Matrix Population Models for Wildlife Conservation and Management

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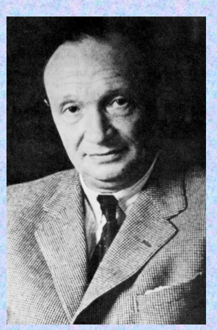
1

Matrix model formulation



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

2

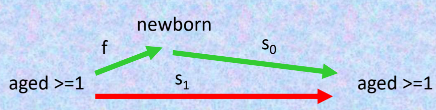
Matrix model formulation

- Two simple examples
- Some numerical results
- A first look at different generalizations

3

A simple example

QUANTITATIVE LIFE CYCLE
in a house sparrow *Passer domesticus* population



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

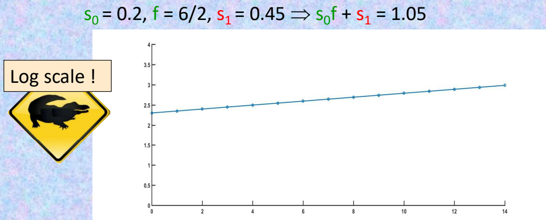
4

A simple example

QUANTITATIVE LIFE CYCLE
in a house sparrow population

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

$s_0 = 0.2$, $f = 6/2$, $s_1 = 0.45 \Rightarrow s_0 f + s_1 = 1.05$



5

A simple example

Discrete time vs Continuous time

Discrete time: $N(t+1) = (s_0 f + s_1)\, N(t) = \lambda\, N(t)$

Continuous time: $N'(t) = r\, N(t) \Rightarrow$

$N(t) = N(0) \exp(rt)$

$N(t+1) = N(0) \exp(r(t+1)) = N(0) \exp(rt+r) = N(0) \exp(rt)\exp(r)$

Hence $N(t+1) = \exp(r)\, N(t)$

$\exp(r) = \lambda$

or, equivalently $r = \mathrm{Ln}(\lambda)$

6

A simple example

Discrete time vs Continuous time
Two different points of view

Discrete time: $N(t+1) = (s_0 f + s_1)\, N(t) = \lambda\, N(t)$

- Uses only overall seasonal survival probabilities and fecundity

Continuous time: $N(t+1) = \exp(r)\, N(t)$

- Based on constant r throughout (within as well as among years)
- Or, in presence of within year (seasonal) variation in demography, requires to integrate changes induced by variation in instantaneous rates to produce overall annual r

However, within year changes in, e.g., survival, most often inaccessible … and not needed in discrete time models

7

A simple example

Density Dependence

Density independent model

$\lambda = 0.45+0.2 * 3 = 0.45+0.6 = 1.05$

Density Dependent model

Assume fecundity decreases with population size as 3 *exp(-0.001*N(t))
then

$\lambda = 0.45+ 0.6 * \exp(-0.001*N(t))$

8

A simple example

Density Dependence

Density Dependent model

$\lambda = 0.45+ 0.6 * \exp(-0.001*N(t))$

- λ is a monotonously decreasing function of N
- Equals 1 iff exp(-0.001*N(t) = (1-0.45)/0.6 = 11/12
- i.e. when N = -1000 * Ln(11/12) = 87.0114

