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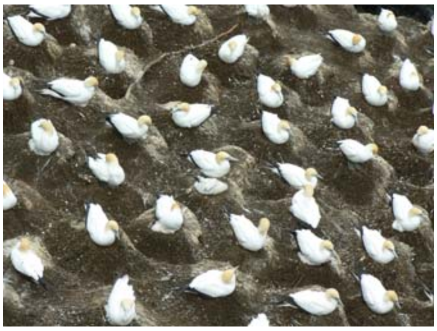
Lecture 5: Modelling Population Dynamics – N(t)

Part II: Stochastic limited growth



Jürgen Groeneveld
SGGES, University of Auckland, New Zealand

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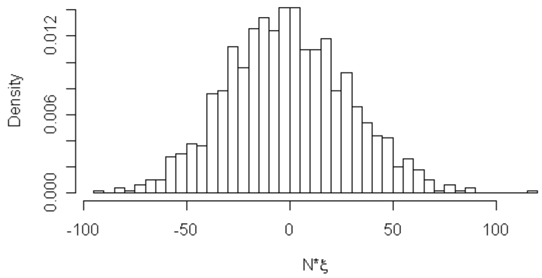
How to deal with noise?

$$N_{t+1} = RN_t\left(1 - \frac{N_t}{K}\right) + N_t + N_t\xi(\mu, \sigma)$$

ξ a normally distributed random variable with $\mu = 0$ and $\sigma = 0.05$



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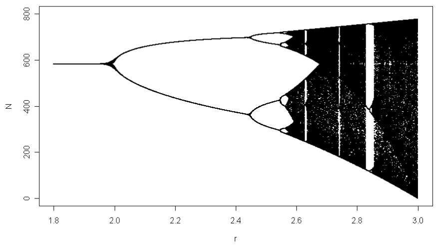
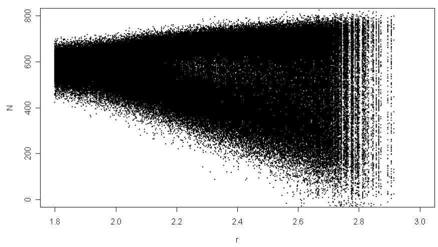


$\sigma = 0$



$\sigma = 0.05$

Extinctions more likely

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ξ a normally distributed random variable with $\mu = 0$ and $\sigma = 0.05$

Are there continuous descriptions of this problem?

$$\frac{dN(t)}{dt} = rN(t)\left(1-\frac{N(t)}{K}\right) + N(t)\xi(\eta,\sigma)$$

Langevin equation

But only specialists really work with them

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Stochastic differential equation:

$$\frac{dN(t)}{dt} = rN(t)\left(1-\frac{N(t)}{K}\right) + N(t)\xi(\eta,\sigma)$$

↓

Ito´s Lemma, Stratonovich

↓

Partial differential equation (**Fokker Planck**)

$$\frac{\partial P(N,t)}{\partial t} = -\frac{\partial}{\partial N}\left[A_1(N)P(N,t)\right] + 0.5\frac{\partial^2}{\partial N^2}\left[A_2(N)P(N,t)\right]$$

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So, can we calculate P(N,t)?

$$\frac{\partial P(N,t)}{\partial t} = -\frac{\partial}{\partial N}\left[A_1(N)P(N,t)\right] + 0.5\frac{\partial^2}{\partial N^2}\left[A_2(N)P(N,t)\right]$$

Well, I can't and most often it is not tractable, but if dynamics end in an equilibrium and the system has no memory than…..

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$$P^*(N) = c\exp\left\{\left[\frac{2r}{\sigma^2} - 1\right]\ln(N) - \frac{2rN}{K\sigma^2}\right\}$$

Maximum of P*:

$$N_{max} = K\left(1 - \frac{\sigma^2}{2r}\right)$$

if $\sigma^2 = 0$, than $N_{max} = K$

Mean of P*:

$$\overline{N} = K$$

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$$P^*(N) = c\exp\left\{\left[\frac{2r}{\sigma^2} - 1\right]\ln(N) - \frac{2rN}{K\sigma^2}\right\}$$

Good old Paramecium

r = 0.81
K = 582.5
σ = 0.05

Software implemented by
Lorenz Fahse

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But system also has to reach stationary stage:

```
# Simulation example for comparison with Fokker-Planck result
comp<-function(sigma,repe)
{
r<-exp(0.81)-1

N <- rep(1, times = 1000)
K <- 582.5
All <- c(1:repe)

for(j in 1:repe)
{
for (i in 1:1000)
{

    N[i+1] <- N[i]+(r*N[i]*(1-N[i]/K) + N[i]*rnorm(1,0,sigma))
    if (N[i+1]<0) N[i+1] = 0
}
All[j]=N[i]
}

hist(All,freq=T, xlim=c(0,1500),breaks=30)
}
```

