

Matrix models for population management and conservation



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All you always wanted to know about Matrix Models....

- Matrix model formulation
- Some (palatable) elements of demographic theory
- Special emphasis on conservation and management
- The theory of exploited populations
- Aimed at giving you autonomy
- Hands-on work: exercises with program ULM
- Hands-on work: your material, data and questions
- Lectures and exercises: interactivity needed

EXERCISES WITH SOLUTIONS

EXERCISE	WHEN	TOPIC	BIOLOGICAL MATERIAL
1	Day 1 AM	Introduction to matrix models and ULM	Barn swallow
2	Day 1 PM	Sensitivities and elasticities	White stork
3	Day 2 AM	Multisite/multistate models	Black-headed gull
4	Day 2 AM	Random Environment	Chamois
5			Kidneywetch
6	Day 2 PM	Exploited populations	Red Deer
7	Day 2 PM	Density dependence	Cormorant
8		Density-dependence, chaos	Ricker model
9	Day 3 AM	Demographic stochasticity	House Sparrow



*If you are faced by a difficulty or
a controversy in science,
an ounce of algebra is worth
a ton of verbal argument*

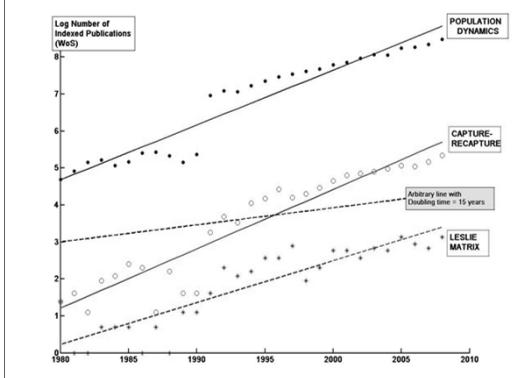
J.B.S. Haldane



Hunting Book, Gaston Phoebus, 1390



The wildlife techniques manual, 2012



Lecture 1

Matrix model formulation



Patrick "George" LESLIE,
whose famous 1945 paper
launched the development
of « matrix models »



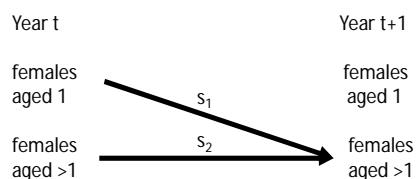
Matrix model formulation

- A simple example
- Some numerical results
- A first quick look to different generalizations



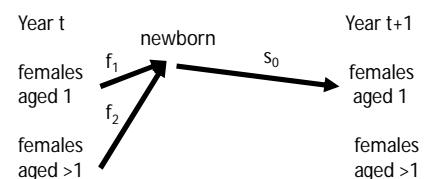
A simple example

1) SURVIVAL in a barn swallow *Hirundo rustica* population



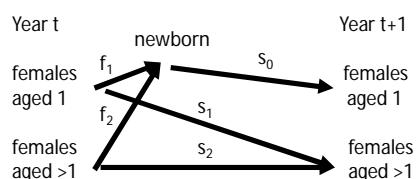
A simple example

2) REPRODUCTION in a barn swallow population



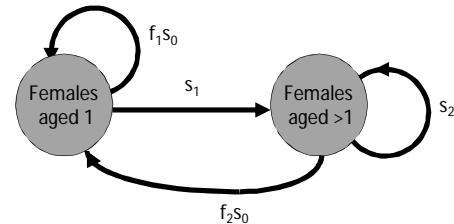
A simple example

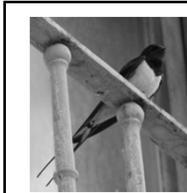
OVERALL LIFE CYCLE in a barn swallow population



A simple example

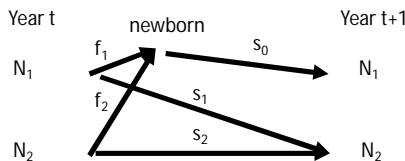
LIFE CYCLE graph in a barn swallow population





A simple example

QUANTITATIVE LIFE CYCLE in a barn swallow population



A simple example

QUANTITATIVE LIFE CYCLE in a barn swallow population

$$N_1(t+1) = s_0 f_1 N_1(t) + s_0 f_2 N_2(t)$$

$$N_2(t+1) = s_1 N_1(t) + s_2 N_2(t)$$



A Mathematical Model

- i.e., a mathematical object (linear equations)...
- based on assumptions
(discrete time scale, life cycle, **constant parameters**)
- potentially useful (numerical & formal calculations)
- to answer biological questions (is the pop. growing?)
- easily generalizable



A simple example

PARAMETER ESTIMATES in a barn swallow population

$s_0 = 0.20$ $f_1 = 3/2$ $f_2 = 6/2$
(50 % breed at age 1, 6 young produced,
divide by 2 for balanced- sex ratio)

$s_1 = 0.50$ $s_2 = 0.65$
(analysis of dead recoveries)



A simple example

QUANTITATIVE LIFE CYCLE in a barn swallow population

Two linear
Equations

$$N_1(t+1) = 0.30 N_1(t) + 0.60 N_2(t)$$

$$N_2(t+1) = 0.50 N_1(t) + 0.65 N_2(t)$$

One matrix
Equation

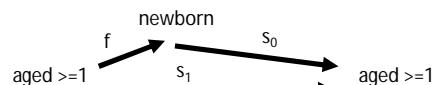
$$\begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_{t+1} = \begin{bmatrix} 0.30 & 0.60 \\ 0.50 & 0.65 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_t$$

$$N_{t+1} = M N_t, \text{ alike a product of scalars}$$



An even simpler example

QUANTITATIVE LIFE CYCLE in a house sparrow population



$$\text{One linear scalar equation } N(t+1) = (s_0 f + s_1) N(t)$$



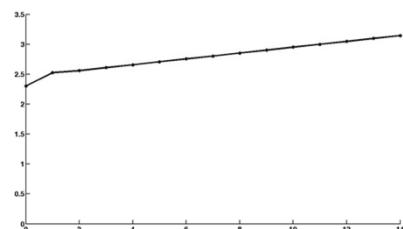
Some Numerical Results

QUANTITATIVE LIFE CYCLE
in a barn swallow population

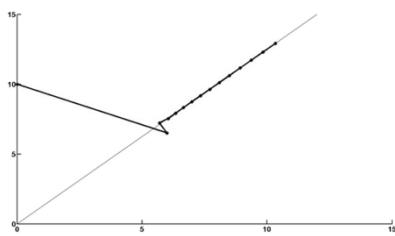
Two linear Equations $N_1(t+1) = 0.30 N_1(t) + 0.60 N_2(t)$
 $N_2(t+1) = 0.50 N_1(t) + 0.65 N_2(t)$

$t =$	0	1	2	3	...
$N =$	0	6	5.7	6.05	...
	10	6.5	7.7	7.55	...

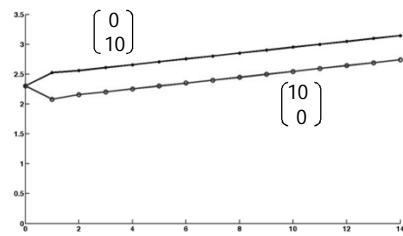
Trajectory over time
Asymptotically exponential growth



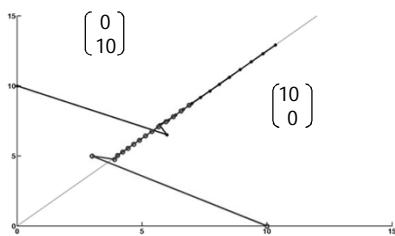
Trajectory in the phase plane
Asymptotically stable age structure



Trajectory over time
two different initial vectors



Trajectory in the phase plane
two different initial vectors



A simple example

- Regular (asymptotic) behaviour
- Partially dependent on initial conditions
- Encourages formal analysis (next lecture)
- A key assumption: constant parameters

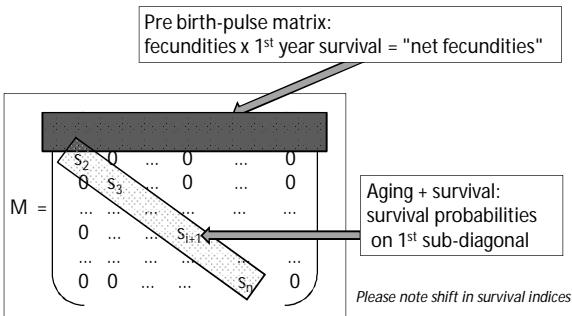
Model as a tool: use it to answer questions

- Growth ?
- Structure ?
- Change in parameters ?
- Sustainability of human induced action ?
- Effect of evolutionary change ?
- ...

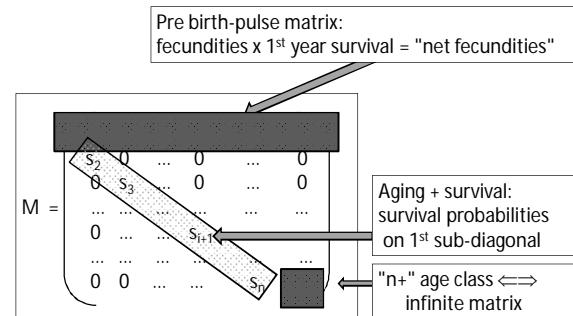
Model as a tool: suggested modeling process

- Biological Questions
- Review Information available
- Build model
- Translate biological Q. into technical Q.
- Use model to answer Questions

Matrix Models: the basic Leslie age-structured model



Matrix Models: a first variation

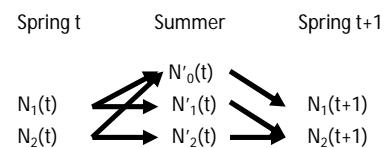


Matrix Models: a variety of structures

- Age classes and time scale
- Stages
- Sites
- Sexes
- Seasonal models
- Age x Sites



Matrix Models: seasonal models





Matrix Models: seasonal models

Spring t Summer Spring t+1

$N(t)$ $N'(t)$ $N(t+1)$

M_1 M_2

$$M_1 = \begin{bmatrix} f_1 & f_2 \\ 1 & 0 \\ 0 & 1 \end{bmatrix} \quad M_2 = \begin{bmatrix} s_0 & 0 & 0 \\ 0 & s_1 & s_2 \end{bmatrix}$$


Matrix Models: seasonal models

$$M_1 = \begin{bmatrix} f_1 & f_2 \\ 1 & 0 \\ 0 & 1 \end{bmatrix} \quad M_2 = \begin{bmatrix} s_0 & 0 & 0 \\ 0 & s_1 & s_2 \end{bmatrix}$$

$M_2 M_1 = [2 \times 3 \text{ matrix}] \times [3 \times 2 \text{ matrix}]$
is a 2×2 matrix

$$M_2 M_1 = \begin{bmatrix} s_0 f_1 & s_0 f_2 \\ s_1 & s_2 \end{bmatrix}$$

... the 2×2 original matrix



Matrix Models: post birth-pulse model

Spring t Summer Spring t+1

$N(t)$ $N'(t)$ $N(t+1)$

M_1 M_2

$$N'(t+1) = M_2 M_1 N'(t)$$

$$M_2 M_1 = \begin{bmatrix} f_1 s_0 & f_2 s_1 & f_2 s_2 \\ s_0 & 0 & 0 \\ 0 & s_1 & s_2 \end{bmatrix}$$

Matrix Models: a variety of generalizations

Feature	Recurrence equation	Type of model	Math tools	Key reference
Constant parameters	$N_{t+1} = MN_t$	Matrix models <i>stricto sensu</i>	Linear Algebra	Caswell (2001) Matrix population models
Density-dependence	$N_{t+1} = M(N_t)N_t$	Density-dependent matrix models, Discrete time logistic growth	Nonlinear dynamics	Caswell (2001) Matrix population models
Random Environment	$N_{t+1} = \mathbf{M}_t N_t$	Random Environment models	Products of random matrices	Tuljapurkar (1990) Population dynamics in variable environments
Demographic stochasticity	$E(N_{t+1}/N_t) = MN_t$	Branching Processes	Applied Probability	Gosselin, Lebreton (2001) The potential of branching processes... in Ferson & Burgman (Eds)

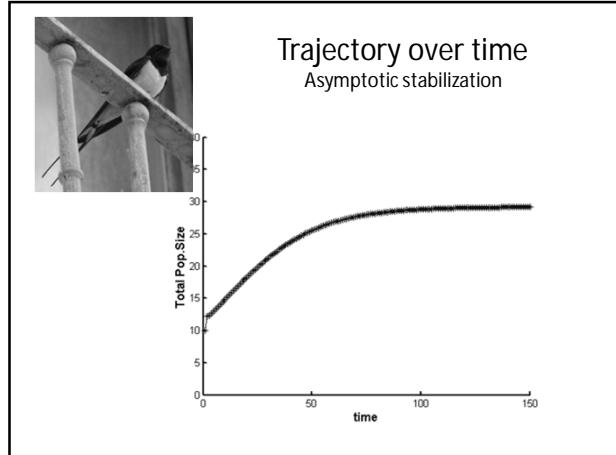


Matrix Models: Density-dependence

$$N_1(t+1) = s_0(N_1(t) + N_2(t)) f_1 N_1(t) + s_0 f_2 N_2(t)$$

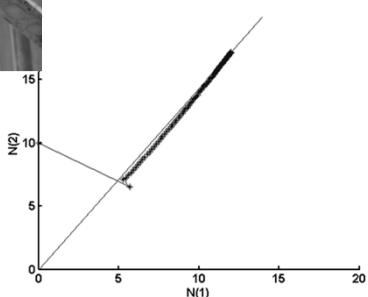
$$N_2(t+1) = s_1 N_1(t) + s_2 N_2(t)$$

e.g. $s_0(N_1(t) + N_2(t)) = 0.2 * \exp(-0.001(N_1(t) + N_2(t)))$





Trajectory in the phase plane
Asymptotically stable age structure



Matrix Models: Density-dependence

- Regular (asymptotic) behaviour too
- Formal analysis feasible too
- Transcribes "Logistic growth" in a realistic (demographic) context

Matrix Models: Overview

- Easily built from life cycle
- Easily generalized to consider relevant sources of variation in demographic parameters
- Easily generalized to any partition of individuals in mutually exclusive « classes »
- Discrete seasons, matrix products, pre/post birth-pulse
- Amenable to formal study (**not only asymptotics!**)

Lecture 2 An introduction to ULM

Stéphane LEGENDRE,
developer of ULM

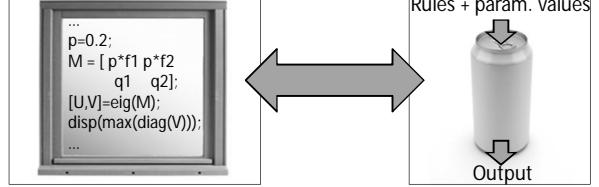
**UNIFIED
LIFE
MODELS**



Ecole Normale Supérieure,
46 Rue d'ULM, Paris

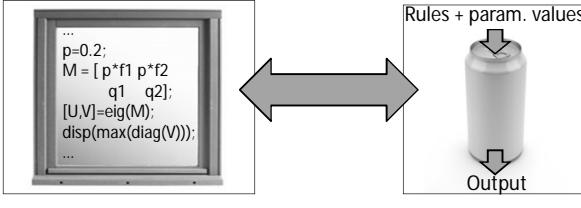


From transparent to canned software



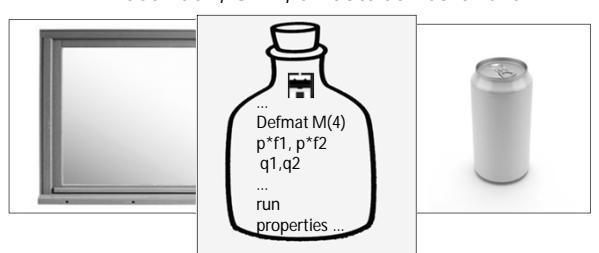
R, MATLAB, MATHEMATICA ...	RAMAS, VORTEX ...
clear control of everything	pro
tedious code writing	con
too general?	con
just write rules	
poor control	
too specialized?	

