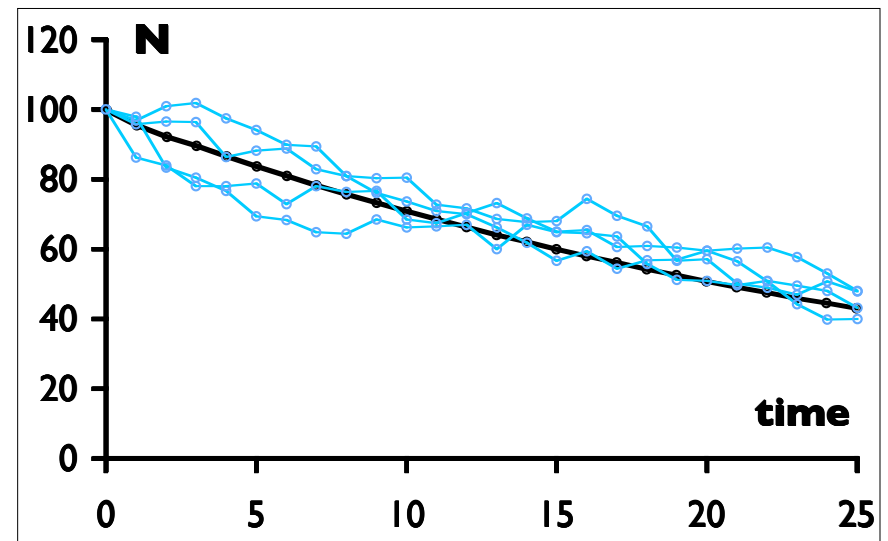
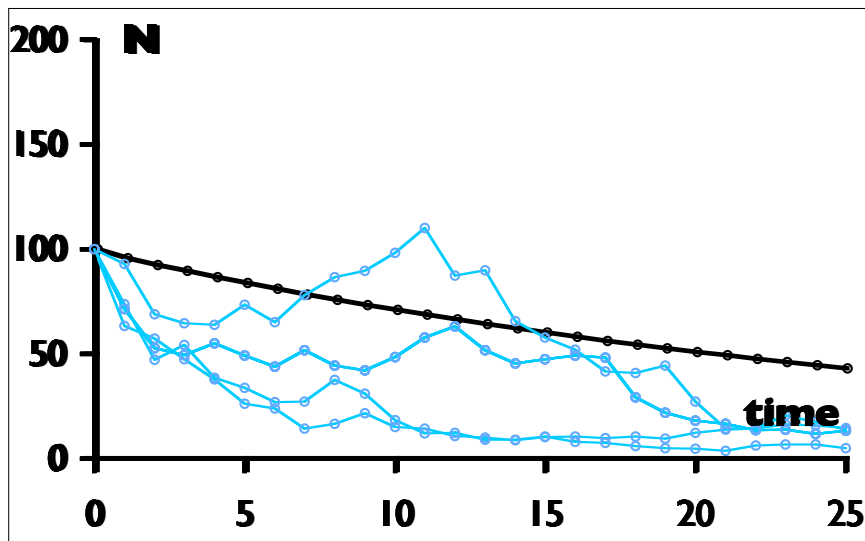
- based on a 5x5 Leslie Matrix

N=100	class age 0	class age 1	class age 2	class age 3	class age 4
class age 0	0	0	1	1	1
class age 1	0.5	0	0	0	0
class age 2	0	0.5	0	0	0
class age 3	0	0	0.7	0	0
class age 4	0	0	0	0.7	0.7