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Modelling population dynamics

	Time discrete	Time continuous
Unlimited growth	$N_{t+1} = R^t N_0$	$N(t) = N(0)\exp(rt)$
Limited growth	Simulations – complex dynamics	$\frac{dN(t)}{dt} = rN(t)\left(1 - \frac{N(t)}{K}\right)$
Stochastic limited growth	Simulations – Extinction	$\frac{dN(t)}{dt} = rN(t)\left(1 - \frac{N(t)}{K}\right) + N\xi(0,\sigma)$

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Example 1: How does individual behaviour influence population dynamics?

Fahse et al. 1998, AmNat

Complex individual-based and spatially explicit simulation model for nomadic lark species (Alaudidae) in a heterogeneous, randomly varying landscape (Nama-Karoo, South Africa)

Optimal flocking and searching strategy?

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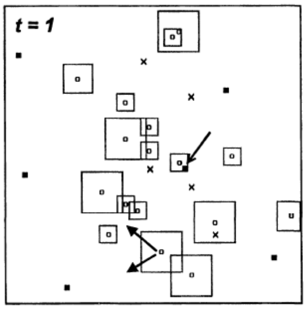
How does individual behaviour influence population dynamics?



modified after Fahse et al. 1998, AmNat

Larks move in small flocks, searching for grass patches to breed

Grass patches occur at random (rain fall) and last only 2 weeks

Grass patch – filled square
Flocks – circles
Breeding Flocks – crosses
Squares – range of vision

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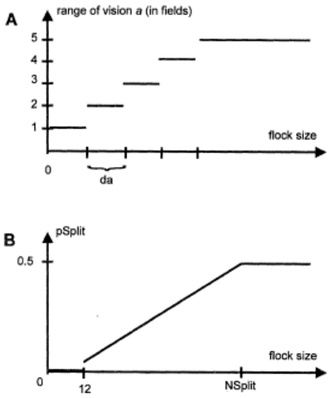
How does individual behaviour influence population dynamics?



Flock dynamics

modified after Fahse et al. 1998, AmNat

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How does individual behaviour influence population dynamics?

Computation would be too time consuming

Growth rate f is a complex function:

dN/dt = f(Nad,Njuv,flock size distribution, da, pSplit, landscape, mortality)

Idea: Population dynamics and behaviour are operating on two time scales

Separation of time scales (Haken 1991)

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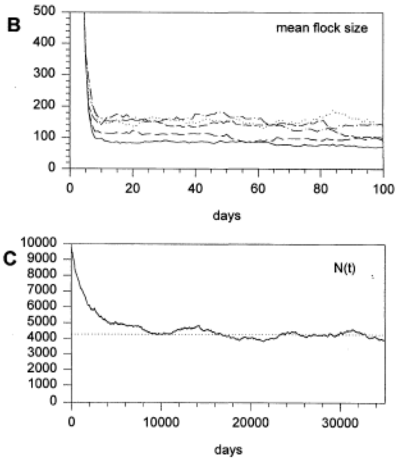
Separation of time scales:

Fast variable: f = dN/dt
Slow variable: N(t)

That means there is a characteristic f for any given N

Therefore it is possible to split the model:

behavioural model
population dynamics model



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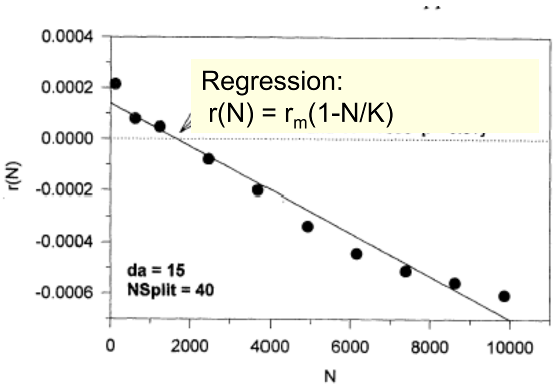
Separation of time scales:

Method:
Switch of demographic processes in the simulation model and determine a Distribution of f(N) for several N´s



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Comparison between full simulation model and the method of separated time scales:

$$\frac{\Delta N(t)}{\Delta dt} = rN(t)\left(1 - \frac{N(t)}{K}\right)$$

derive the parameters from bottom up models

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Population Viability Analysis (PVA)

Application of ecological theory

Following: Grimm and Wissel 2004, OIKOS

The intrinsic mean time to extinction: a unifying approach to analysing persistence and viability of populations

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I Basics of Population Viability Analysis PVA

Population models often aim to assess population viability

Assessing the risk that a population goes extinct

To compare the effect of different measures and scenarios, this risk has to be quantified.