From transparent to canned software



R, MATLAB, MATHEMATICA ...	RAMAS, VORTEX ...
clear control of everything	pro
tedious code writing	con
too general?	con
use libraries / specific code	
just write rules	
poor control	
too specialized?	

From transparent to canned software In-between, ULM, a "bottled" software



clear control	+	simple commands
clear code writing	+	powerful
not too general, not too specialized		

ULM: the basics

Download from
<http://www.biologie.ens.fr/~legendre/ulm/ulm.html>

After installation should have

- ULM program **ulm.exe**
- example model files ***.ulm**
- reference manual **ulmref.pdf**



ULM: the basics

For analysis of matrix models

- discrete time
- discrete population structure

Broad scope: can model

- deterministic models
- environmental stochasticity
- demographic stochasticity
- density dependence
- metapopulations

ULM: the basics

Results: can output

- Population trajectories, growth rate
- Population structure, distributions
- Sensitivities to changes in parameters
- fitness landscapes
- Probability of extinction, quasi-extinction
- Lyapunov exponents, bifurcation diagrams

ULM: creating and running models

Create a model file

- define model structure and inputs
- simple syntax and commands

In main window

- Compile and run the model
- Modify and explore interactively

Or, create input and output files

- specify model outputs,
- variations in settings and inputs

Can use batch files

ULM: model file

```
{ Generic matrix model for passerine
{ female-based, 2 age classes, pre-breeding census

defmod passerine(2)           [Simple programming language]
mat: a
vec: w                         [Must leave a space]
{ population vector
defvec w(2)
n1, n2

{ population matrix
defmat a(2)                     [Recommend using comments]
sigma*s0*f1, sigma*s0*f2
S, V
```

ULM: model file

```
{ initial number of subadults
defvar n1 = 10

{ initial number of adults
defvar n2 = 10

{ total population size
defvar n = n1 + n2

{ juvenile survival rate
defvar s0 = 0.2

{ subadult survival rate
defvar s = 0.35
...
```

ULM: running models

Click on the ULM Icon

Open a model file (*.ulm)

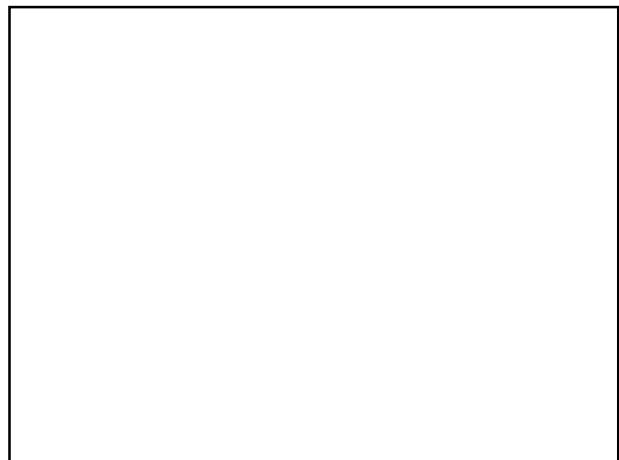
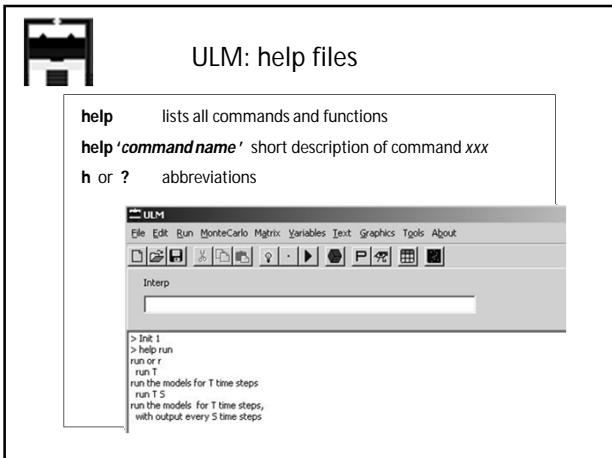
Compile the model file
use button or menu

Run, modify and investigate
use the command line, menus or buttons

View the output
main window – population size, growth rate
menus – formal analysis results
graph window

ULM: running models

Don't forget to check the graph window . . .



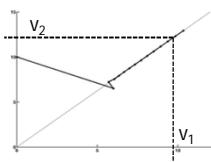
Lecture 3 Matrix model theory

Hal CASWELL,
showing a matrix model to
a Laysan Albatross.



Hal's book (Matrix models, Sinauer, 2001) can be used both as a textbook and as a comprehensive reference.

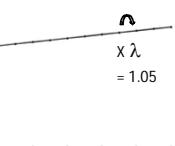
From numerical to formal results



$$M V = \lambda V$$

$$M^t N_0 \rightarrow \alpha(N_0) \lambda^t V$$

asymptotically



$$... \text{in loose notation}$$



From numerical to formal results

$$t = \begin{matrix} 1 \\ 2 \\ 3 \\ \dots \\ 10 \\ 11 \end{matrix}$$

$$M^t = \begin{pmatrix} 0.3000 & 0.6000 \\ 0.5000 & 0.6500 \end{pmatrix} \begin{pmatrix} 0.3900 & 0.5700 \\ 0.4750 & 0.7225 \end{pmatrix} \begin{pmatrix} 0.4020 & 0.6045 \\ 0.5038 & 0.7546 \end{pmatrix} \dots \begin{pmatrix} 0.5666 & 0.8499 \\ 0.7082 & 1.0623 \end{pmatrix} \begin{pmatrix} 0.5949 & 0.8924 \\ 0.7436 & 1.1154 \end{pmatrix}$$

$$M^t / M^{t-1} =$$

Termwise division



From numerical to formal results

$$t = \begin{matrix} 1 \\ 2 \\ 3 \\ \dots \\ 10 \\ 11 \end{matrix}$$

$$M^t = \begin{pmatrix} 0.3000 & 0.6000 \\ 0.5000 & 0.6500 \end{pmatrix} \begin{pmatrix} 0.3900 & 0.5700 \\ 0.4750 & 0.7225 \end{pmatrix} \begin{pmatrix} 0.4020 & 0.6045 \\ 0.5038 & 0.7546 \end{pmatrix} \dots \begin{pmatrix} 0.5666 & 0.8499 \\ 0.7082 & 1.0623 \end{pmatrix} \begin{pmatrix} 0.5949 & 0.8924 \\ 0.7436 & 1.1154 \end{pmatrix}$$

$$M^t / M^{t-1} =$$

Termwise division

$$M^t = M M^{t-1} \approx \lambda M^{t-1}, \text{ similar to } M V = \lambda V$$

$\Rightarrow M^{t-1}$ (and M^t) have columns \approx proportional to V

$$M^t \rightarrow \lambda^t [u_1 V \ u_2 V] = \lambda^t V U' \text{ with } U' = [u_1 \ u_2]$$

... in loose notation

transpose



Transposition and matrix product

the transpose of $U = \begin{pmatrix} u_1 \\ u_2 \end{pmatrix}$ is $U' = \begin{pmatrix} u_1 & u_2 \end{pmatrix}$

if $V = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$, $V U' = \begin{pmatrix} v_1 u_1 & v_1 u_2 \\ v_2 u_1 & v_2 u_2 \end{pmatrix}$, a 2×2 matrix

while $U' V = \begin{pmatrix} v_1 u_1 + v_2 u_2 \end{pmatrix}$ is a 1×1 matrix, i.e. a scalar,
also denoted as $\sum u_i v_i$



From numerical to formal results

$$M^t \rightarrow \lambda^t [u_1 V \ u_2 V] = \lambda^t V U'$$

Or, equivalently and more rigorously

$$\lambda^{-t} M^t \rightarrow V U'$$

$$u_i > 0, v_i > 0$$

$$\lambda^{-(t+1)} M^{t+1} = \lambda^{-1} M \lambda^{-1} M^t \rightarrow \lambda^{-1} M V U' = V U'$$

$$= \lambda^{-t} M^t \lambda^{-1} M \rightarrow V U' \lambda^{-1} M$$

$$\text{Hence } V U' \lambda^{-1} M = V U'$$

Premultiply by U' and simplify by scalar $U' V$, to get:

$$U' M = \lambda U'$$



Of eigenvalues and eigenvectors

Demographic ergodicity

$MV = \lambda V$	eigenvalue and right eigenvector
$U'M = \lambda U'$	eigenvalue and left eigenvector
$\lambda^{-t} M^t \rightarrow V U'$ leads to	
$M^t N_0 \rightarrow \lambda^t V (U' N_0)$	asymptotic exponential growth

Scalar, weighting the components of N_0 by the $u_i = \text{« reproductive values »}$



Of eigenvalues and eigenvectors

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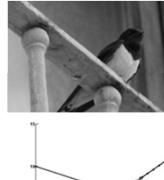


Of eigenvalues and eigenvectors

Usually, no formulas, but easy to get numerically

$MV = \lambda V$	eigenvalue and right eigenvector
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Reproductive values

Figure showing reproductive values over time. The left graph plots N_t against t , showing exponential growth. The right graph plots u_i against t , showing convergence to a steady state.

$MV = \lambda V$	eigenvalue and right eigenvector
$U'M = \lambda U'$	eigenvalue and left eigenvector
$\lambda^{-t} M^t \rightarrow V U'$ leads to	
$M^t N_0 \rightarrow \lambda^t V (U' N_0)$	asymptotic exponential growth

Scalar, weighting the components of N_0 by the $u_i = \text{« reproductive values »}$



Why is it so?

These results do not hold for all matrices
 M is such that M^t , for t large enough, has all its terms > 0
... because M is a primitive, non negative, irreducible matrix



Why is it so?

$n \times n$ Matrices have (in general) n eigenvalues which are complex numbers

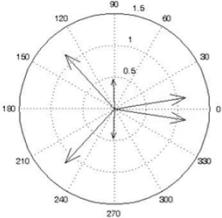
$$M = \begin{pmatrix} 0.6579 & -0.0961 & -0.5214 & -0.3996 & -0.7195 & -0.1503 \\ 0.8771 & 0.6794 & 0.1578 & -0.1972 & -0.4797 & -0.7616 \\ 0.1810 & 0.0652 & 0.7338 & 0.6667 & -0.8264 & -0.0099 \\ -0.1187 & 0.1078 & -0.1864 & -0.1927 & -0.1412 & 0.4128 \\ 0.8838 & 0.3601 & -0.7748 & -0.2196 & -0.4854 & -0.5129 \\ 0.3118 & -0.2656 & -0.1123 & -0.2791 & -0.4049 & 0.5701 \end{pmatrix}$$



Why is it so?

$n \times n$ Matrices have (in general) n eigenvalues which are complex numbers

$M = \begin{pmatrix} 0.6579 & -0.0961 & -0.1 \\ 0.8771 & 0.6794 & 0.1 \\ 0.1810 & 0.0652 & 0 \\ -0.1187 & 0.1078 & -0.1 \\ 0.8838 & 0.3601 & -0.7 \\ 0.3118 & -0.2656 & -0.1 \end{pmatrix}$





Why is it so?

However, positive, nonnegative irreducible matrices ...

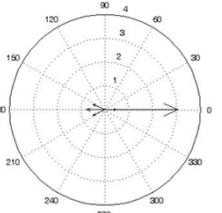
$M = \begin{pmatrix} 0.0842 & 0.0954 & 0.996 & & & \\ 0.1639 & 0.1465 & 0.553 & & & \\ 0.3242 & 0.6311 & 0.515 & & & \\ 0.3017 & 0.8593 & 0.330 & & & \\ 0.0117 & 0.9742 & 0.430 & & & \\ 0.5399 & 0.5708 & 0.491 & & & \end{pmatrix}$



Why is it so?

However, positive, nonnegative irreducible matrices have their largest modulus eigenvalue which is a positive real number

$M = \begin{pmatrix} 0.0842 & 0.0954 & 0.996 \\ 0.1639 & 0.1465 & 0.553 \\ 0.3242 & 0.6311 & 0.515 \\ 0.3017 & 0.8593 & 0.330 \\ 0.0117 & 0.9742 & 0.430 \\ 0.5399 & 0.5708 & 0.491 \end{pmatrix}$

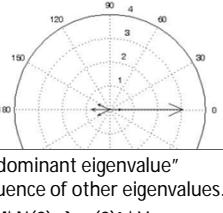




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$M = \begin{pmatrix} 0.0842 & 0.0954 & 0.996 \\ 0.1639 & 0.1465 & 0.553 \\ 0.3242 & 0.6311 & 0.515 \\ 0.3017 & 0.8593 & 0.330 \\ 0.0117 & 0.9742 & 0.430 \\ 0.5399 & 0.5708 & 0.491 \end{pmatrix}$



In products such as M^t , this "dominant eigenvalue" tends to outweigh the influence of other eigenvalues.
i.e., when $t \rightarrow \infty M^t N(0) \rightarrow \alpha(0)\lambda^t V$



Of eigenvalues and eigenvectors

Usually, no formulas, but easy to get numerically

Eigenvalues are the roots of $\det(M - \lambda \begin{pmatrix} 1 & 0 & \dots & 0 \\ 0 & 1 & \dots & 0 \\ 0 & 0 & \dots & 1 \\ 0 & 0 & \dots & 0 \end{pmatrix}) = 0$

General Numerical Analysis software (Matlab, Mathematica...) or specialized software (ULM...) will get eigenvalues and eigenvectors for you.



Of eigenvalues and eigenvectors

The largest root of $\det \begin{pmatrix} pf_1 - \lambda & pf_2 \\ q_1 & q_2 - \lambda \end{pmatrix} = \lambda^2 - (pf_1 + q_2)\lambda + pf_1 q_2 - pf_2 q_1 = 0$

is
$$\frac{pf_1 q_2 + \sqrt{(pf_1 + q_2)^2 - 4(pf_1 q_2 - pf_2 q_1)}}{2}$$



Of eigenvalues and eigenvectors

Even when there is a formula, λ is not a linear or simple function of the parameters

$$\frac{pf_1 q_2 + \sqrt{(pf_1+q_2)^2 - 4(pf_1 q_2 - pf_2 q_1)}}{2}$$


Of eigenvalues and eigenvectors

Even when there is a formula, λ is not a linear or simple function of the parameters

$$\frac{pf_1 q_2 + \sqrt{(pf_1+q_2)^2 - 4(pf_1 q_2 - pf_2 q_1)}}{2}$$

Yet, we need to know how λ varies when one or several parameter values change



Sensitivity analysis

What if swallows were not nesting at age 1?

$$M = \begin{pmatrix} 0.30 & 0.60 \\ 0.50 & 0.65 \end{pmatrix} \Rightarrow \lambda = 1.05$$

$$M = \begin{pmatrix} 0 & 0.60 \\ 0.50 & 0.65 \end{pmatrix} \Rightarrow \lambda = 0.9619$$


Sensitivity analysis What if?