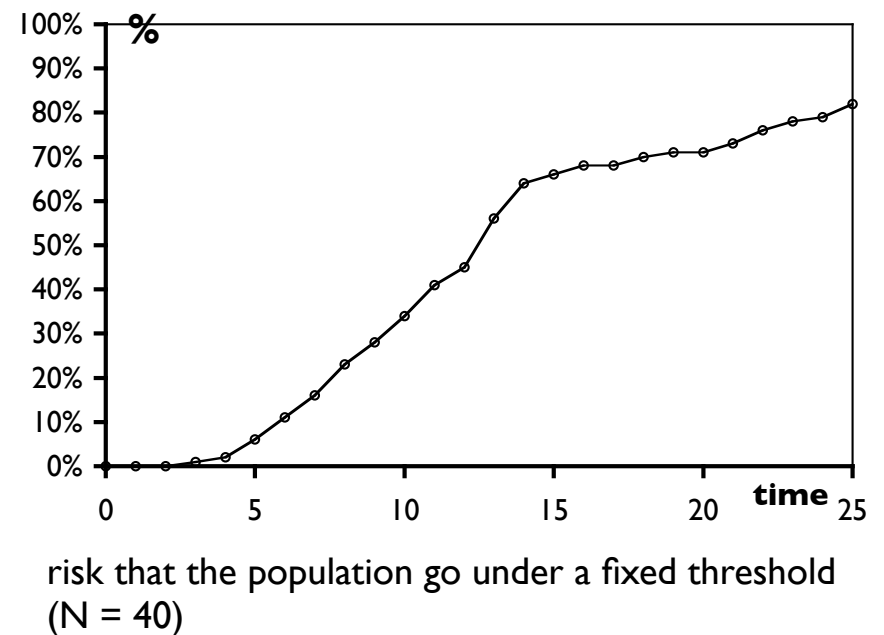
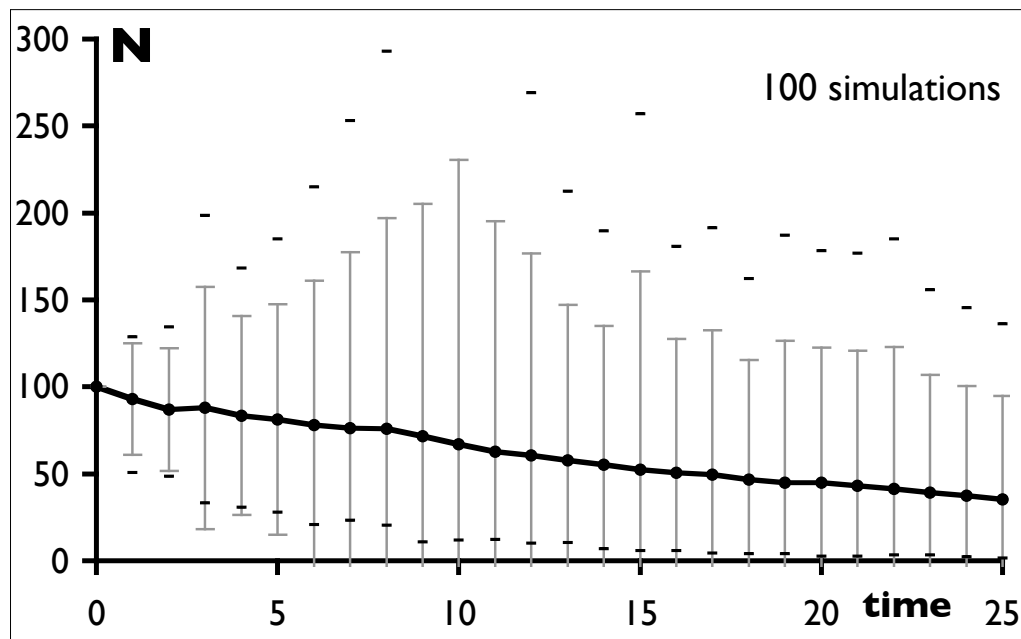
Population Viability Analysis: *add complexity in the model*