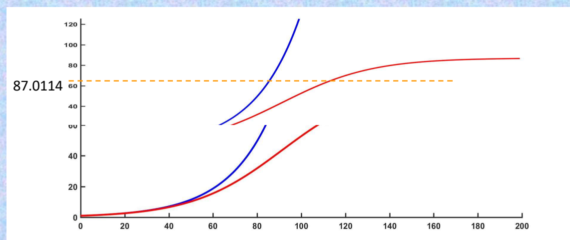
9

A simple example

Density Dependence

$\lambda = 0.45+0.6 = 1.05$

$\lambda = 0.45+ 0.6 * \exp(-0.001*N(t))$



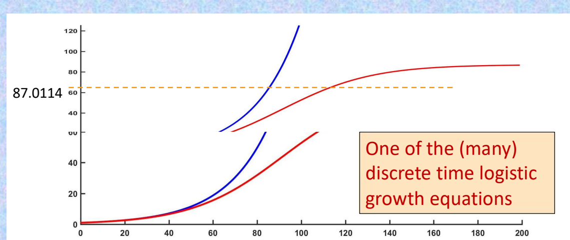
10

A simple example

Density Dependence

$\lambda = 0.45+0.6 = 1.05$

$\lambda = 0.45+ 0.6 * \exp(-0.001*N(t))$



11

Another simple example

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

Year t

females aged 1

females aged >1

s_1

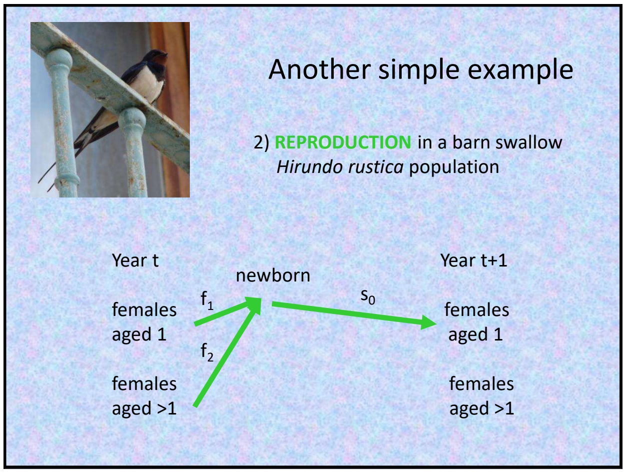
s_2

Year t+1

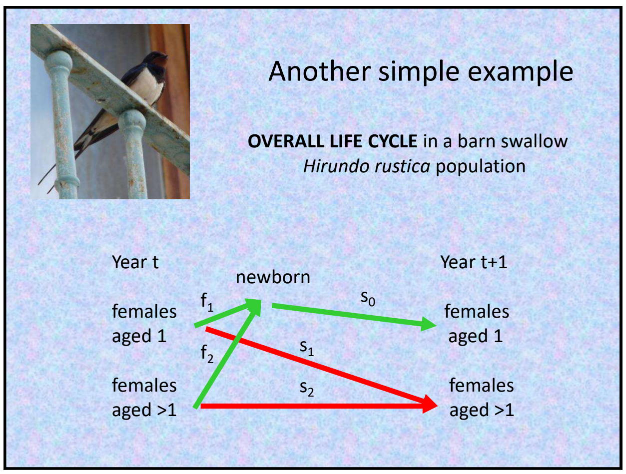
females aged 1

females aged >1

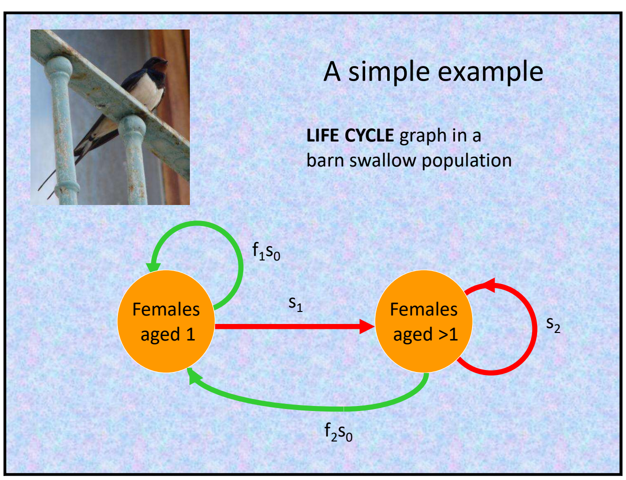
12


Another simple example
2) REPRODUCTION in a barn swallow
Hirundo rustica population
Year t
newborn
Year t+1
females aged 1
f_1
s_0
females aged 1
f_2
females aged >1
females aged >1

13


Another simple example
OVERALL LIFE CYCLE in a barn swallow
Hirundo rustica population
Year t
newborn
Year t+1
females aged 1
f_1
s_0
females aged 1
s_1
f_2
s_2
females aged >1
females aged >1

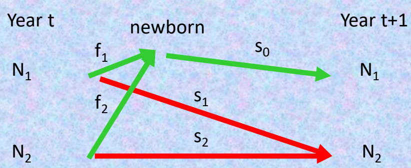
14


A simple example
LIFE CYCLE graph in a
barn swallow population
f_1s_0
Females aged 1
s_1
Females aged >1
s_2
f_2s_0

15

Another simple example

QUANTITATIVE LIFE CYCLE
in a barn swallow population



16

Another simple example

QUANTITATIVE LIFE CYCLE
in a barn swallow population

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

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

17

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

18

Another 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)