What if we harvest a proportion h of a population?

$$M \rightarrow M_h = (1-h)M \quad MV = \lambda V \Rightarrow (1-h)MV = (1-h)\lambda V$$

Hence $M_h V = (1-h)\lambda V$

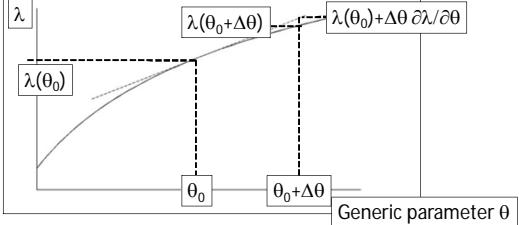
$$\lambda \rightarrow \lambda_h = (1-h)\lambda, \text{ asymptotic structure } V \text{ unchanged}$$

If you harvest each year 30 % of a roe deer population whose growth rate is 40 % ($\lambda=1.4$), λ_h is $1.4 * (1-0.3) = 0.98$, i.e. the population will drop at a rate of 2 % per year



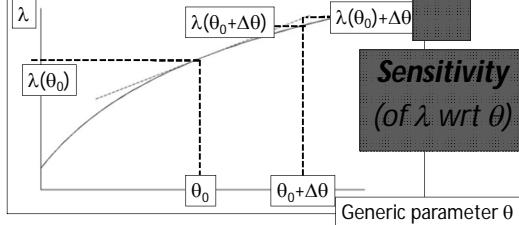
Sensitivity Analysis

In more general cases, λ can be approximated by a linear function




Sensitivity Analysis

In more general cases, λ can be approximated by a linear function





Sensitivity and Elasticity

Sensitivity $\partial \lambda / \partial \theta$
**Absolute change in λ vs
Absolute change in θ**

Elasticity
 $\partial \log \lambda / \partial \log \theta = (\theta / \lambda) \partial \lambda / \partial \theta = (\partial \lambda / \lambda) / (\partial \theta / \theta)$
 Relative change in λ vs relative change in θ

Matrix element $\theta = m_{ij}$
Lower-level parameter e.g. $\theta = f_1$ or $\theta = s_1$



Sensitivity to matrix element: perturbation analysis

$\partial \lambda / \partial m_{ij}?$

$MV = \lambda V$ [1] $(M+dM)(V+dV) = (\lambda + d\lambda)(V + dV)$ [2]

$MV + dM V + MdV + dM dV = \lambda V + d\lambda V + \lambda dV + d\lambda dV$ [2']
 ~~$MV + dM V + MdV + dM dV = \lambda V + d\lambda V + \lambda dV + d\lambda dV$~~

From [1]: ~~$MV + dM V + MdV = \lambda V + d\lambda V + \lambda dV$~~ [2'']

$U' x [2'']:$ $U'dM V + U'MdV = U'd\lambda V + \lambda U'dV$

$U'M = \lambda U':$ $U'dM V = U'd\lambda V$ i.e. $U'dM V = d\lambda U'V$ [3]



Sensitivity to matrix element: perturbation analysis

for a change in a single matrix term
 $m_{ij} \rightarrow m_{ij} + dm_{ij},$

$$dM = \begin{pmatrix} 0 & 0 & \dots & 0 \\ 0 & \dots & dm_{ij} & \dots & 0 \\ \vdots & & & & \vdots \\ 0 & 0 & \dots & 0 \end{pmatrix}$$

hence $U'dM V = u_i v_j dm_{ij}$ [4]



Sensitivity to matrix element: perturbation analysis

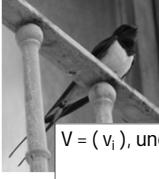
$\partial \lambda / \partial m_{ij}?$

$U'dM V = d\lambda U'V$ [3]
 $U'dM V = u_i v_j dm_{ij}$ [4]

$\partial \lambda / \partial m_{ij} = u_i v_j / U'V = u_i v_j / \sum u_i v_i$

a beautiful result due to Hal Caswell (1978)

$\partial \log \lambda / \partial \log m_{ij} = u_i v_j / U'V = m_{ij} u_i v_j / \lambda \sum u_i v_i$



Sensitivity to matrix element: perturbation analysis

$V = (v_i)$, under $\sum v_i = 1$, is the stable structure

$m_{ij} u_i v_j / \lambda$, under $\sum u_i v_i = 1$, is the *relative contribution*,
in asymptotic regime, of component i to component j ,
expressed with reproductive value as the currency.

As a consequence, *elasticities* (wrt the m_{ij}) sum up to 1

Normalization used in general obvious from the context.
 When speaking of sensitivity, we will use $\sum u_i v_i = 1$

Then, $\partial \lambda / \partial m_{ij} = u_i v_j$



Sensitivity to lower-level par. the chain rule

$\partial \lambda / \partial \theta?$

$\partial \lambda / \partial \theta = \sum_i \sum_j (\partial \lambda / \partial m_{ij}) \times (\partial m_{ij} / \partial \theta)$

Barn Swallow example:
 $\partial \lambda / \partial s_0 = \partial \lambda / \partial m_{11} \times \partial m_{11} / \partial s_0 + \partial \lambda / \partial m_{12} \times \partial m_{12} / \partial s_0$
 $= u_1 v_1 f_1 + u_1 v_2 f_2$
 $s_0 \partial \lambda / \partial s_0 = u_1 (v_1 f_1 s_0 + v_2 f_2 s_0)$
 $MV = \lambda V \Rightarrow v_1 f_1 s_0 + v_2 f_2 s_0 = \lambda v_1,$
 hence the elasticity of λ wrt s_0 :
 $s_0 / \lambda \times \partial \lambda / \partial s_0 = u_1 v_1$

Lecture 4 Generation time

Alfred J. LOTKA,
The father of « mathematical demography »



Like most mathematicians, he takes the hopeful biologist to the edge of a pond, points out that a good swim will help his work, and then pushes him in and leaves him to drown.

Charles ELTON

A classical age-dependent Leslie matrix

Pre birth-pulse matrix:
fecundities x 1st year survival = « net fecundities »

$$M = \begin{bmatrix} & & & & \\ & s_2 & 0 & \dots & 0 & \dots & 0 \\ & 0 & s_3 & \dots & 0 & \dots & 0 \\ & \dots & \dots & \dots & \dots & \dots & \dots \\ & 0 & \dots & \dots & s_{i+1} & \dots & \dots \\ & \dots & \dots & \dots & \dots & \dots & \dots \\ & 0 & 0 & \dots & \dots & s_p & 0 \end{bmatrix}$$

Aging + survival:
survival probabilities
on 1st sub-diagonal

MANY age classes over ONE time step

$$\begin{array}{l} t-1 \quad t \\ N_1 \rightarrow N_1 = \sum f_i s_1 N_i(t-1) \\ N_2 \rightarrow N_2 = s_2 N_1(t-1) \\ N_3 \rightarrow N_3 = s_3 N_2(t-1) \\ \dots \\ N_{n-1} \rightarrow N_{n-1} = s_{n-1} N_{n-2}(t-1) \\ N_n \rightarrow N_n = s_n N_{n-1}(t-1) \end{array}$$

MANY age classes over ONE time step

$$\begin{array}{l} t-1 \quad t \\ N_1 \rightarrow N_1 = \sum f_i s_1 N_i(t-1) \\ N_2 \rightarrow \\ N_3 \rightarrow \\ \dots \\ N_{n-1} \rightarrow \\ N_n \rightarrow \end{array} \text{expands as}$$

MANY age classes over ONE time step

$$\begin{array}{l} t-1 \quad t \\ N_1 \rightarrow N_1 = f_1 s_1 N_1(t-1) \\ N_2 \rightarrow + f_2 s_1 N_2(t-1) \\ N_3 \rightarrow + f_3 s_1 N_3(t-1) \\ \dots \\ N_{n-1} \rightarrow + \dots \\ N_n \rightarrow + f_{n-1} s_1 N_{n-1}(t-1) \\ + f_n s_1 N_n(t-1) \end{array}$$

ONE age class over MANY time steps

$$\begin{array}{ccccccccc} t-n & \dots & t-3 & t-2 & t-1 & t \\ N_1 \rightarrow & & N_1 \rightarrow & N_2 \rightarrow & N_1 \rightarrow & N_1 = f_1 s_1 N_1(t-1) + \\ \dots & & \dots & N_2 \rightarrow & N_2 \rightarrow & + f_2 s_1 s_2 N_1(t-2) \\ N_1 \rightarrow & & N_1 \rightarrow & N_3 \rightarrow & N_2 \rightarrow & + f_3 s_1 s_2 s_3 N_1(t-3) \\ \dots & & \dots & \dots & \dots & + \dots \\ N_{n-1} \rightarrow & & N_{n-1} \rightarrow & N_n \rightarrow & N_{n-1} \rightarrow & + f_{n-1} s_1 s_2 \dots s_{n-1} N_1(t-n+1) \\ N_n \rightarrow & & N_n \rightarrow & N_1 \rightarrow & N_n \rightarrow & + f_n s_1 s_2 \dots s_n N_1(t-n) \end{array}$$

Renewal equation $N_1(t) = \sum f_i I_i N_1(t-i)$ with $I_i = S_1 \dots S_i$

Euler-Lotka equation

$$N_1(t) = \sum f_i l_i N_1(t-i) \quad \text{with } l_i = s_1 \dots s_i$$

However, under asymptotic regime: $N_1(t-i) = \lambda^{-i} N_1(t)$

Hence: $N_1(t) = \sum f_i l_i \lambda^{-i} N_1(t)$

i.e.

$$1 = \sum f_i l_i \lambda^{-i}$$

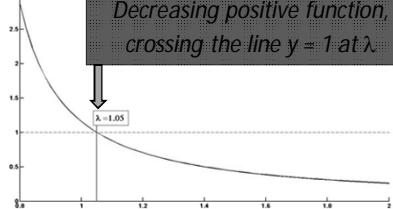
*Valid for any number
of age classes (even ∞)*

Euler - Lotka equation
1760 and 1911, respectively

Euler-Lotka equation Swallow example



*Decreasing positive function,
crossing the line $y = 1$ at λ*



Two sides of the same coin



Stable Pop. Theory
Euler - Lotka equation
1760 and 1911, respectively

Leslie Matrices
Age-structured Matrix models
1945, 1948

Stable Population Theory
to be expanded later
to stage-structured matrix models

Generation time

time	$t-n$	\dots	$t-3$	$t-2$	$t-1$	t
contribution	$f_n l_n \lambda^{-n}$	\dots	$f_3 l_3 \lambda^{-3}$	$f_2 l_2 \lambda^{-2}$	$f_1 l_1 \lambda^{-1}$	$\Sigma = 1$
age of mothers at t	n	\dots	3	2	1	

Stable distribution of the Age of mothers at birth

Mean age of mothers at birth (in asymptotic regime)

$$T = \sum i f_i l_i \lambda^{-i}$$

\bar{T} , Generation time, Leslie 1966,
Hereafter denoted as T

Derived quantities

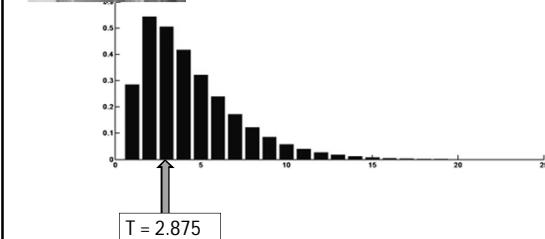
Number of individuals per mother in next generation

$$R_0 = \sum f_i l_i$$

Mean age of child birth along a mother's life

$$T_C = \sum i f_i l_i / \sum f_i l_i$$

Generation time Swallow example



Nathan Keyfitz,
1913-2010

Generation time and Sensitivity Analysis

The Euler-Lotka equation is an implicit function, linking any generic parameter θ and λ :

$$\phi(\theta, \lambda) = \sum f_i(\theta) l_i(\theta) \lambda^{-i} = 1$$

If $\theta \rightarrow \theta + d\theta$, $\lambda \rightarrow \lambda + d\lambda$, but ϕ remains equal to 1, i.e. $d\phi = 0$

As a consequence $0 = \frac{\partial \phi}{\partial \lambda} d\lambda + \frac{\partial \phi}{\partial \theta} d\theta$

Hence $d\lambda/d\theta = -(\partial \phi / \partial \theta) / (\partial \phi / \partial \lambda)$

Generation time and Sensitivity Analysis

$$d\lambda/d\theta = -(\partial \phi / \partial \theta) / (\partial \phi / \partial \lambda)$$

$$\text{From } \phi = \sum f_i l_i \lambda^{-i}, \quad \partial \phi / \partial \lambda = \sum i f_i l_i \lambda^{-i-1} = -T / \lambda$$

$$\text{From } l_i = s_1 \dots s_i, \quad \partial \phi / \partial s_i = \sum f_i (l_i / s_1) \lambda^{-i} = (1/s_1) \sum f_i l_i \lambda^{-i} = 1/s_1$$

Sensitivity $d\lambda/ds_1 = \lambda/(s_1 T)$

Elasticity $(s_1/\lambda) d\lambda/ds_1 = 1/T$

same result for a change in all fecundities
same result for all parameters < 1st reprod.
(« immature parameters »)

Generation time and turnover

Elasticity $(s_1/\lambda) d\lambda/ds_1 = 1/T$

However $(s_1/\lambda) d\lambda/ds_1 = u_1 v_1$
under $\sum u_i v_i = 1$

Hence $\boxed{u_1 v_1} = u_1 v_1$ under $\sum u_i v_i = 1$

A measure of turnover:

- the proportion of new individuals in reproductive value
- Also the (asympt.) increase in mean generation number per year



Sensitivity analysis Survival

$$M \rightarrow M_h = (1-h)M \quad MV = \lambda V \Rightarrow (1-h)MV = (1-h)\lambda V$$

Hence $M_h V = (1-h)\lambda V$

$$\lambda \rightarrow \lambda_h = (1-h)\lambda, \text{ asymptotic structure } V \text{ unchanged}$$

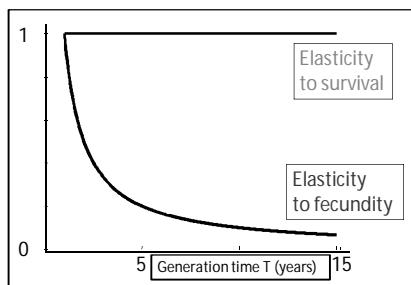
x % change in all $s_i \rightarrow$ x % change in λ

The elasticity of λ wrt to $\{s_1, s_2, \dots, s_i, \dots\}$ is 1

Jean
Clobert

Sensitivity analysis Fecundity and Survival

Lebreton and Clobert 1991



Sensitivity analysis and Generation time



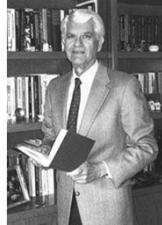
Albatross, T≈24 y:
-30 % in Fecundity ⇒
-1.25 % in growth rate

In any sharp-decline of a long lived species,
first suspect a change in survival

Lecture 5 Multistate matrix models



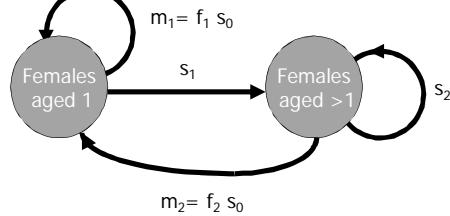
Hervé LE BRAS and Andrei ROGERS,
who developed a generalization of
the Euler-Lotka equation for
multistate matrix models



A simple age-classified model



LIFE CYCLE graph in a
barn swallow population



A simple age-classified model

QUANTITATIVE CYCLE in a barn swallow population

Two linear Equations $N_1(t+1) = m_1 N_1(t) + m_2 N_2(t)$
 $N_2(t+1) = s_1 N_1(t) + s_2 N_2(t)$

One matrix Equation $\begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_{t+1} = \begin{bmatrix} m_1 & m_2 \\ s_1 & s_2 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_t$

$$N_{t+1} = M N_t$$



Expanding over age-classes

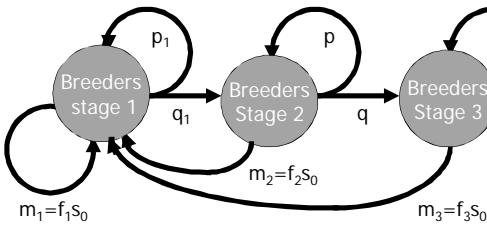
INFINITELY MANY AGE CLASSES

$$M(\infty) = \begin{bmatrix} m_1 & m_2 & m_2 & m_2 & m_2 & \dots \\ s_1 & 0 & 0 & 0 & 0 & \dots \\ 0 & s_2 & 0 & 0 & 0 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 0 & \dots & s_2 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{bmatrix}$$



A simple stage-classified model

LIFE CYCLE GRAPH



A simple stage-classified model

MATRIX EQUATION

$$\begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix}_{t+1} = \begin{bmatrix} m_1 + p_1 & m_2 & m_3 \\ q_1 & p & 0 \\ 0 & q & s \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix}_t$$

$$\begin{aligned} m_1, m_2, m_3 &= 0.3, 0.6, 1.0 \\ p_1, q_1 &= 0.25, 0.25 \\ p, q &= 0.25, 0.40 \\ s &= 0.65 \end{aligned}$$

$$\lambda_1 = 1.05, \lambda_2 \text{ & } \lambda_3 \in \mathbb{C}$$

$$\text{Elasticity}(m) = 0.3166$$

$$T = 1/E(f) = 3.158 ??$$

Stage-classified models

- How to obtain Generation time and measures of turnover?
- How to make age explicitly present?