What would be good measures?

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Simple deterministic case:

Remember age structured models

$$\begin{pmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix} \bullet \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \end{pmatrix} = \begin{pmatrix} n_{1,t+1} \\ n_{2,t+1} \\ n_{3,t+1} \end{pmatrix}$$

The growth rate λ is a good measure

If $\lambda \geq 1$, population will persist forever
If $\lambda < 1$, population will deterministically go extinct

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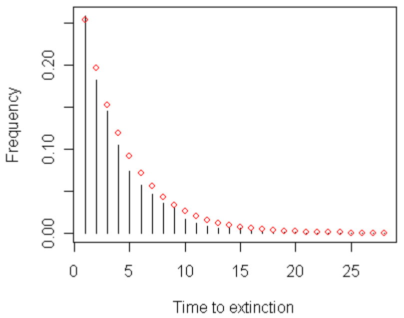
Stochastic case:

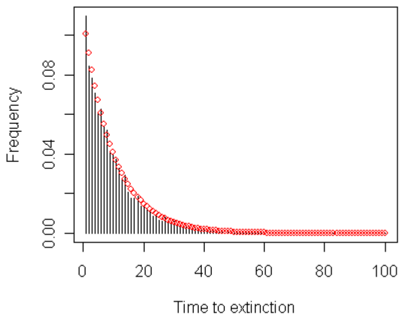
All populations have a certain risk of extinction!

$$f = \lambda \exp(-\lambda t) \qquad < f >= 1/\lambda$$



$\lambda = 0.25$

Mean ~ 3.9



$\lambda = 0.1$

Mean ~ 10

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What is the currency of our PVA?

Usually people are interested in the Risk P_0 that a population has gone extinct during a time t.

$$P_0(t,T_M) = \langle f \rangle = \frac{1}{T_M}\int_0^t \exp\left(\frac{t}{T_M}\right)dt$$

Relationship of $P_0(t)$ and T_m

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So far, we assumed that extinction times are exponentially distributed.

Lets analyse general demographic models

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Master Equation – Markov model
Birth and death type

$$\frac{dP_n(t)}{dt} = b_{n-1}P_{n-1}(t) + d_{n+1}P_{n+1}(t) - b_nP_n(t) - d_nP_n(t)$$

$P_n(t)$: Probability having n individuals at time t

b_n: birth rate

d_n: death rate

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Birth and death type

$$\frac{dP_n(t)}{dt} = b_{n-1}P_{n-1}(t) + d_{n+1}P_{n+1}(t) - b_nP_n(t) - d_nP_n(t)$$

State of t does only depend on the state t-1 and not on previous time steps (no memory)

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Equation from first principles

$$\frac{dP_n(t)}{dt} = b_{n-1}P_{n-1}(t) + d_{n+1}P_{n+1}(t) - b_nP_n(t) - d_nP_n(t)$$

Solution of $P_0(t)$ can be approximated!

No detailed description here – see Grimm and Wissel 2004 for further references.

Main idea: Set of linear (differential) equations, i.e. Solution can be expressed by its eigenvectors and eigenvalues! Largest eigenvalue and eigenvector will dominate the solution and therefore the contribution of all other eigenvectors can be neglected.

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$$\frac{dP_n(t)}{dt} = b_{n-1}P_{n-1}(t) + d_{n+1}P_{n+1}(t) - b_nP_n(t) - d_nP_n(t)$$

Note that b and d can be functions, e.g. logistic equation, Equation must be linear in P

$$P_n(t) = \sum_i u_{n,i} c_i \exp(-\omega_i t)$$

$u_{n,i}$ is the n-th component of the normalized i-th right hand side eigenvector ω_1 is the i-th eigenvalue of the i-th eigenvector (right hand side)

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$$P_n(t) = \sum_i u_{n,i} c_i \exp(-\omega_i t)$$