- stochasticity



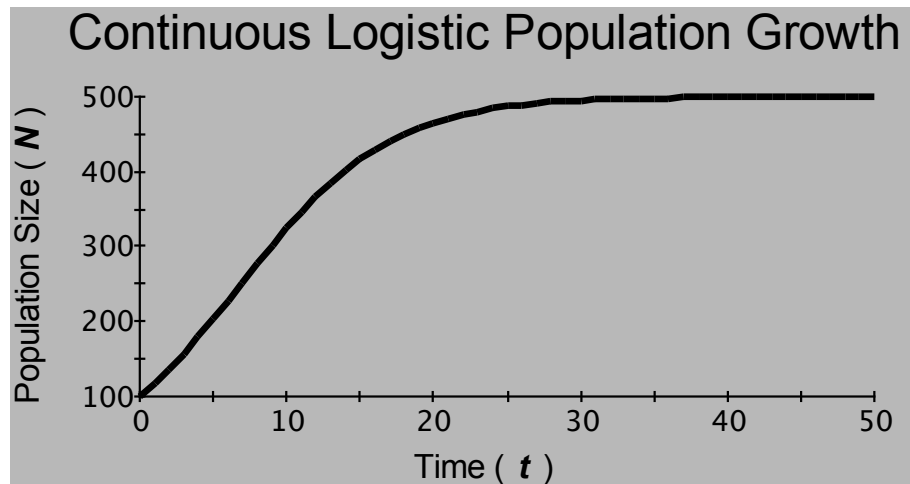
Population Viability Analysis: *add complexity in the model*