A simple stage-classified model



MATRIX EQUATION

$$\begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}_{t+1} = \begin{pmatrix} m_1 + p_1 & m_2 & m_3 \\ q_1 & p & 0 \\ 0 & q & s \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}_t$$

$$F = \begin{pmatrix} m_1 & m_2 & m_3 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

$$T = \begin{pmatrix} p_1 & 0 & 0 \\ q_1 & p & 0 \\ 0 & q & s \end{pmatrix}$$

A simple stage-classified model



DECOMPOSING THE MATRIX EQUATION
(Caswell, 2001 ch.5)

$$F = \begin{pmatrix} m_1 & m_2 & m_3 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

$$T = \begin{pmatrix} p_1 & 0 & 0 \\ q_1 & p & 0 \\ 0 & q & s \end{pmatrix}$$

$$M = F + T$$

Expanding over age-classes



INFINITELY MANY AGE CLASSES

$$M(\infty) = \begin{pmatrix} F & F & F & \dots & F & \dots \\ T & 0 & 0 & \dots & 0 & \dots \\ 0 & T & 0 & \dots & 0 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 0 & \dots & T & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{pmatrix}$$

Block Matrix notation



Expanding over age-classes



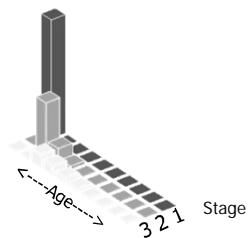
MULTISTATE STABLE POPULATION THEORY
LEBRETON, Theor.Pop.Biol., 1996

- The Le Bras-Rogers equation, a multistate generalization of the Euler-Lotka equation

$$\det(F\lambda^{-1} + FT\lambda^{-2} + \dots + FT^{i-1}\lambda^{-i} + \dots - I) = 0$$
- Largest root = dominant eigenvalue of M, as the equation reduces to $\det(F+T-\lambda I)=0$
- Distribution of age of mothers at birth naturally appears as weighted by reproductive value of offspring

Stage classified models expanded over age classes

Distribution of age of mothers at birth, by stage



Generation time T, weighted mean age of mothers at childbirth, is equal to 3.158

$$E(m) = 1 / T = 0.3166$$

Stage classified models expanded over age classes

Applies to any stage-classified model, via the Le Bras - Rogers equation and the multistate stable population theory

$$M(\infty) = \begin{pmatrix} F & F & F & \dots & F & \dots \\ T & 0 & 0 & \dots & 0 & \dots \\ 0 & T & 0 & \dots & 0 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 0 & \dots & T & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{pmatrix}$$

Age x Stage classified models

Also applicable to age *and* stage-classified model, via...

$$M(\infty) = \begin{pmatrix} F_1 & F_2 & F_3 & \dots & F_n & \dots \\ T_2 & 0 & 0 & \dots & 0 & \dots \\ 0 & T_3 & 0 & \dots & 0 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 0 & \dots & T_n & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{pmatrix}$$


...and, again, the multistate stable population theory

Multistate models

- Stages = a set of mutually exclusive states
- Think of "states" rather than "stages"
- States can be sites:
 - "multisite models",
 - "regional population models"
 -

Multisite models

2 sites

$$R = \begin{pmatrix} a & 0 \\ 0 & b \end{pmatrix} \quad D = \begin{pmatrix} p & 1-q \\ 1-p & q \end{pmatrix}$$

REACTION - DIFFUSION

$$N_{t+1} = R.D.N_t = \begin{pmatrix} a p & b (1-q) \\ a (1-p) & b q \end{pmatrix} N_t$$

Multisite models

2 sites

$$R = \begin{pmatrix} a & 0 \\ 0 & b \end{pmatrix}$$

Independent sites with growth rates a and b, respectively

REACTION - DIFFUSION

$$N_{t+1} = R.D.N_t = \begin{pmatrix} a p & b (1-q) \\ a (1-p) & b q \end{pmatrix} \quad \begin{array}{l} \text{Common growth} \\ \text{rate } \lambda, \text{ with } a < \lambda < b \end{array}$$

Leslie Matrices

2 age classes, 2 *non-connected* sites

site	1	1	2	2
age	1	2	1	2
site	1	2	1	2
1	1	$\begin{pmatrix} 0 & f_1 \\ s_1 & s_1 \end{pmatrix}$	0	0
1	2	$\begin{pmatrix} 0 & f_1 \\ s_1 & s_1 \end{pmatrix}$	0	0
2	1	$\begin{pmatrix} 0 & 0 \\ 0 & f_2 \end{pmatrix}$	0	f_2
2	2	$\begin{pmatrix} 0 & 0 \\ 0 & s_2 \end{pmatrix}$	s_2	s_2

Coupling Leslie Matrices

2 age classes, 2 sites

$$\begin{array}{ccccc}
 & \text{site} & 1 & 1 & 2 & 2 \\
 & \text{age} & 1 & 2 & 1 & 2 \\
 \text{site} & \text{age} & & & & \\
 1 & 1 & \begin{pmatrix} 0 & f_{11} \\ s_1 & s_1 \end{pmatrix} & 0 & f_{21} & \\
 1 & 2 & \begin{pmatrix} 0 & f_{12} \\ 0 & f_{22} \end{pmatrix} & 0 & 0 & \\
 2 & 1 & 0 & 0 & \begin{pmatrix} 0 & f_{12} \\ s_2 & s_2 \end{pmatrix} & \\
 2 & 2 & 0 & 0 & 0 &
 \end{array}$$

Coupling Leslie Matrices

2 age classes, 2 sites

$$\begin{array}{ccccc}
 & \text{site} & 1 & 1 & 2 & 2 \\
 & \text{age} & 1 & 2 & 1 & 2 \\
 \text{site} & \text{age} & & & & \\
 1 & 1 & \begin{pmatrix} 0 & f_{11} \\ s_1 & s_1 \end{pmatrix} & 0 & f_{21} & \\
 1 & 2 & \begin{pmatrix} 0 & f_{12} \\ 0 & f_{22} \end{pmatrix} & 0 & 0 & \\
 2 & 1 & 0 & f_{12} & \begin{pmatrix} 0 & f_{22} \\ s_2 & s_2 \end{pmatrix} & \\
 2 & 2 & 0 & 0 & 0 &
 \end{array}$$

Coupling by first-year dispersal

Coupling Leslie Matrices

2 age classes, 2 sites: SITE \subset AGE

$$\begin{array}{ccccc}
 & \text{age} & 1 & 1 & 2 & 2 \\
 & \text{site} & 1 & 2 & 1 & 2 \\
 \text{age} & \text{site} & & & & \\
 1 & 1 & \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix} & \begin{pmatrix} f_{11} & f_{21} \\ f_{12} & f_{22} \end{pmatrix} & & \\
 1 & 2 & \begin{pmatrix} 0 & 0 \\ s_1 & 0 \end{pmatrix} & \begin{pmatrix} f_{11} & f_{21} \\ f_{12} & f_{22} \end{pmatrix} & & \\
 2 & 1 & \begin{pmatrix} s_1 & 0 \\ 0 & s_2 \end{pmatrix} & \begin{pmatrix} s_1 & 0 \\ 0 & s_2 \end{pmatrix} & & \\
 2 & 2 & \begin{pmatrix} 0 & s_2 \\ 0 & s_2 \end{pmatrix} & \begin{pmatrix} 0 & s_2 \\ 0 & s_2 \end{pmatrix} & &
 \end{array}$$

Coupling Leslie Matrices

2 age classes, 2 sites: SITE \subset AGE

$$\begin{array}{ccccc}
 & \text{age} & 1 & 1 & 2 & 2 \\
 & \text{Site} & 1 & 2 & 1 & 2 \\
 \text{age} & \text{site} & & & & \\
 1 & 1 & \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix} & \begin{pmatrix} f_{11} & f_{21} \\ f_{12} & f_{22} \end{pmatrix} & & \\
 1 & 2 & \begin{pmatrix} 0 & 0 \\ f_{12} & f_{22} \end{pmatrix} & \begin{pmatrix} f_{11} & f_{21} \\ f_{12} & f_{22} \end{pmatrix} & &
 \end{array}$$

$M = \begin{pmatrix} F_1 & F_2 \\ T & T \end{pmatrix}$ fecundity and survival parameters appear as 2×2 matrices, and, in block-matrix notation the overall matrix is a Leslie matrix

This structure links this matrix model to the Le Bras -Rogers equation and the multistate stable population theory

Coupling Leslie Matrices

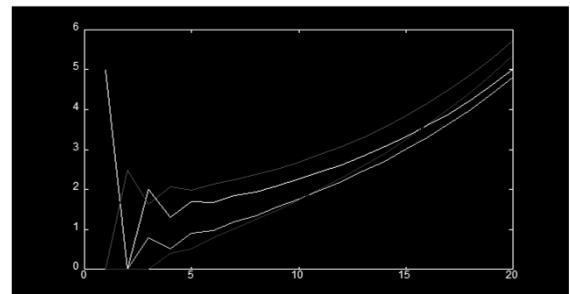
2 age classes, 2 sites: SITE \subset AGE

$$\begin{array}{ccccc}
 & \text{age} & 1 & 1 & 2 & 2 \\
 & \text{Site} & 1 & 2 & 1 & 2 \\
 \text{age} & \text{site} & & & & \\
 1 & 1 & \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix} & \begin{pmatrix} f_{11} & f_{21} \\ f_{12} & f_{22} \end{pmatrix} & & \\
 1 & 2 & \begin{pmatrix} 0 & 0 \\ s_1 & 0 \end{pmatrix} & \begin{pmatrix} f_{11} & f_{21} \\ f_{12} & f_{22} \end{pmatrix} & & \\
 2 & 1 & \begin{pmatrix} s_1 & 0 \\ 0 & s_2 \end{pmatrix} & \begin{pmatrix} s_1 & 0 \\ 0 & s_2 \end{pmatrix} & & \\
 2 & 2 & \begin{pmatrix} 0 & s_2 \\ 0 & s_2 \end{pmatrix} & \begin{pmatrix} 0 & s_2 \\ 0 & s_2 \end{pmatrix} & &
 \end{array}$$

ULM recognizes multistate Leslie matrices if states \subset ages

Asymptotically exponential Growth

2 age classes, 2 sites

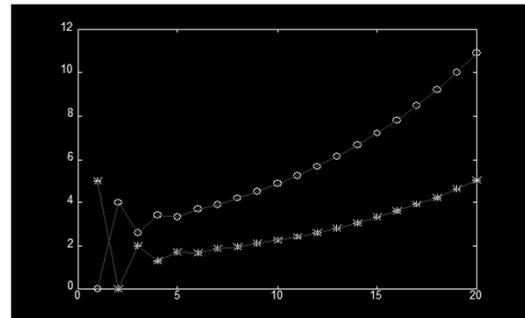


Asymptotically exponential Growth

	$N_{t+1} = M N_t$	
	$N_t \rightarrow c \lambda^t V$	
QUANTITY	MEANING	FORMAL NATURE
V	stable structure by age and site	right eigenvector
λ	asymptotic multiplication rate	largest eigenvalue
$c = \sum u_i N_i(0)$	function of initial values	U : left eigenvector

Spatial reproductive value

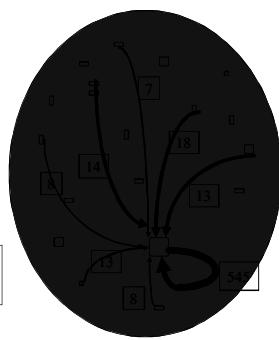
effect of initial values, via $c = \sum u_i N_i(0)$



Dispersal and Recruitment Black-headed gull (Forez, central France)



resightings as breeders of gulls ringed as chicks



Coupling Leslie Matrices

5 age classes, 2 sites
Black-Headed Gull Population

AGE SITE	1 1	1 2	2 1	2 2	3 1	3 2	4 1	4 2	5 1	5 2
AGE SITE	1 1	1 2	2 1	2 2	3 1	3 2	4 1	4 2	5 1	5 2
1 1	0	0	.096	0	.160	0	.224	0	.320	0
1 2	0	0	0	.100	0	.160	0	.200	0	.200
2 1	(.600)	(.300)	0	0	0	0	0	0	0	0
2 2	(.200)	(.500)	0	0	0	0	0	0	0	0
3 1	0	0	.820	0	0	0	0	0	0	0
3 2	0	0	0	.820	0	0	0	0	0	0
4 1	0	0	0	0	.820	0	0	0	0	0
4 2	0	0	0	0	0	.820	0	0	0	0
5 1	0	0	0	0	0	0	.820	0	.820	0
5 2	0	0	0	0	0	0	0	.820	0	.820

Coupling Leslie Matrices

5 age classes, 2 sites
Black-Headed Gull Population

Common growth rate (0.997), but \neq reproductive values
Stable structure (by age and site)
Multisite generation time T
Sensitivity results easily generalized:
e.g., elasticity(fecundities) = $1/T = .130$

Lecture 6

Time-Varying and Random environment Matrix models



Shripad TULJAPURKAR ("Tulja")
who extensively developed the
theory of population models in
random environment

When the model matrix
varies from year to year....

Time-Varying Models:

... in a known fashion over finite time window

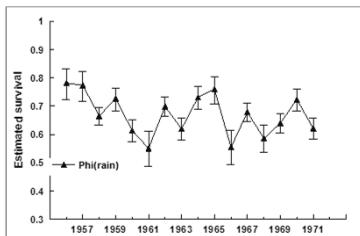
- Recorded sequence of bad and poor years
- Relationship between demographic parameter and env. covariate
- MAIN AIM: model a known trajectory

Random Environment:

... in a random fashion over a finite or infinite time window

- Projection of relationship between parameter and env. covariate
- Unexplained year-to-year (environmental) variation
- MAIN AIM: projection, asymptotic behavior

Survival of storks in Baden-Württemberg estimated with rainfall in Sahel as a covariate



Model	(S_t, p)	(S_{rain}, p)	(S, p)
AIC	1349.50	1339.15	1356.10

$$\log(S / (1 - S)) = a + b \text{ rain}$$

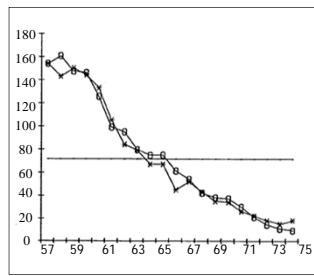
Storks in Baden-Württemberg: Modelling numbers with survival driven by rainfall in Sahel

Year	57	58	...	i	i+1	...	74
Rain	x_{57}	x_{58}	...	x_i	x_{i+1}	...	x_{75}
Survival	ϕ_{57}	ϕ_{58}	...	ϕ_i	ϕ_{i+1}	...	ϕ_{75}
Matrix	M_{57}	M_{58}	...	M_i	M_{i+1}	...	M_{75}

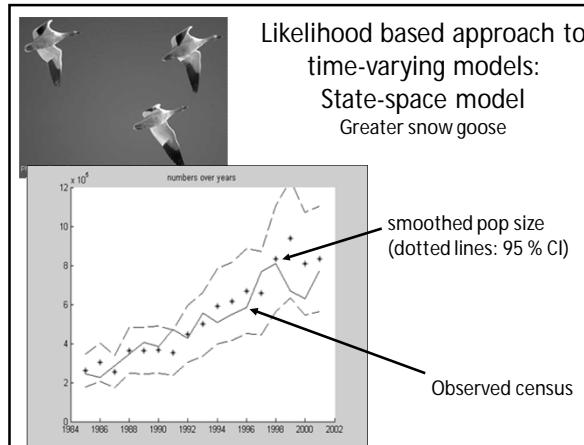
Numbers obtained by a « time-varying matrix model »
(using N_{56} based on average stable age structure):
 $N_{i+1} = M_i * N_i$