If $\omega_1 >> \omega_i$ for all i > 1 and using that all u_i are normalized

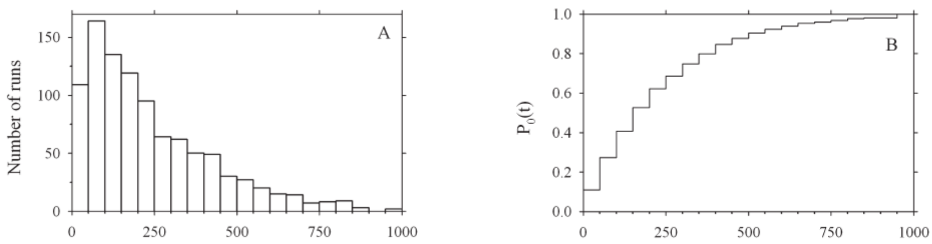
$$P_0(t) = 1 - c_1 \exp(-\omega_1 t)$$

What do the parameters mean?

$$\omega_1 = \frac{1}{T_M}$$

Meaning of c_1?

Grimm and Wissel 2004 suggest a protocol to derive the intrinsic mean time T_M to extinction from simulations



Time to extinction   Time to extinction

modified after Grimm and Wissel 2004

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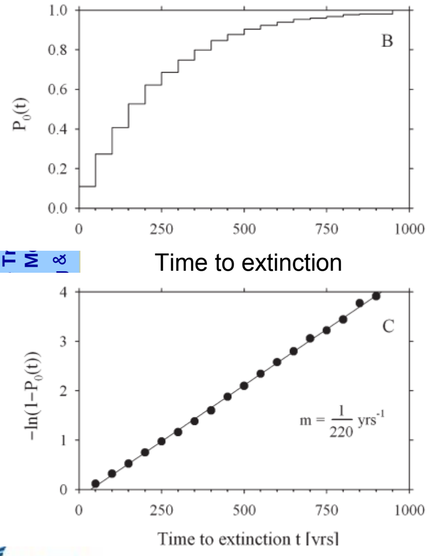
modified after Grimm and Wissel 2004



$$P_0(t) = 1 - c_1 \exp\left(-\frac{1}{Tm}t\right)$$

$$-\log(1 - P_0(t)) = -\frac{1}{Tm}t + \log(c_1)$$

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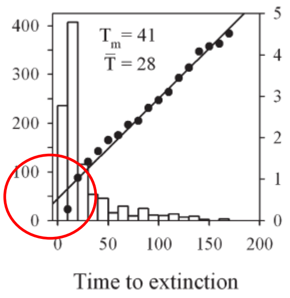
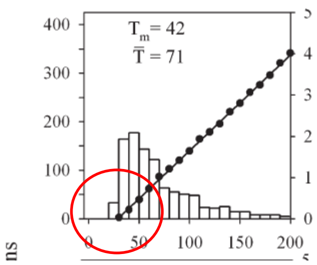
Theoretically it can be shown that c_1 reflects the initial conditions

Bad conditions



Population much below its capacity at the start of the simulation

Good conditions



Population at its capacity at the start of the simulations

modified after Grimm and Wissel 2004

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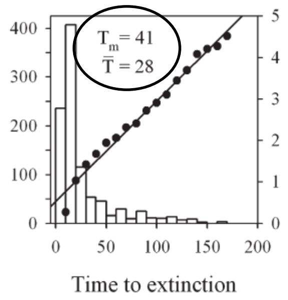
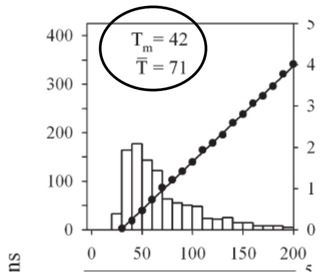
T_m does not depend on the initial conditions!

Bad conditions



Good conditions



Population much below its capacity at the start of the simulation

Population at its capacity at the start of the simulations

Modified after Grimm and Wissel 2004

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Modelling population dynamics

	Time discrete	Time continuous
Unlimited growth	$N_{t+1} = R^t N_0$	$N(t) = N(0)\exp(rt)$
Limited growth	Simulations – complex dynamics	$\frac{dN(t)}{dt} = rN(t)\left(1 - \frac{N(t)}{K}\right)$
Stochastic limited growth	Simulations – Extinction	$\frac{dN(t)}{dt} = rN(t)\left(1 - \frac{N(t)}{K}\right) + N\xi(0,\sigma)$

Equation based modelling provides important ways to aggregate, understand and to communicate results of simulation models

Simulation models might be needed to parameterize equation based models

Ecological theory can provide robust measures (e.g. Tm)

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But grey is all theory…

Thank you for your attention!

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