- stochasticity

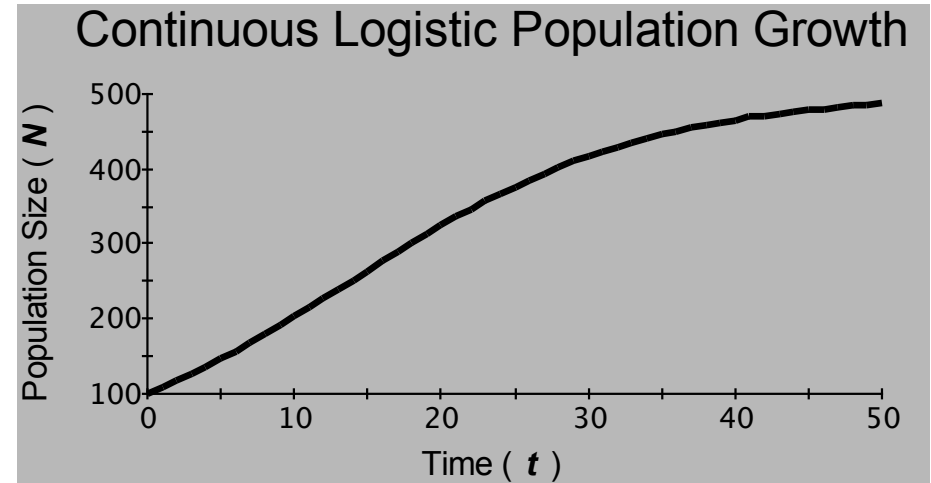


Population Viability Analysis: *add complexity in the model*

- stochasticity
- density dependence



$N_0=100; K=500; r=0.2$



$N_0=100; K=500; r=0.1$

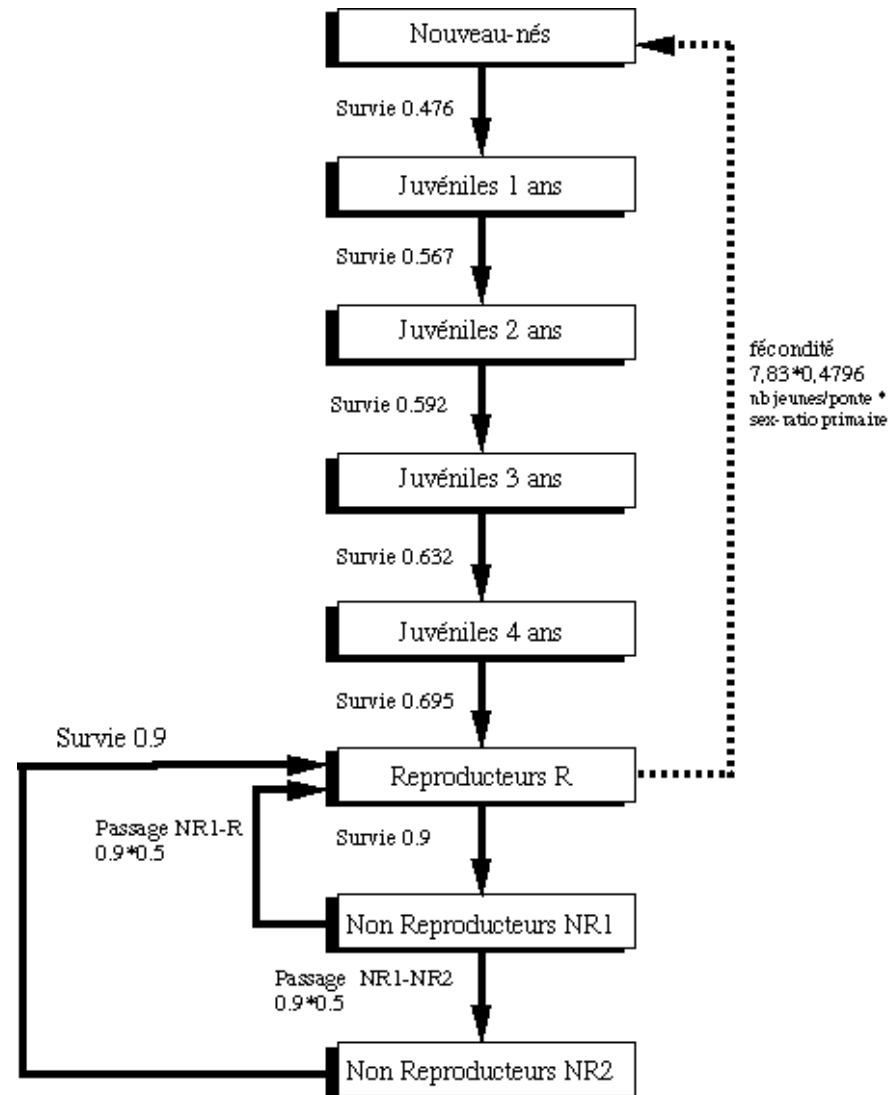
Population Viability Analysis: *sensitivity analysis*

- try to define the impact on the population size of changes in a single parameter
 - ▶ example:
 - with an increase of 10% of the survival rate of the adults, the population will increase by 5% every year
 - with an increase of 10% of the survival rate of the juveniles, the population will increase by 1% every year
 - with an increase of 90% of the fecundity, the population will increase by 5% every year
- important for conservation aspect
 - ▶ determine on which parameter the impact of improvement will be the highest
- example: *Vipera berus*



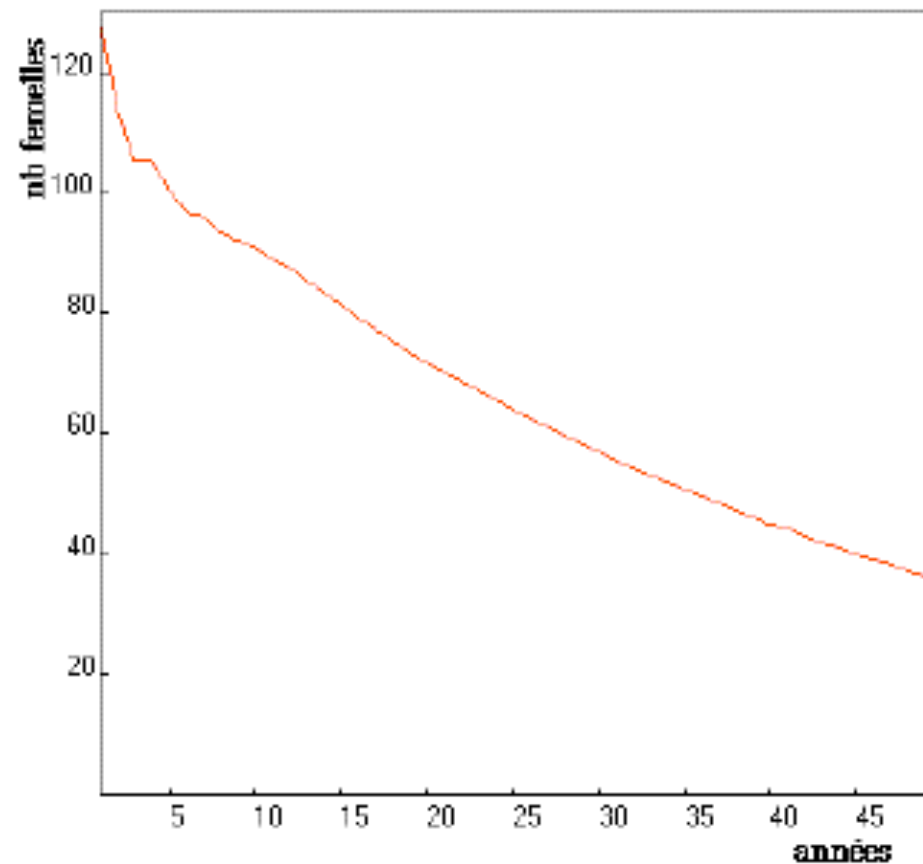
Population Viability Analysis: *Vipera berus*