Storks in Baden-Württemberg: Modelling numbers with survival driven by rainfall in Sahel

An "ad hoc"
comparison
(o = model)
(x = census)
based on
 $a_3 N_i(3) + N_i(4)$
(Nr of breeders)



Likelihood based approach to
time-varying models:
State-space model
Greater snow goose



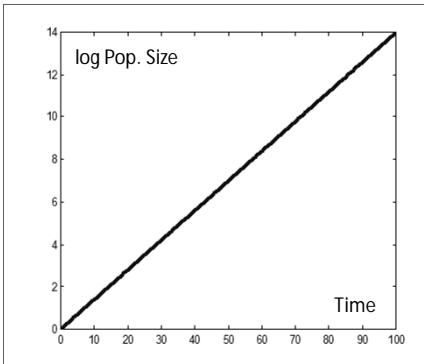
Random Environment
 the scalar exponential model
 (no stage/age classes)

$n(t) = A_t n(t-1)$
 A_t random scalar (i.i.d.) , with $E(A_t) = \lambda$
 $E(n(t)/n(t-1)) = \lambda n(t-1)$
 $E(n(t)/n(0)) = \lambda^t n(0)$

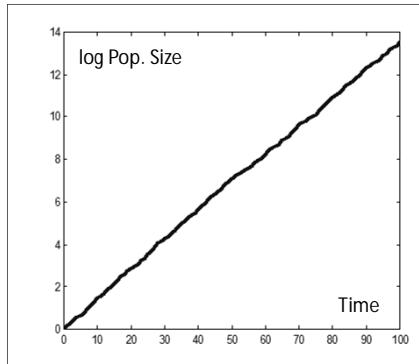
Random environment
 Increasing variability

$A_t = 1.15$ with probability 1 $\Rightarrow \lambda = 1.15$
 $A_t = 1.2$ and 1.1 with prob. 0.5 $\Rightarrow \lambda = 1.15$
 $A_t = 1.4$ and 0.9 with prob. 0.5 $\Rightarrow \lambda = 1.15$
 $A_t = 2.0$ and 0.3 with prob. 0.5 $\Rightarrow \lambda = 1.15$

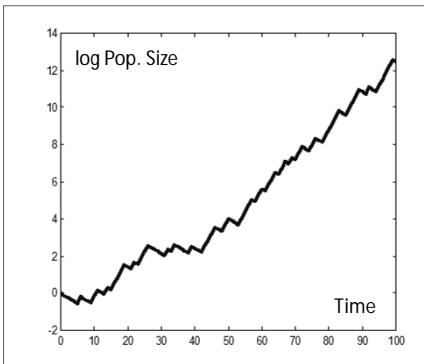
$A_t = 1.15$ with probability 1 $\Rightarrow \lambda = 1.15$



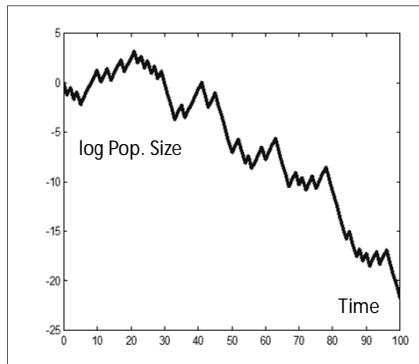
$A_t = 1.2$ and 1.1 with prob. 0.5 $\Rightarrow \lambda = 1.15$



$A_t = 1.4$ and 0.9 with prob. 0.5 $\Rightarrow \lambda = 1.15$



$A_t = 2.0$ and 0.3 with prob. 0.5 $\Rightarrow \lambda = 1.15$



Where is the paradox ?

$$\begin{aligned}
 n(t) &= A_t n(t-1) \Rightarrow n(t) = n(0) \prod A_i \\
 \log n(t) - \log n(0) &= \sum \log A_i \\
 \text{Central Limit Theorem: } \sum \log A_i &\approx \text{Normal distribution} \\
 \log n(t) - \log n(0) &\approx \text{Normal}(\mu_t, \sigma^2_t) \\
 a = E(\log A_t), v = \text{var}(\log A_t) &\Rightarrow \mu_t = a t \quad \sigma^2_t = v t
 \end{aligned}$$

The paradox is still there

$$\begin{aligned}
 \log n(t) - \log n(0) &\approx \text{Normal}(\mu_t, \sigma^2_t) \\
 \mu_t &= a t, \quad \sigma^2_t = v t \\
 \Rightarrow (\log n(t) - \log n(0))/t &\approx \text{Normal}(a, v/t) \\
 1/t \log n(t) &\approx \text{Normal}(a, v/t) \\
 v/t \rightarrow 0 \text{ when } t \rightarrow \infty &\Rightarrow \\
 1/t \log n(t) &\rightarrow \log \lambda_s = E(\log A_t) \\
 \text{However } 1/t \log E(n(t)) &\rightarrow \log \lambda = \log E(A_t)
 \end{aligned}$$

Is the paradox still there ?

A_t values	λ	EXPECTED	MOST PROBABLE
		$\log \lambda$	$\log \lambda_s$
1.15	1.15	0.1398	0.1398
1.2 1.1	1.15	0.1398	0.1388
1.4 0.9	1.15	0.1398	0.1156
2.0 0.3	1.15	0.1398	-0.2554

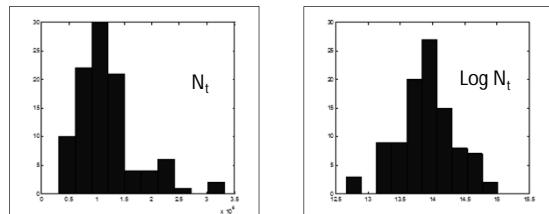
Most probable and expected trajectories differ 

There is no real paradox

$n(t) \rightarrow$ log-normal distribution \Rightarrow Median < Expectation

$A_t = 1.2$ and 1.1 with prob. 0.5

Distribution for a large t

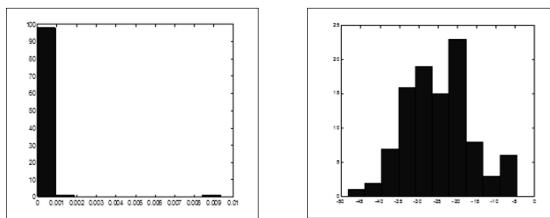


There is no real paradox

$n(t) \rightarrow$ log-normal distribution \Rightarrow Median < Expectation

$A_t = 2.0$ and 0.3 with prob. 0.5

Distribution for a large t



There is no real paradox

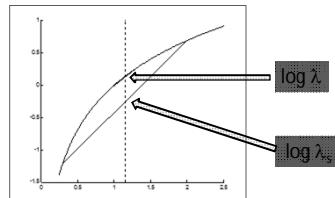
A few trajectories with large growth rate keep the expected growth rate equal to $\log \lambda = \log E(A_t)$

Most probable trajectories are concentrated around $\log \lambda_s = E(\log A_t)$ (more and more when $t \rightarrow \infty$)

$\log \lambda_s$ is a relevant measure of growth rate

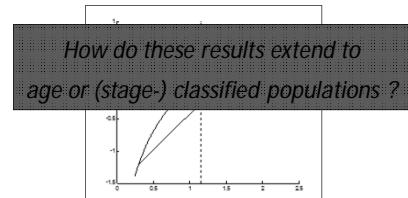
Environmental variability influences population growth

Jensen's inequality: $\log \lambda_s = E(\log A_t) \leq \log \lambda = \log E(A_t)$



Environmental variability depresses Population growth
A deterministically growing population may decrease

The effect of Environmental variability on Population growth



The Barn Swallow example

1st y $n_1(t-1)$
After 1st y $n_2(t-1)$



Average values
 $s_0 = 0.2$ $f_1, f_2 = 3/2, 6/2$
 $s_1 = 0.5$ $s_2 = 0.65$

$$A = \begin{pmatrix} f_1 s_0 & f_2 s_0 \\ s_1 & s_2 \end{pmatrix}$$

+ random Survival with variance σ^2

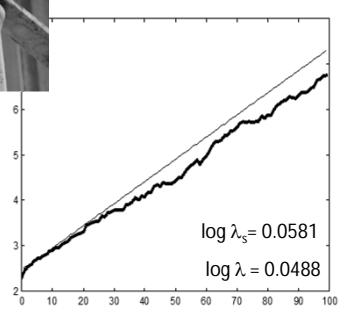
$E(\log N(t))$, Constant Environment



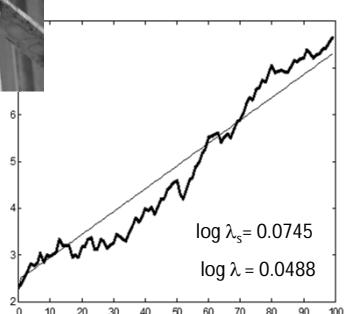
$\log \lambda_s = 0.0488$
 $\log \lambda = 0.0488$

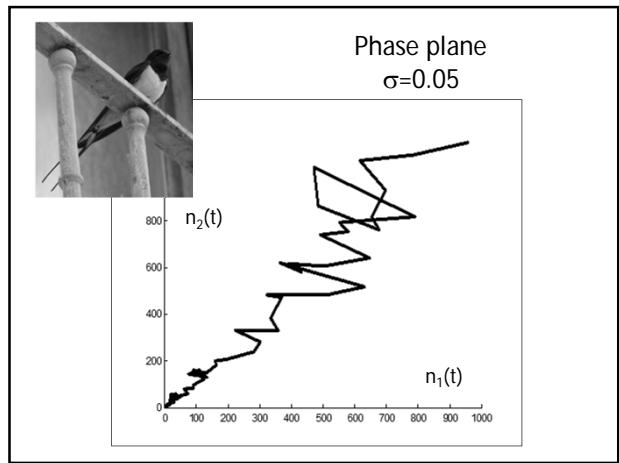
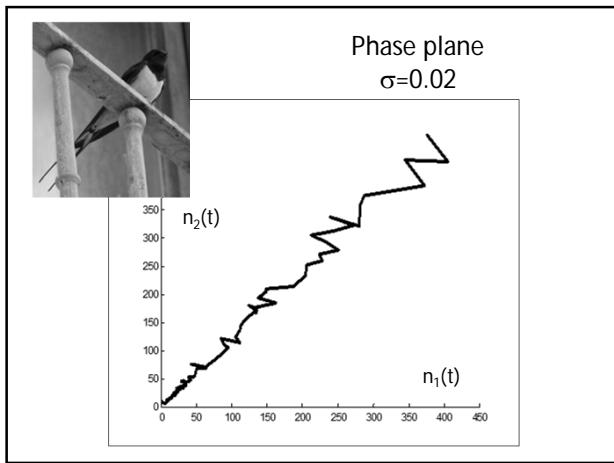
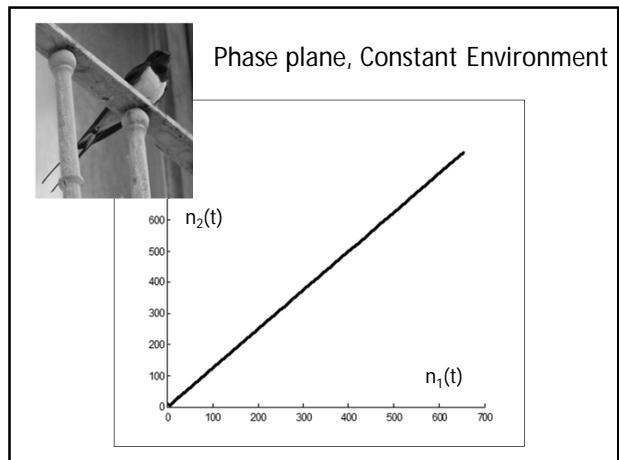
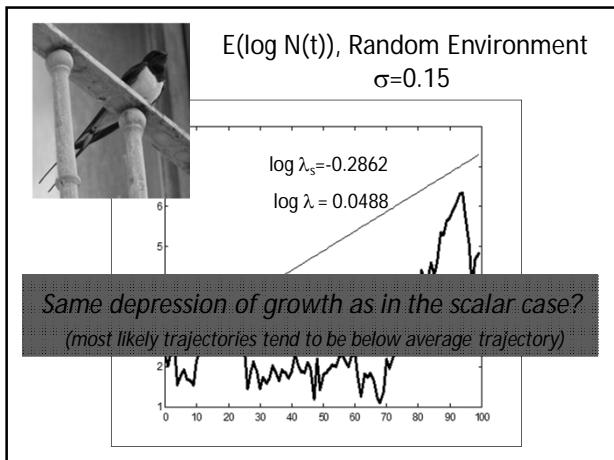
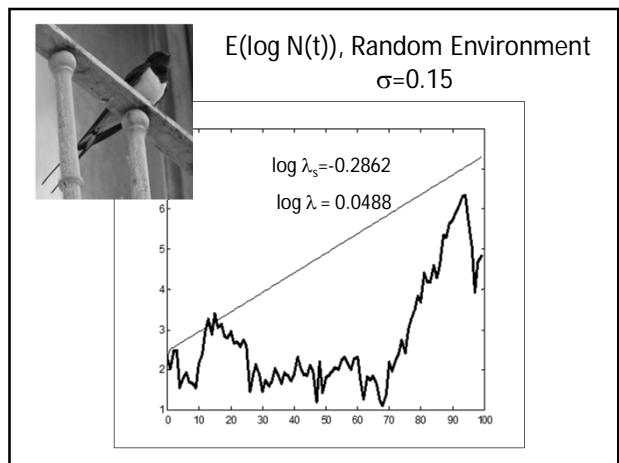
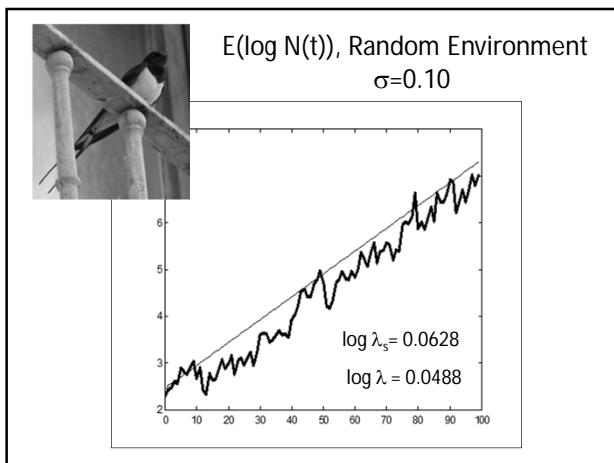


$E(\log N(t))$, Random Environment $\sigma=0.02$



$E(\log N(t))$, Random Environment $\sigma=0.05$





Same depression as above ...plus a constant mismatch in age structure

$$\begin{aligned}\log \lambda_s &\neq \log(E(A_t)) = \log \lambda \\ \log \lambda_s &\neq E(\log(A_t)), A_t \text{ being a matrix} \\ \log \lambda_s &\neq \log E(\lambda(A_t)), n_t \neq \text{eigenvector of } A\end{aligned}$$

Convergence of $1/t \log c' n(t)$ to $\log \lambda_s$
even under correlated environments
("ergodic theorems on products of random matrices")

How to calculate the asymptotic growth rate ?

"The computation is considerably more involved than in the scalar case" — S.Tuljapurkar (1990) 

Simulation or Approximation

Estimation of $\log \lambda_s$ Simulation and approximation

Simulation: Matlab, 

Large number of repetitions needed

Approximation : valid from small variability

For uncorrelated parameters:

$$\log \lambda_s \approx \log \lambda - \frac{1}{2 \lambda^2} \sum \left[\frac{\partial \lambda}{\partial \theta} \right]^2 \text{var}(\theta)$$



Estimation of $\log \lambda_s$ Approximation

σ	λ	$\log \lambda$	APPROXIMATE $\log \lambda_s$
0.00	1.05	0.0488	0.0488
0.01	1.05	0.0488	0.0486
0.05	1.05	0.0488	0.0442
0.10	1.05	0.0488	0.0304
0.15	1.05	0.0488	0.0075
0.10	1.05	0.0488	-0.0246

Random Environment simulation in ULM

In batch file (or using interpreted command "changevar").
Just define the parameter of interest as random.
Several continuous distributions are available.
The parameter value will be evaluated at each time step.
"0.1+rand(0.2)" \iff 0.1 + Unif[0, 0.2] \iff Unif[0.1, 0.3]

Fixed environment

```
{ juvenile survival rate
defvar s0 = 0.2
{ subadult survival rate
defvar s = 0.35
{ adult survival rate
defvar v = 0.5
```

Random Environment

```
{ juvenile survival rate
defvar s0 = 0.1+rand(0.2)
{ subadult survival rate
defvar s = 0.35
{ adult survival rate
defvar v = 0.5
```

Lecture 7

Exploited populations, the comparative approach, management and conservation

Fedor Illyich BARANOV,
A pioneer of the theory of exploited populations.