19

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

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

20

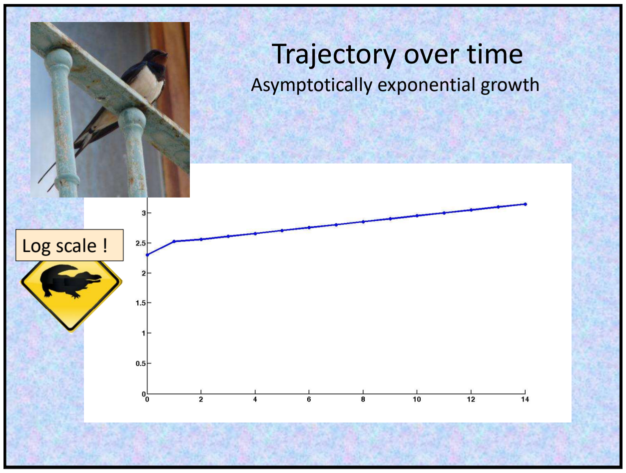
Some Numerical Results

QUANTITATIVE LIFE CYCLE
in a barn swallow population

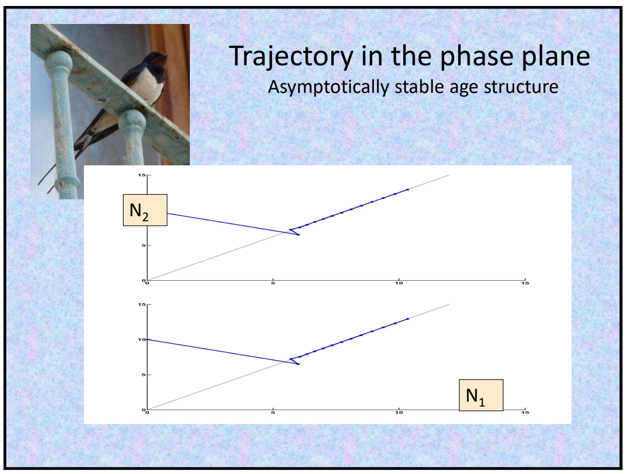
Two linear Equations
$N_1(t+1) = 0.30\ N_1(t) + 0.60\ N_2(t)$
$N_2(t+1) = 0.50\ N_1(t) + 0.65\ N_2(t)$

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

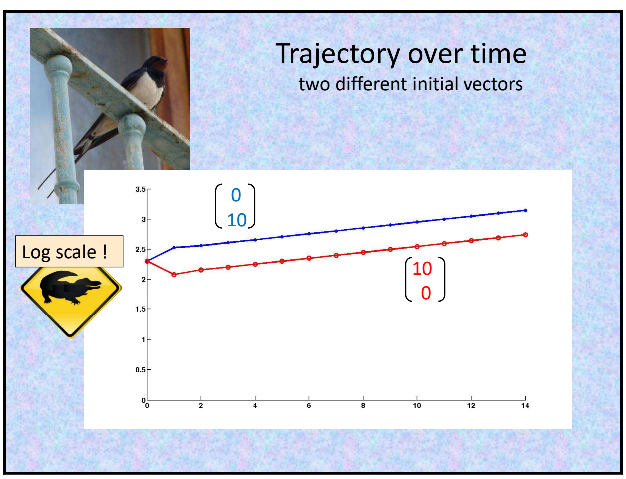
21


Trajectory over time
Asymptotically exponential growth
Log scale !

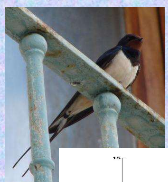
22


Trajectory in the phase plane
Asymptotically stable age structure
N_2
N_1

23

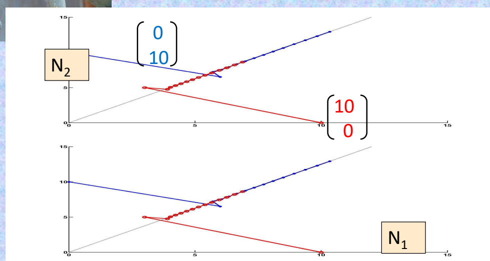

Trajectory over time
two different initial vectors
Log scale !
$\begin{bmatrix} 0 \\ 10 \end{bmatrix}$
$\begin{bmatrix} 10 \\ 0 \end{bmatrix}$

24



Trajectory in the phase plane

two different initial vectors



25

Another simple example

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

26

Model as a tool: use it to answer questions

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

27

Model as a tool: suggested modeling process

- Biological Questions
- Review Information available
- Build model
- Translate biological Q. into technical Q.
- Proceed to parameter estimation (CMR)
- Use model to answer Biological Questions