Model I



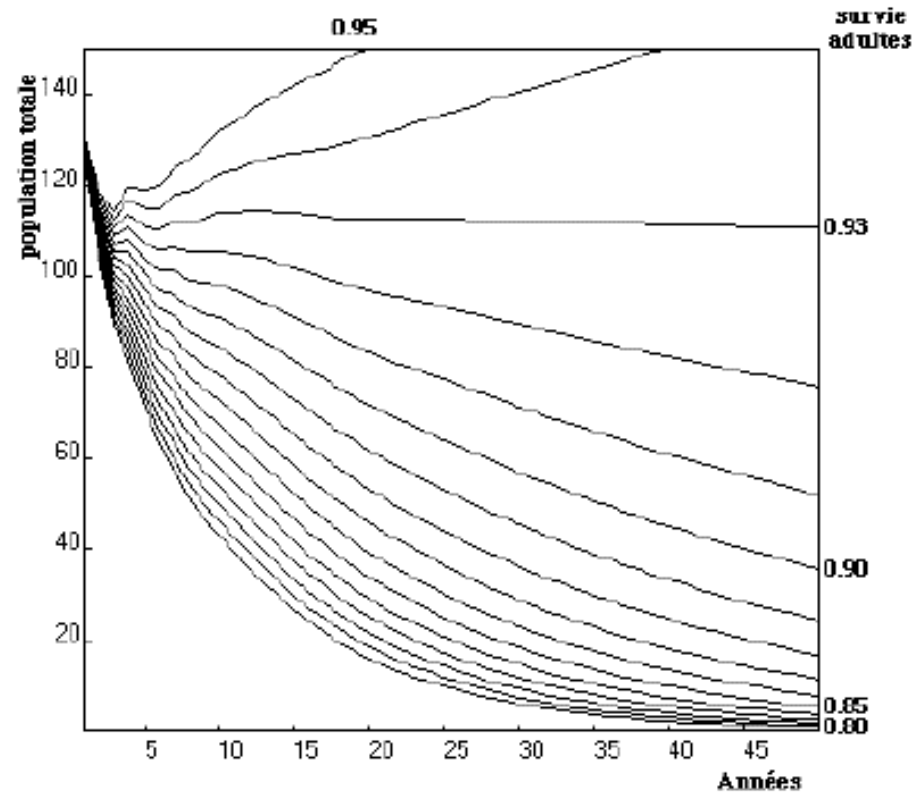
Population Viability Analysis: *Vipera berus*