W.E. RICKER taught himself
the Russian to be able to read
BARANOV's works.



Sensitivity analysis Survival

$$M \rightarrow M_h = (1-h)M \quad MV = \lambda V \Rightarrow (1-h)MV = (1-h)\lambda V$$

Hence $M_h V = (1-h)\lambda V$

$$\lambda \rightarrow \lambda_h = (1-h)\lambda, \text{ asymptotic structure } V \text{ unchanged}$$

$x\%$ change in all $s_i \rightarrow x\%$ change in λ

The elasticity of λ wrt to $\{s_1, s_2, \dots, s_i, \dots\}$ is 1

Sensitivity analysis Survival

$$M \rightarrow M_h = (1-h)M \quad MV = \lambda V \Rightarrow (1-h)MV = (1-h)\lambda V$$

Hence $s_i \rightarrow s_i(1-h)$

$\lambda \rightarrow \lambda_h = (1-h)\lambda,$
if harvest or incidental mortality
entirely before or after natural mortality.

Then $\lambda \rightarrow \lambda(1-h)$

$x\%$ change in all $s_i \rightarrow x\%$ change in λ

The elasticity of λ wrt to $\{s_1, s_2, \dots, s_i, \dots\}$ is 1

Exploitation in continuous time: mortality and exploitation as competing risks (Baranov, 1918)

"natural" dynamics of death: $n(t+dt) - n(t) = -m n(t) dt$

with exploitation: $n(t+dt) - n(t) = -(m+h) n(t) dt$

m, h : natural mortality and harvest *instantaneous rates*

two sources of mortality assumed additive, with total rate $z = m+h$

However, the number of individuals at risk for both sources of mortality varies with total mortality z as $n(t) = n(0) \exp(-z t)$

Exploitation in continuous time: mortality and exploitation as competing risks over $[0, T]$

$$\begin{aligned} \text{Number of natural deaths} & \int n(t) m dt = m/z n(0)(1-e^{-zT}) \\ \text{Number of deaths from exploitation} & = h/z n(0)(1-e^{-zT}) \\ \text{Proportion of deaths from exploitation} & H = h/z (1-e^{-zT}) \\ \text{Overall proportion of survivors} & S = e^{-zT} \\ \text{Proportion of survivors if no exploitation} & S_0 = e^{-mT} \\ \Rightarrow \text{a complex relationship between } S, H, \text{ and } S_0: & 1 - H/(1 - S) = \log(S_0) / \log(S) \\ \dots S \text{ cannot be worked out as a simple function of } H \text{ and } S_0 & \end{aligned}$$

Exploitation in continuous time: approximation of additive competing risks

However, for high S_0 or low H , $S = f(S_0, H)$ (continuous lines)
is well approximated by line $S \approx S_0(1-H)$ (dashed lines)

0.9 Overall survival S

I

0.3

0

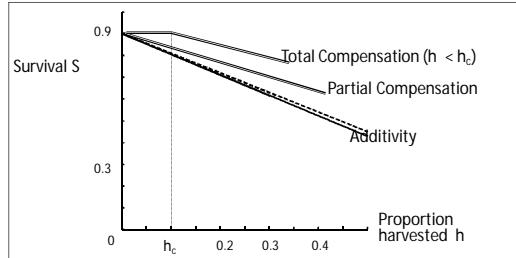
0.1 0.2 0.3 0.4

Proportion harvested H

*Similar results for variable
rates $m(t)$ and $h(t)$
For low S_0 , split in shorter
intervals*

Compensatory mortality

Does survival decrease with harvest h less rapidly than under "additive" mortality effects: $S > S_0(1-h)$?



Compensatory mortality and Density-dependence

- Compensatory mortality implies m decreases for high h
- Such a change can be mediated by density-dependence
- $h=10\%$ totally compensated
iff - 10% in numbers $\Rightarrow + 10\%$ survival
- Weak partial compensation expected in most cases
- Controversial evidence (Anderson & Burnham, 1976)
- Compensatory recruitment/reproduction?

Individual Frailty *Lindberg et al. in prep.*



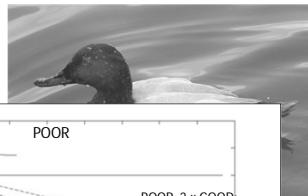
- Canvasback
Aythya valisineria
- 2 classes of "demographic quality" (purely phenotypical)
POOR and GOOD
- A discrete mixture model for a continuous heterogeneity
- "POOR" individuals more vulnerable to hunting than "GOOD"

Individual Frailty *Lindberg et al. in prep.*



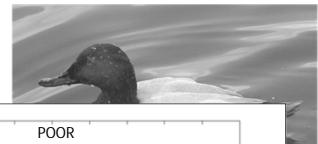
AGE	1	1	2+	2+	
QUALITY	POOR	GOOD	POOR	GOOD	
AGE	QUALITY				
1	POOR	0	$a_{1g} * f_{gp} * S_{1p} * (1-h_p)$	$a_p * f_{pp} * S_{1p} * (1-h_p)$	$a_g * f_{gp} * S_{1p} * (1-h_p)$
1	GOOD	0	$a_{1g} * f_{gg} * S_{1g} * (1-h_g)$	$a_p * f_{pg} * S_{1g} * (1-h_g)$	$a_g * f_{gg} * S_{1g} * (1-h_g)$
2+	POOR	$S_p * (1-h_p)$	0	$S_p * (1-h_p)$	0
2+	GOOD	0	$S_g * (1-h_g)$	0	$S_g * (1-h_g)$

Individual Frailty *Lindberg et al. in prep.*



"POOR" individuals more vulnerable to hunting than "GOOD"
"Die from hunting before dying from other cause" = compensation
Even under exchange between POOR and GOOD

Individual Frailty *Lindberg et al. in prep.*



POOR

POOR=2 x GOOD: COMPENSATION

GOOD

POOR-GOOD : ADDITIVITY

λ

h

Intimately linked with "REPRODUCTIVE VALUE"
 $P1 = 0.1544 \quad G1 = 1.1233 \quad P2+ = 0.2233 \quad G2+ = 1.1233$
 Contribution to future growth = common currency

Reproductive Value (RV) and compensation

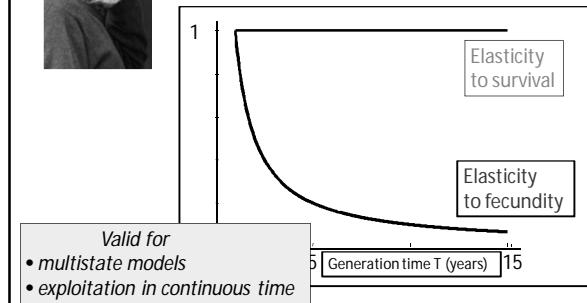
Compensation by heterogeneity
 $=$
harvest of low reproductive value
Biologically significant iff RV strongly uneven

RV (autumn) < RV(spring)
 RV(young) < RV(adult)
 RV(sink) < RV(source)
 RV(ill) < RV(healthy)



Sensitivity analysis Fecundity and Survival

Lebreton and Clobert 1991



Sensitivity analysis and Generation time



Albatross, $T \approx 24$ y:
 -30 % in Fecundity \Rightarrow
 -1.25 % in growth rate

*In any sharp decline of a long lived species,
 first suspect a change in survival*

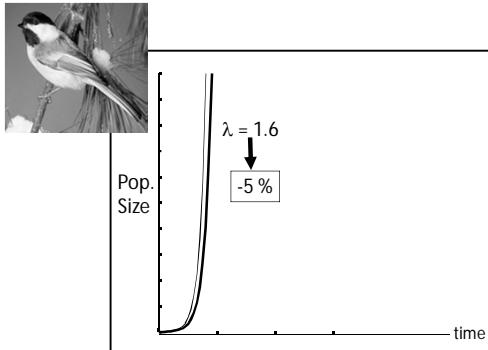
Sensitivity analysis and Generation time



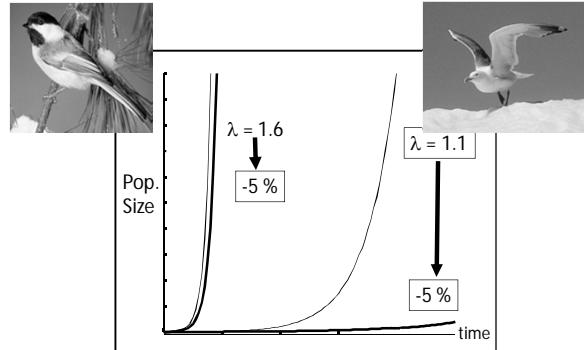
Albatross, $T \approx 24$ y:
 -30 % in Fecundity \Rightarrow
 -1.25 % in growth rate

*In any sharp decline of a long lived species,
 first suspect a change in survival*
 Ok, but does not say WHY long-lived species
 so often face conservation problems?

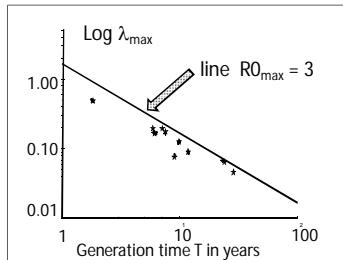
Effect of exploitation on growth rate



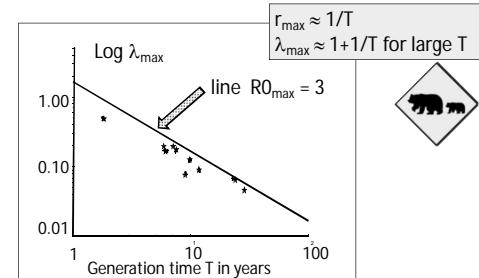
Effect of exploitation on growth rate



Constancy of MGR per Generation among Bird species (Niel & Lebreton, 2005)



Constancy of MGR per Generation among Bird species (Niel & Lebreton, 2005)

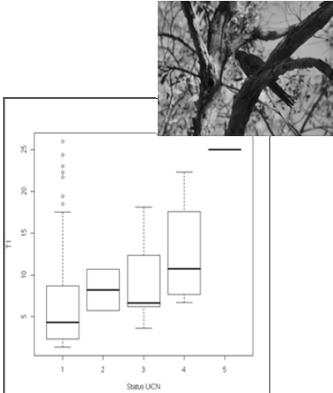


Generation time and conservation status (IUCN)

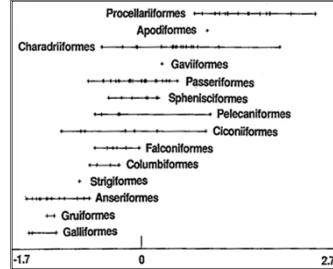
118 species with decently complete demographic info

Susceptibility to harvest \leftrightarrow
Max growth rate
Max growth rate \leftrightarrow
Generation time
Generation time \leftrightarrow
Conservation status

Susceptibility to harvest \leftrightarrow
Conservation status

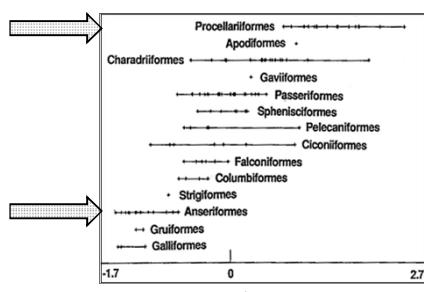


The slow fast gradient



← Fast 1st PC Slow →
PCA of Log Age at 1st repro., Log Ad. life expectancy, Log Fecundity,
corrected for body size
Gaillard et al. 1989, *Oecologia*

The slow fast gradient



← Fast 1st PC Slow →
PCA of Log Age at 1st repro., Log Ad. life expectancy, Log Fecundity,
corrected for body size
Gaillard et al. 1989, *Oecologia*

Adult survival among Anseriforms

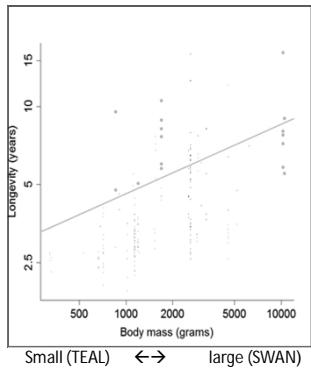
Devineau Ph.D., Devineau et al., in prep.

- 53 species, with replications over populations
- Estimated annual adult survival probability (CMR, Recoveries)
- Categorical index of hunting pressure

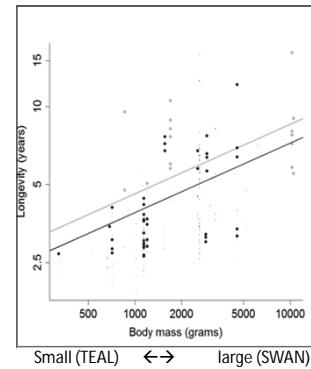
$h = 0$ No hunting
 $h = 1$ low
 $h = 2$ medium
 $h = 3$ high

Spécie	Information chasse	HP
<i>Anas acuta</i>	"hunter effort (...) was consistently high"	2
<i>Anas superciliosa</i>	"exposed to heavy hunting pressure"	3
<i>Anas platyrhynchos</i>	"regulations were stable and relatively liberal"	2
<i>Anas platyrhynchos</i>	"regulations were restrictive"	1
<i>Anser a. albifrons</i>	"restrictive measure have been imposed on shooting"	1
<i>Aythya collaris</i>	"the population (...) is heavily harvested"	3
<i>Lophodytes cucullatus</i>	"because of their low harvest rate"	1

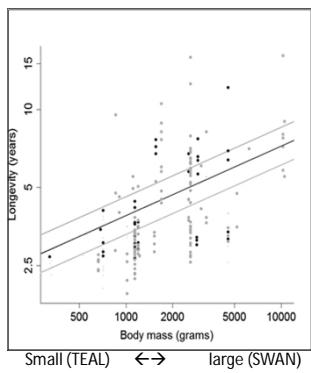
Adult survival among Anseriforms



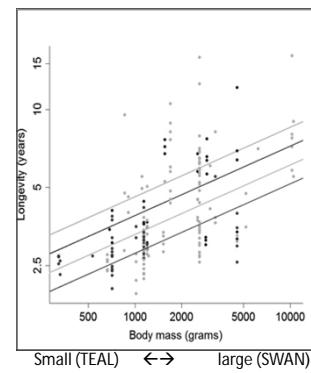
Adult survival among Anseriforms



Adult survival among Anseriforms

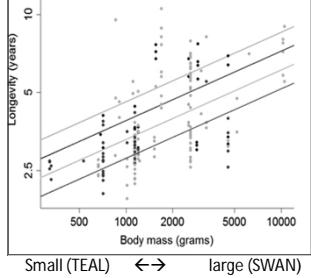


Adult survival among Anseriforms



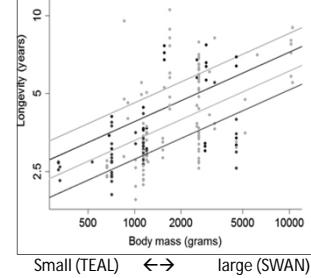
Adult survival among Anseriforms

- Survival does increase allometrically with Body mass
- Survival does decrease with hunting pressure
- Hunting level quantifiable from change in survival



Adult survival among Anseriforms

- Survival does increase allometrically with Body mass
- Survival does decrease with hunting pressure
- Hunting level quantifiable from change in survival