28

Matrix Models: the basic Leslie age-structured model

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

$$M = \begin{pmatrix} f_1s_1 & f_2s_1 & \dots & f_is_1 & \dots & f_ns_1 \\ s_2 & 0 & \dots & 0 & \dots & 0 \\ 0 & s_3 & \dots & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & \dots & s_{i+1} & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & \dots & s_n & 0 \end{pmatrix}$$

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

note shift in
survival indices

29

Matrix Models: a first variation

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

$$M = \begin{pmatrix} f_1s_1 & f_2s_1 & \dots & f_is_1 & \dots & f_ns_1 \\ s_2 & 0 & \dots & 0 & \dots & 0 \\ 0 & s_3 & \dots & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & \dots & s_{i+1} & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & \dots & s_n & s_{n+1} \end{pmatrix}$$

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

"n+" age class $\Longleftrightarrow$
infinite matrix

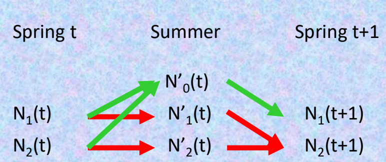
30

Matrix Models: a variety of structures

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

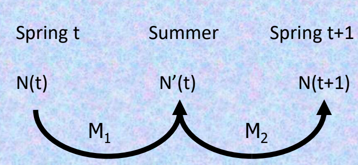
31

Matrix Models: seasonal models



32

Matrix Models: seasonal models



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

33

Matrix Models: seasonal models

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

M_2M_1 = [2x3 matrix] x [3 x 2 matrix]
is a 2 x 2 matrix

$$M_2M_1 = \begin{pmatrix} s_0f_1 & s_0f_2 \\ s_1 & s_2 \end{pmatrix}$$

… the 2 x 2 original matrix

34

Matrix Models: post birth-pulse model

Spring t	Summer	Spring t+1
N(t)	N'(t)	N(t+1)

$$N(t) \xrightarrow{M_1} N'(t) \xrightarrow{M_2} N(t+1)$$

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

$$M_1 M_2 = \begin{pmatrix} f_1s_0 & f_2s_1 & f_2s_2 \\ s_0 & 0 & 0 \\ 0 & s_1 & s_2 \end{pmatrix}$$

35

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 *stricto sensu*	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)

36

Matrix Models: Density-dependence

$N_1(t+1) = \boxed{s_0(N_1(t) + N_2(t))} \times [\, f_1 N_1(t) + f_2 N_2(t) \,]$

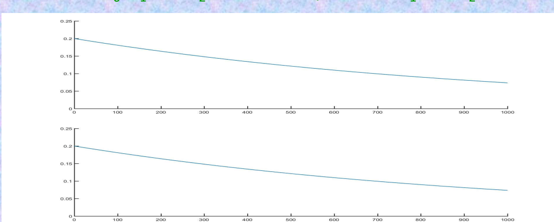
$N_2(t+1) = s_1 N_1(t) + s_2 N_2(t)$

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

37

Matrix Models: Density-dependence

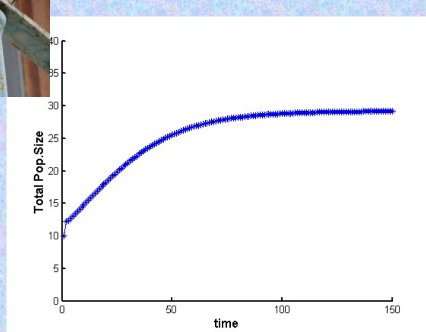
$s_0(N_1(t) + N_2(t)) = 0.2 * \exp(-0.001\, (N_1(t) + N_2(t)))$



38

Trajectory over time

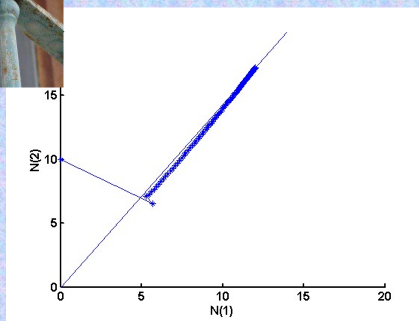
Asymptotic stabilization



39

Trajectory in the phase plane

Asymptotically stable age structure



40

Matrix Models: Density-dependence

- Regular (asymptotic) behaviour too
- Formal analysis feasible too
- Transcribes "Logistic growth"

  in a realistic (demographic) context

41

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 » (« stages », « states »)
- Discrete seasons, matrix products, pre/post birth-pulse
- Parameter estimation often drives choice of generalization (e.g. random environment)
- Amenable to formal study (**not only asymptotics**!)

42

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43