PVA: mean female adult population size



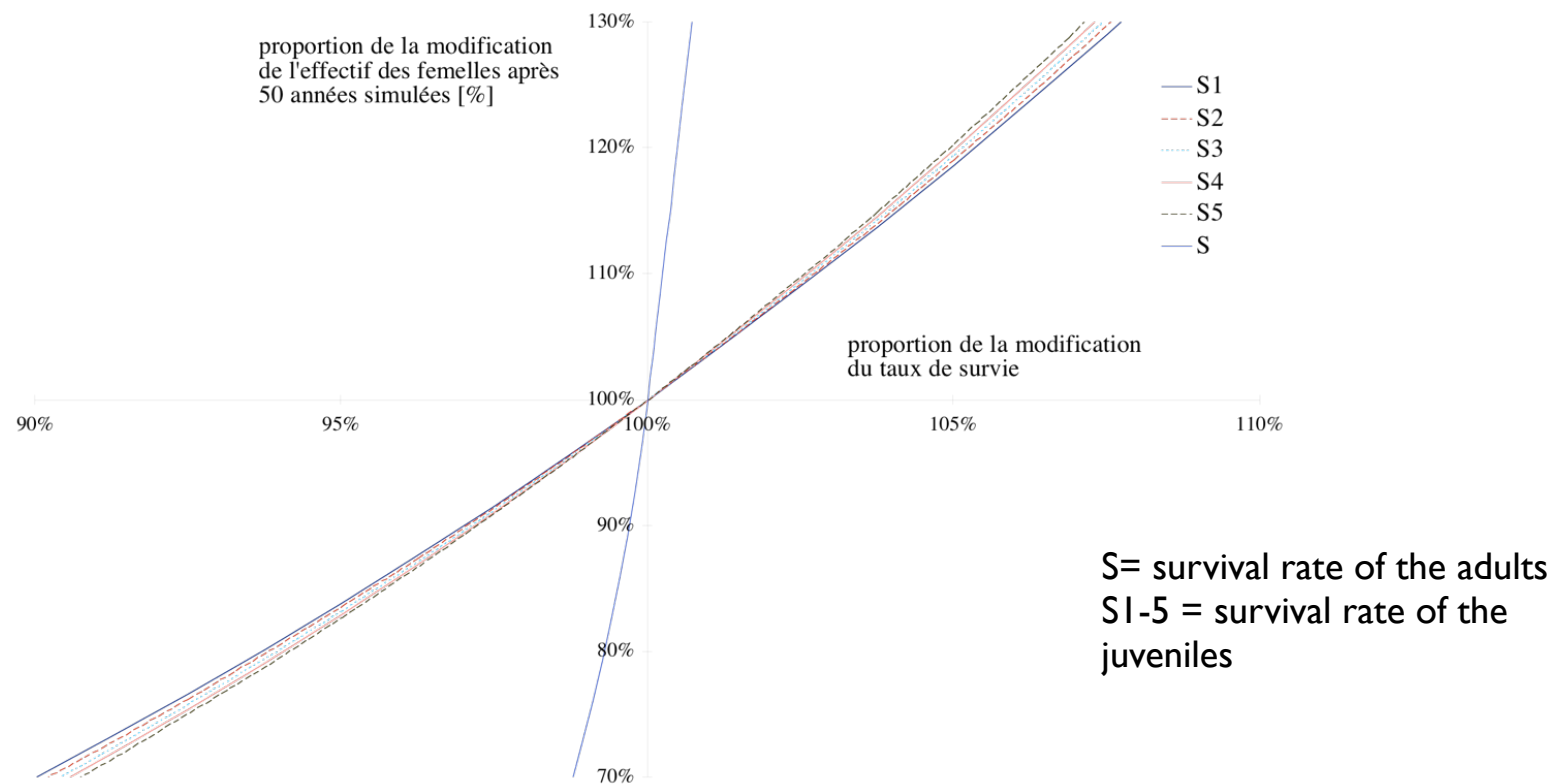
Population Viability Analysis: *Vipera berus*