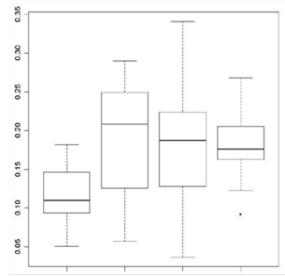


$$\begin{aligned} S &= S_0 \\ S &= S_0 \cdot (1 - H_{\text{low}}) \\ H_{\text{low}} &\approx 11\% \\ S &= S_0 \cdot (1 - H_{\text{medium}}) \\ H_{\text{medium}} &\approx 26\% \\ S &= S_0 \cdot (1 - H_{\text{high}}) \\ H_{\text{high}} &\approx 45\% \end{aligned}$$

Management choices match estimated max growth rate

Estimated maximum growth rate
1/T

Index of hunting pressure 0 1 2 3



Sensitivity analysis and Generation time



Albatross, T≈24 y:
-30 % in Fecundity ⇒
-1.25 % in growth rate

*In any sharp-decline of a long lived species,
first suspect a change in survival*

Longline fisheries and Black-Footed Albatross



- Demography similar to other albatross
- (adult survival ≈ 0.93)
- Matrix model: T ≈ 25 y



- 60 000 pairs => 300 000 individuals
- 1/T ≈ 0.04 => Maximum by-catch < 12 000
- Other sources of man-induced mortality (plastic ingestion...)
- ⇒ A warning of deleterious character of by-catch by longline fisheries (≈ 12 500 ind., Melvin, pers.comm.)
- Confirmed since by detailed analyses and modeling

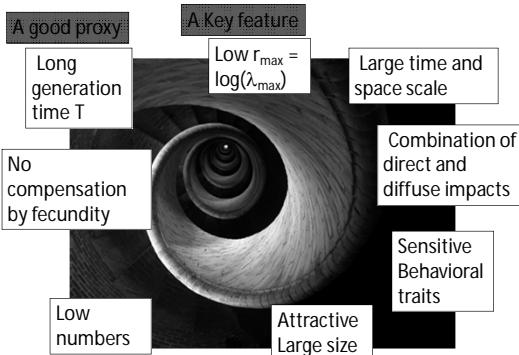
The malediction of long-lived species

- Long generation time
- Low maximum growth rate
- Man-induced exploitation, even incidental, often not sustainable

*As a capital with a low interest rate,
they cannot sustain
the tax of human impacts*



The malediction of long-lived species



The malediction of long-lived species

Choose your example



Lecture 8 Density Dependence



Robert MAY and David LACK, who contributed in very different fashions to our understanding of « Density-Dependence »



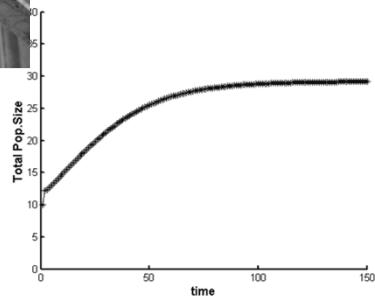
Matrix Models: Density-dependence

$$\begin{aligned} N_1(t+1) &= s_0(N_1(t) + N_2(t)) f_1 N_1(t) + s_0 f_2 N_2(t) \\ N_2(t+1) &= q_1 N_1(t) + q_2 N_2(t) \end{aligned}$$

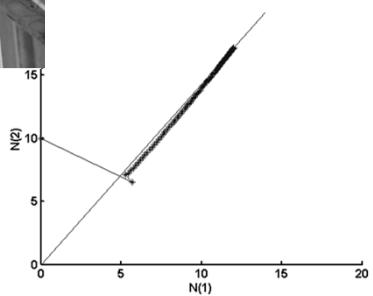
$$\text{e.g. } s_0(N_1(t) + N_2(t)) = 0.2 * \exp(-0.001 (N_1(t) + N_2(t)))$$



Trajectory over time Asymptotic stabilization



Trajectory in the phase plane Asymptotically stable age structure



Density-dependence and space A minimal Metapopulation model

$$N_{t+1} = R.D. N_t = \begin{pmatrix} a(N_t)p & b(1-q) \\ a(N_t)(1-p) & b q \end{pmatrix} N_t$$

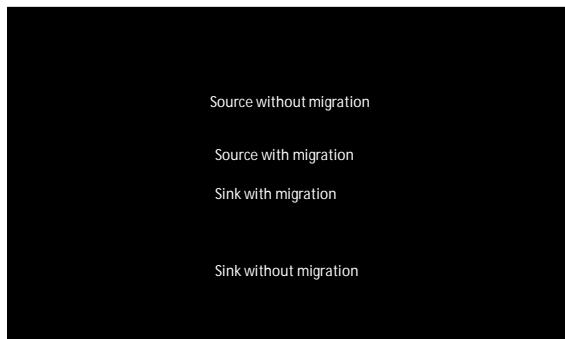
$$\begin{aligned} a(N_t) &= \exp(r(1 - N_t(1)/K)) && (\text{Source}) \\ b < 1 & && (\text{Sink}) \\ p < 1 & && (\text{migration, Source to Sink}) \\ q = 1 & && (\text{no migration from Sink to Source}) \end{aligned}$$

Density-dependence and space A minimal Metapopulation model

$$N_{t+1} = R.D. N_t = \begin{pmatrix} a(N_t)p & 0 \\ a(N_t)(1-p) & b \end{pmatrix} N_t$$

$$\begin{aligned} a(N_t) &= \exp(r(1 - N_t(1)/K)) && (\text{Source}) \\ b < 1 & && (\text{Sink}) \\ p < 1 & && (\text{migration, Source to Sink}) \\ q = 1 & && (\text{no migration from Sink to Source}) \end{aligned}$$

Effect of migration from a Source to a Sink

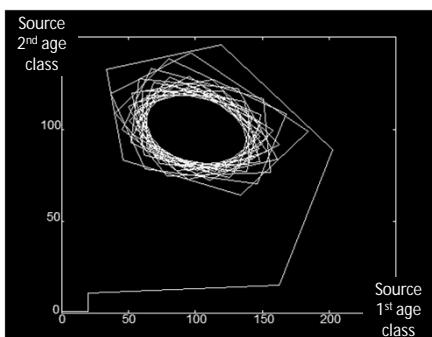


A diversity of behaviors

- Stages x ages etc...
- Dependence on total population size
- Dependence on some components:
e.g., number of breeders
- Dependence of various parameters:
e.g. probability of breeding
- Further complexity due to discrete time
stable equilibrium for low λ_{\max}
periodic equilibrium for higher values
chaos for high values
- ... even more in multistate models



Source-sink 2 age classes, 2 sites



Estimating intensity of Density-Dependence Issues resulting from uncertainty in population size estimates

Lebreton and Gimenez, JWM, 2013

- From series of population size estimates
 - Tricky
 - Strong risk of overestimation
 - State-space models promising
 - No fully standardized approach
- On traits (e.g. Capture-recapture data)
 - Straightforward
 - Conservative, i.e. tendency to underestimation

Modeling density-dependence often speculative
rather than directly based on empirical evidence



Lecture 9

Demographic stochasticity



Krishna ATHREYA



Peter NEY



Peter JAGERS



Eugene SENETA

Major contributors to the theory of branching processes,
a natural framework for modeling demographic stochasticity

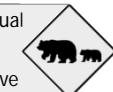


A simple example



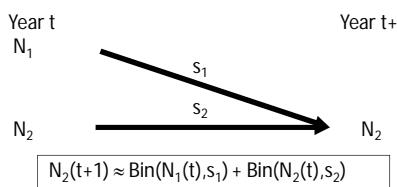
- Death / Survival as a coin tossing experiment
- Reproduction as a discrete distribution
(e.g. Clutch size \sim Poisson distribution)
- Independence of individuals

- As usual, "random" stands for residual variation after adequate stratification
- Independence may be more restrictive

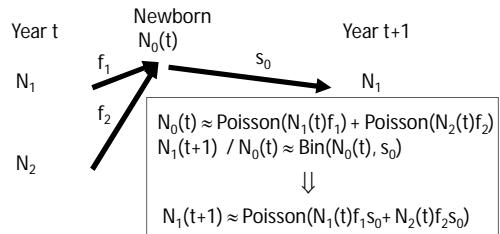


Death/Survival

In what follows, everything is conditional on $N_1(t)$ and $N_2(t)$



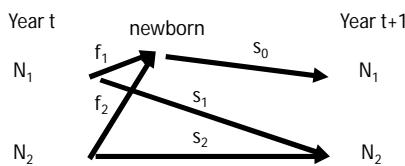
Reproduction



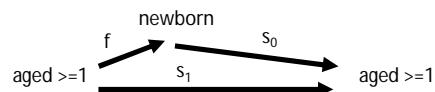
Overall model: a branching process

$$N_1(t+1) \approx \text{Poisson}(N_1(t)f_1s_0 + N_2(t)f_2s_0)$$

$$N_2(t+1) \approx \text{Bin}(N_1(t), s_1) + \text{Bin}(N_2(t), s_2)$$



An even simpler example of branching process



Demographic vs Environmental stochasticity

Demographic

$$\begin{aligned} N(t+1) &\approx \text{Poisson}((pf+q)N(t)) = \text{Poisson}(\lambda N(t)) \\ E(N(t+1)/N(t)) &= \lambda N(t) \quad \text{var}(N(t+1)/N(t)) = \lambda N(t) \\ \text{More generally } \text{var}(N(t+1)/N(t)) &= \alpha N(t) \end{aligned}$$

Demographic

$$\begin{aligned} N(t+1) &\approx \text{Poisson}((pf+q)N(t)) = \text{Poisson}(\lambda N(t)) \\ E(N(t+1)/N(t)) &= \lambda N(t) \quad \text{var}(N(t+1)/N(t)) = \lambda N(t) \\ \text{More generally } \text{var}(N(t+1)/N(t)) &= \alpha N(t) \end{aligned}$$

Environmental

$$\begin{aligned} N(t+1)/N(t) &\approx \Lambda N(t), \Lambda \text{ random variable, } E(\Lambda) = \lambda \\ E(N(t+1)/N(t)) &= \lambda N(t) \quad \text{var}(N(t+1)/N(t)) = \sigma^2 N(t)^2 \\ \text{More generally } \text{var}(N(t+1)/N(t)) &= \alpha N(t)^2 \end{aligned}$$

Demographic vs Environmental stochasticity

Demographic

$$\begin{aligned} N(t+1) &\approx \text{Poisson}((pf+q)N(t)) = \text{Poisson}(\lambda N(t)) \\ E(N(t+1)/N(t)) &= \lambda N(t) \quad \text{var}(N(t+1)/N(t)) = \lambda N(t) \\ \text{More generally } \text{var}(N(t+1)/N(t)) &= \alpha N(t) \end{aligned}$$

Environmental

$$\begin{aligned} N(t+1)/N(t) &\approx \Lambda N(t), \Lambda \text{ random variable, } E(\Lambda) = \lambda \\ E(N(t+1)/N(t)) &= \lambda N(t) \quad \text{var}(N(t+1)/N(t)) = \sigma^2 N(t)^2 \\ \text{More generally } \text{var}(N(t+1)/N(t)) &= \alpha N(t)^2 \end{aligned}$$

Demographic	$\text{var}(N(t+1)/N(t))$
Environmental	$\alpha N(t)$
	$\alpha N(t)^2$



Demographic vs Environmental stochasticity

Demographic	$\text{var}(N(t+1)/N(t))$
Environmental	$\alpha N(t)$
	$\alpha N(t)^2$

- Environmental Stochasticity prevails over Demographic Stochasticity in large populations
- Demographic Stochasticity prevails over Environmental Stochasticity in small populations
- Demographic Stochasticity may be non negligible in large, multistate populations (small number of individuals in some states)

Demographic stochasticity and extinction

- In Branching processes, population size is an integer
- Extinction is unambiguously defined as reaching a population size equal to 0
- ... or a vector population size equal to (0, 0, ..., 0) in the case of a structured population
- Many formal results in mathematical literature
- e.g., extinction certain iff $\lambda \leq 1$
- Simulation straightforward in ULM



Demographic stochasticity in ULM

"rel" = recurrence relationships

```
{ Swallow with demographic stochasticity
defmod swallowDS(2)
rel : rn1,rn2

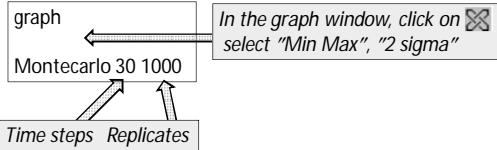
{ relation for n1
defrel rn1
n1 = poisson(n1*s0*(f1+f2))

{ relation for n2
defrel rn2
n2 = binomf(n1,s1) + binomf(n2,s2)
```

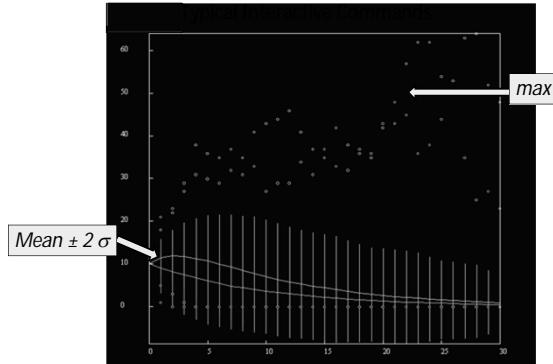
Demographic stochasticity in ULM declaring variables and parameters

```
{ initial numbers
defvar n1 = 10
defvar n2 = 10
{ total number
defvar n = n1 + n2
{ 1st year survival prob.
defvar s0 = 0.3
{ 2nd year survival prob.
defvar s1 = 0.50
{ After 2nd year survival prob.
defvar s2 = 0.65
{ subadult female fecundity
defvar f1 = 3.0/2
{ adult female fecundity
defvar f2 = 6.0/2
```

Demographic stochasticity in ULM Typical Interactive Commands



Demographic stochasticity in ULM



Demographic stochasticity and Density-dependence

If $\lambda > 1$, asymptotically $P(N(t)=0) + P(N(t)=\infty) = 1$, i.e. the population either goes extinct or escapes to ∞

If DD is added to stabilize the population, then, asymptotically $P(N(t)=\infty) = 0$

Hence asymptotically $P(N(t)=0) = 1$, i.e. extinction is certain

Demographic stochasticity and Density-dependence



```
defmod sparrow(1)
rel : rn1
{ relation for n1
defrel rn1
n = poisson(n*s0*f)+binomf(n,s1)
{ initial numbers
defvar n = 10
{ FY survival probability
defvar s0 = 0.2*exp(-0.01*n)
{ AFY survival probability
defvar s1 = 0.5*exp(-0.01*n)
{ female fecundity
defvar f = 6.0/2
```

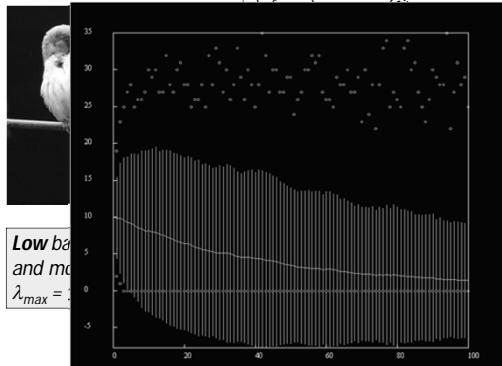
Demographic stochasticity and Density-dependence



```
defmod sparrow(1)
rel : rn1
{ relation for n1
defrel rn1
n = poisson(n*s0*f)+binomf(n,s1)
{ initial numbers
defvar n = 10
{ FY survival probability
defvar s0 =
{ AFY survival probability
defvar s1 =
{ female fecundity
defvar f = 6.0/2
```

**Low baseline survival
and moderate DD**
 $\lambda_{max} = 1.1$

Demographic stochasticity and Density-dependence



Demographic stochasticity and Density-dependence



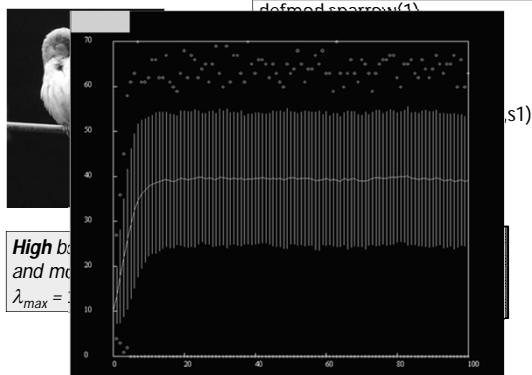
High baseline survival and moderate DD
 $\lambda_{max} = 1.5$

```
defmod sparrow(1)
rel : rn1
{ relation for n1
defrel rn1
n = poisson(n*s0*f)+binomf(n,s1)

{ initial numbers
defvar n = 10

{ FY survival probability
defvar s0 =
{ AFY survival probability
defvar s1 =
{ female fecundity
defvar f = 6.0/2
```

Demographic stochasticity and Density-dependence



Demographic stochasticity and Density-dependence

If DD is added to stabilize the population, extinction is certain

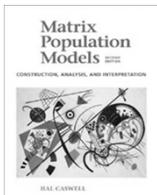
- Population size stabilizes conditional on non extinction (**Quasi-stationary distribution, QSD**)
- $\Pr(\text{extinction in one time step})$ becomes constant
- Time to extinction: geometric distribution
- $\Pr(\text{Extinction over finite time window})$ often negligible

The QSD concept leads to a continuum from decreasing population doomed to close extinction to stable DD populations with negligible risk of extinction



Lecture 10

Uncertainty, Process Variance, and Retrospective Perturbation Analysis



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UNCERTAINTY

- If you attended the multi-event workshop or have similarly dealt with parameter estimation, great attention is paid to
 - Accuracy
 - Precision
- Have not yet talked about how to incorporate sampling uncertainty into the analysis of a matrix model

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UNCERTAINTY

- For example, a deterministic matrix model does not depict uncertainty in parameter estimates

Vital Rate	Mean	s.e.
F_1	0.50	0.05
F_{2+}	1.00	0.10
S_1	0.25	0.02
S_{2+}	0.50	0.05

$$\mathbf{A} = \begin{bmatrix} 0.5 & 1 \\ 0.25 & 0.5 \end{bmatrix}$$

$$\lambda = 1.00$$

- How can we estimate uncertainty in λ ?

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UNCERTAINTY

- A robust frequentist method is to create 'Bootstrapped' datasets from your data
 - Sample individuals from the data with replacement to create a new data set
 - Re-estimate vital rates
 - Re-parameterize matrix model
 - Re-calculate λ
 - Repeat steps 1-4 1000 times (or more)
 - Order values of λ
 - 25th and 975th values make up the 95% Confidence Interval for λ (or more generally, the 0.025 and 0.975 quantiles)

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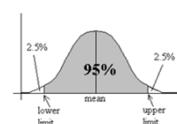
UNCERTAINTY

- Boot-Strap limitations
 - Do not always have the original datasets available to sample from
 - Does not perform well with small samples
- Monte Carlo simulations

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UNCERTAINTY

- Monte Carlo simulations (MC)
 - Each vital rate is *sampled* from a unique probability distribution
 - The uncertainty measured in each vital rate (sampling variation) defines the 95% confidence limits on the *sampling distribution*



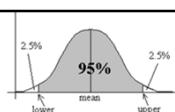
- Randomly draw vital-rate values from within these limits

252

UNCERTAINTY

- Monte Carlo Simulations

- Randomly draw vital-rate values from within these limits
- Re-parameterize matrix model with random vital rate values
- Calculate λ for each random trial
- Repeat 1-3 1000 times (or more)
- Order the 1000 values of λ
- 0.025 and 0.975 quantiles of λ make up the 95% C.I.



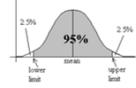
$$\mathbf{A} = \begin{bmatrix} 0.5 & 1 \\ 0.25 & 0.5 \end{bmatrix}$$

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UNCERTAINTY

- Monte Carlo Simulations

- What if you don't know the type of distribution that a vital rate is sampled from (e.g., Beta, log-normal, etc.)?



- A conservative and perhaps more appropriate assumption in a frequentist setting is to use a Uniform Distribution that spans from the LCL to UCL for each vital rate



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UNCERTAINTY

- Monte Carlo Example

$$\mathbf{A} = \begin{bmatrix} 0.5 & 1 \\ 0.25 & 0.5 \end{bmatrix}$$

Vital Rate	Mean	s.e.	LCL	UCL
F_1	0.50	0.05	0.40	0.60
F_{2+}	1.00	0.10	0.80	1.20
S_1	0.25	0.02	0.21	0.29
S_{2+}	0.50	0.05	0.40	0.60

- Assume uniform distributions for each vital rate ranging from respective lower and upper confidence limits

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UNCERTAINTY

- Monte Carlo Example

- Randomly draw vital-rate values from these uniform distributions
 - using R, ULM, Matlab, Excel or any program with such capabilities
- Parameterize matrix model with random vital rate values
- Calculate λ for each trial
 - using Eigen Analysis (like in the exercises) $\mathbf{A} = \begin{bmatrix} r.v. & r.v. \\ r.v. & r.v. \end{bmatrix}$
- Repeat 1000 times
 - e.g., using a `for` loop in a programming language (R, Matlab, etc.)

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UNCERTAINTY

- Monte Carlo Simulations

- Order the 1000 values of λ
 - ⋮
 - 1.11
 - 1.10
 - 1.09
 - ⋮
 - ⋮
 - 0.90
 - 0.89
 - 0.88
 - ⋮
- 0.025 and 0.975 quantiles for λ make up the 95% confidence intervals
- λ 95% C.I. = [0.89, 1.10]

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UNCERTAINTY

- Advanced approach to estimating uncertainty in population dynamics

- Integrated Population Models
 - A combination of matrix modeling in an estimation framework
- Maximum Likelihood Estimation of parameters in matrix model, population structure, and population growth rate with the Kalman Filter
- Bayesian estimation

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VARIANCE COMPONENTS

- Often want to know the actual process variation in demographic parameters
 - e.g., the variation driven by temporal or spatial variation in the environment
 - Resource variability
 - That driven by conservation and management actions
- Most useful for projecting stochastic population dynamics (population viability / recovery / control analysis)

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VARIANCE COMPONENTS

- Estimates of variance* also include sampling variation (a.k.a. observation error)
 - A measure of precision and repeatability
 - Occurs whenever studying a *finite* random sample from a larger population (i.e., sampling universe)
 - Observer has some control over sampling variation through study design (e.g., sample size, stratification and replication, selection of covariates, etc.)

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VARIANCE COMPONENTS

- Challenge is to separate variance components

$$\hat{V}_{total} \approx \hat{V}_{process} + \hat{V}_{sampling}$$

$$\hat{V}_{process} \approx \hat{V}_{temporal} + \hat{V}_{spatial}$$

$\hat{V}_{individual}$

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VARIANCE COMPONENTS

- Burnham et al. 1987 post hoc approach
 - Go to: http://welcome.warnercnr.colostate.edu/class_info/fw663/ for fisheries monograph
 - Sampling variance in a *single* Survival Probability:

$$\hat{V}_{sampling} = \frac{\hat{S}(1-\hat{S})}{n}$$

$$\hat{V}_{sampling} = [s.e.(\hat{S})]^2$$

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VARIANCE COMPONENTS

- Using a (temporal) string of survival probabilities

Year	N	Lived	S	Sampling Var
1981	46	15	0.3269	0.001915
1982	114	38	0.3333	0.001915
1983	118	5	0.0437	0.00034
1984	106	19	0.17925	0.00139
1985	155	59	0.38065	0.00152
1986	161	61	0.37688	0.00146
1987	116	15	0.12931	0.00097
7 =Count			Sum=	0.01241

- Post hoc estimator for total variation in the data:

$$\hat{V}_{total} = \frac{\sum_{t=1}^n (\hat{S}_t - \bar{\bar{S}})^2}{n-1} \quad V_{process} = V_{total} - V_{sampling}$$

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VARIANCE COMPONENTS

- Burnham et al. (1987) estimator of process variance weights each sample by its relative sampling precision

$$weight_t = \frac{1}{\hat{V}_{process} + \hat{V}_{sampling,t}}$$

$$\frac{1}{T-1} \sum_{t=1}^T weight_t (\hat{S}_t - \bar{\bar{S}})^2 = 1$$

- Use Excel's 'Solver' or R's 'Optim' function to find solution to process variation

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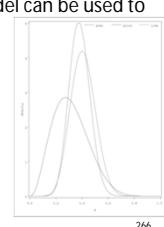
VARIANCE COMPONENTS

- Same approach can be used to decompose spatial process variation from total variation
- Also useful for extracting process variation in meta-analyses of published studies (applicable to any parameter of interest)
- Extensions by Kendall 1998 & Ackakaya 2002 provided in the *popbio* package for R; Gould & Nichols 1998 offer another extension

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VARIANCE COMPONENTS

- Hierarchical methods
 - Data model (observation model)
 - Estimate sampling variation
 - Process model linked to the data model
 - Random effect terms in process model can be used to estimate process (co)variation
 - Formal way to estimate process (co)variance



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PERTURBATION ANALYSIS

- Prospective Perturbation Analysis
 - Forward looking
 - Assess how dynamics would change if demographic parameters were to change
- Retrospective Perturbation Analysis
 - Examining the past
 - Assess how past changes in demographic parameters affected population dynamics

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MOTIVATION

- Retrospective Perturbation Analysis
 - Assessing ecological capacity and scope for demographic parameters to change, and in turn cause change in population dynamics
 - Assessing *actual* impacts of management, conservation actions, and experiments on observed population dynamics
 - Given existing biological constraints

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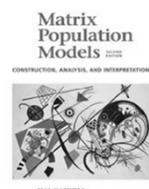
LTRE

- Life Table Response Experiments (LTRE)
 - Used to examine the effect of past variation in vital rates on population growth rates
- Treatments (or time or space) affect the various vital rates
- Set of vital rates (matrix) are the intermediate response variables in an experimental design or observational study
- λ most frequently used statistic to evaluate the population-level effect of the treatments or environmental variation

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LTRE DESIGNS

- Analogous to:
 - ANOVA Designs
 - One-way fixed effects
 - Factorial fixed effects
 - Regression Designs
 - Continuous covariate effects
 - Random Effects Design
 - Spatial or temporal process variance



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L TRE EXAMPLE

- One-way fixed design
 - Vital rates measured in treatment areas (t) and control areas (c)

$$\mathbf{A}_t = \begin{bmatrix} 0 & \mathbf{0.197} & \mathbf{0.393} \\ 0.891 & 0 & 0 \\ 0 & 0.891 & 0.891 \end{bmatrix} \quad \lambda = 1.158$$

$$\mathbf{A}_c = \begin{bmatrix} 0 & \mathbf{0.098} & \mathbf{0.197} \\ 0.891 & 0 & 0 \\ 0 & 0.891 & 0.891 \end{bmatrix} \quad \lambda = 1.046$$

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L TRE EXAMPLE

- Calculate the mean matrix

$$\mathbf{A}_m = \frac{(\mathbf{A}_t + \mathbf{A}_c)}{2}$$

$$\mathbf{A}_m = \begin{bmatrix} 0 & 0.148 & 0.295 \\ 0.891 & 0 & 0 \\ 0 & 0.891 & 0.891 \end{bmatrix}$$

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L TRE EXAMPLE

- Calculate the sensitivities for the mean matrix \mathbf{A}_m

$$S_m = \begin{bmatrix} 0 & 0.122 & 0.507 \\ 0.188 & 0 & 0 \\ 0 & 0.168 & 0.697 \end{bmatrix}$$

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L TRE EXAMPLE

- Calculate the difference between \mathbf{A}_t and \mathbf{A}_c

$$\mathbf{D} = \mathbf{A}_t - \mathbf{A}_c$$

$$\mathbf{D} = \begin{bmatrix} 0 & 0.099 & 0.196 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$$

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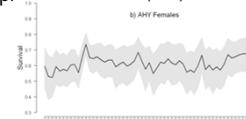
L TRE EXAMPLE

- Multiply the differences by the sensitivities
 - (element-by-element multiplication: Hadamard product)
- $\mathbf{C} = \mathbf{D} \circ S = \begin{bmatrix} 0 & 0.012 & 0.099 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$
- Results in the contributions of the differences in the vital rates to the actual difference in λ between treatment and control

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- Random effects L TRE design

- Vital rates vary over time, some of which is attributable to temporal process variation (var) Riernham et al 1987, Kendall 1998 & Ackakaya 2002



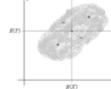
- Process variation in λ is a function of process variation in vital rates and their respective sensitivity values

$$\text{var}(\lambda) \approx \sum_x \text{var}(x) \times \text{sens}_x^2$$

- Contribution of each vital rate to this variation is a component of this equation

$$\text{contribution}_x = \text{var}(x) \times \text{sens}_x^2$$

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- Random effects LTRE design
 - Vital rates may co-vary with one another over time
 
 - More generally, process variation in λ is a function of process co-variation in vital rates and sensitivity values

$$\text{var}(\lambda) \approx \sum_x \sum_y \text{cov}(x, y) \times \text{sens}_x \times \text{sens}_y$$
 - Contribution of each vital rate to this variation is a component of this equation

$$\text{contribution}_x = \sum_y \text{cov}(x, y) \times \text{sens}_x \times \text{sens}_y$$

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PERTURBATION ANALYSIS

- Parameters with greatest elasticities will have the greatest relative impact on λ 'if changed'
 - Sometimes they may not be 'manageable'
- Parameters with greatest contribution to past variation can be indicative of ecological process and management opportunity
- Valuable to conduct both prospective and retrospective perturbation analyses when developing management & conservation plans

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Lecture 11

Overview



Main points

- The flexibility of matrix models
 - Multistate
 - Constant parameters, RE, DD, Demographic stochasticity
- Coherent theory
 - Stable population theory
 - Multistate stable population theory
 - Random environment and product of random matrices
 - Demographic stochasticity and branching processes
 - The theory of exploited populations
- Simulation / numerical abilities
- Links with parameter estimation
 - Sensitivity
 - LTRE

A few thoughts on modeling

- Models are tools to answer questions, not beautiful and fancy representations of reality
- There is no good or bad model; there are useful, less useful, or useless models

Would you say a hammer is good or bad ?
- Data have not been generated by models: the best you can hope is that **on some selected criteria**, outputs of the model behave like the real world
- Do not expect a model to be exhaustive

"Models are playthings relative to reality"

R.M. Cormack

How to proceed

- Review your questions
 - Growth ?
 - Sustainable exploitation ?
 - Extinction risk
 - Disease dynamics
 - ...
- Decide of model structure based on
 - Demographic structure (stage ? Age ? ...)
 - Key features in relation with your questions
 - Information available
 - Use guess-timates when needed (+ comparative approach)
- Link with theory
 - Numerical evidence is not a proof
 - Theory links with otherwise overlooked features

Numerical evidence is not a proof

$$\sum_{i=1}^{\infty} \frac{1}{i} ?$$

Numerical evidence is not a proof

$$\sum_{i=1}^{\infty} \frac{1}{i} ?$$

Numerical Simulation $\sum_{i=1}^n \frac{1}{i}$ for different values of n

n	100,000	500,000	1,000,000	1,500,000	2,000,000
Sum	12.0901	13.6996	14.3927	14.3927	14.3927

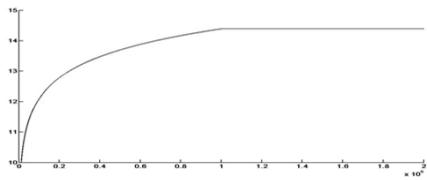
Seems to bring a fair proof of convergence to 14.3927

However

Numerical evidence is not a proof

$$\sum_{i=1}^{\infty} \frac{1}{i} ?$$

- the illusion of convergence results from "underflow":
- once $1/i < 10^{-6}$, $1/i$ is forced to 0 on the computer used
- The sum above is indeed not convergent



How to proceed

- Bottom-up approach

- To understand which result comes from which model feature
- For better communication / publication
- To keep focus on your questions

"Modeling is the art of oversimplification"