PVA: mean female adult population size: impact of female survival rate



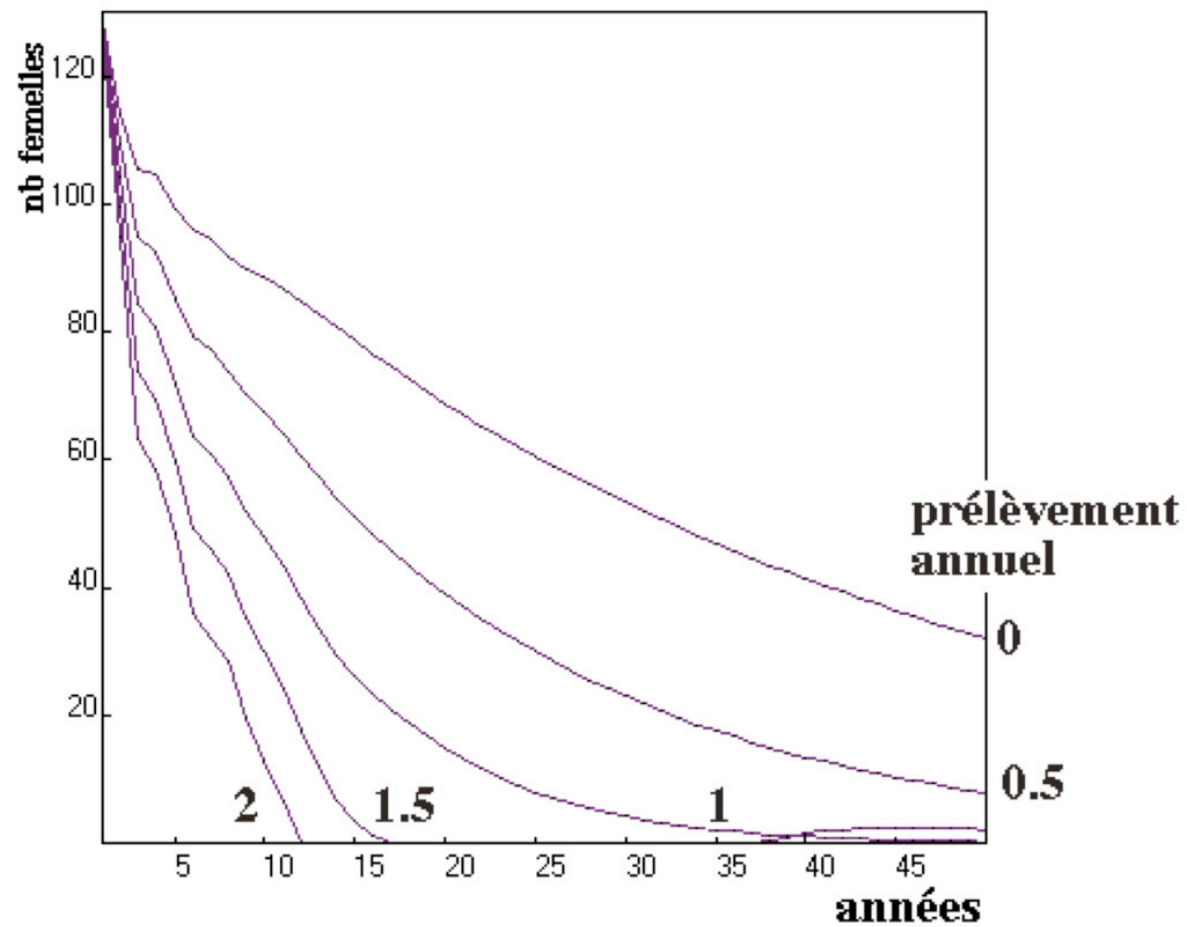
Population Viability Analysis: *Vipera berus*

PVA: sensitivity analysis: variation of survival rate and it impact on the population size after 50 years



Population Viability Analysis: *Vipera berus*

PVA: mean female adult population size: with additional culling



Conclusions

- simple models can already explain observed/expected increase/decrease/fluctuation of populations
- complexity for complex life cycles
- test the complete life cycle
- important impact on conservation aspects

some softwares and links

- RAMAS: www.ramas.com
 - ▶ most commonly used software
 - ▶ not free!
- ULM: <http://www.biologie.ens.fr/~legendre/ulm/ulm.html>
 - ▶ free
 - ▶ numerous models, high level of complexity
- POPULUS: <http://www.cbs.umn.edu/populus/>
 - ▶ very simple, numerous models
 - ▶ more for demo than for analyses