Matrix Population Models for Wildlife Conservation and Management

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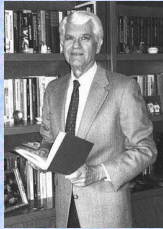
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Multistate matrix models

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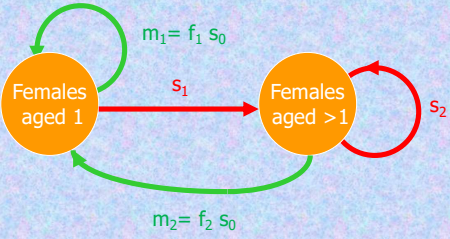
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A simple age-classified model

LIFE CYCLE graph in a barn swallow population

$m_1 = f_1 \, s_0$

s_1

Females aged 1

Females aged >1

s_2

$m_2 = f_2 \, s_0$

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

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

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Expanding over age-classes

INFINITELY MANY AGE CLASSES

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

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A simple stage-classified model

LIFE CYCLE GRAPH

p_1 p s

Breeders stage 1 q_1 Breeders Stage 2 q Breeders Stage 3

$m_2 = f_2 s_0$

$m_1 = f_1 s_0$ $m_3 = f_3 s_0$

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A simple stage-classified model

MATRIX EQUATION

$$\begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}_{t+1} = \begin{pmatrix} m_1 + p_1 & m_2 & m_3 \\ q_1 & p & 0 \\ 0 & q & s \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}_t$$
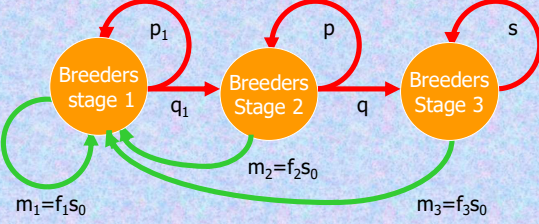
$m_1, m_2, m_3 = 0.3, 0.6, 1.0$
$p_1, q_1 \quad = 0.25, 0.25$
$p, q \quad = 0.25, 0.40$
$s \quad = 0.65$

$\longrightarrow$

$\lambda_1 = 1.05, \lambda_2 \ \& \ \lambda_3 \in C$
Elasticity(m)=0.3166

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

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Stage-classified models

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

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Slide 9

A simple stage-classified model

MATRIX EQUATION

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

$$F = \begin{pmatrix} m_1 & m_2 & m_3 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \qquad P = \begin{pmatrix} p_1 & 0 & 0 \\ q_1 & p & 0 \\ 0 & q & s \end{pmatrix}$$

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A simple stage-classified model

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

$$F = \begin{pmatrix} m_1 & m_2 & m_3 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \qquad P = \begin{pmatrix} p_1 & 0 & 0 \\ q_1 & p & 0 \\ 0 & q & s \end{pmatrix}$$

$$M = F + P$$

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A simple stage-classified model

Stage	1	2	3	1	2	3	1	2	3	...
Age	1	1	1	2	2	2	3	3	3	...

S A										
1 1	m_1	m_2	m_3	m_1	m_2	m_3	m_1	m_2	m_3	
2 1	0	0	0	0	0	0	0	0	0	...
3 1	0	0	0	0	0	0	0	0	0	...
1 2	p_1	0	0	0	0	0	0	0	0	...
2 2	q_1	p	0	0	0	0	0	0	0	...
3 2	0	q	s	0	0	0	0	0	0	...
1 3	0	0	0	p_1	0	0	0	0	0	...
2 3	0	0	0	q_1	p	0	0	0	0	...
3 3	0	0	0	0	0	s	0	0	0	...
...			...			...			...	...

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Expanding over age-classes

INFINITELY MANY AGE CLASSES

$$M(\infty) = \begin{pmatrix} F & F & F & ... & F & ... \\ P & 0 & 0 & ... & 0 & ... \\ 0 & P & 0 & ... & 0 & ... \\ ... & ... & ... & ... & ... & ... \\ 0 & ... & 0 & ... & P & ... \\ ... & ... & ... & ... & ... & ... \end{pmatrix}$$

Block Matrix notation

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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

$$\det (F \lambda^{-1} + F P \lambda^{-2} + \ldots + F P^{i-1} \lambda^{-i} + \ldots - I) = 0$$

- Largest root = dominant eigenvalue of M,
  as the equation reduces to $\det (F+P- \lambda I) = \det (M - \lambda I) -=0$

- Distribution of age of mothers at birth naturally appears as
  weighted by reproductive value of offspring

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Stage classified models expanded over age classes

Distribution
of age of
mothers
at birth,
by stage

<----Age---->

3 2 1   Stage

Generation time T, weighted mean age of mothers
at childbirth, with reproductive value as unit,
is equal to 3.158

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

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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
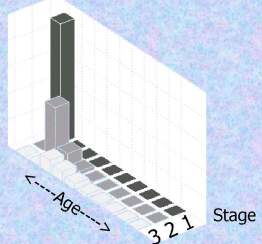
$$M(\infty) = \begin{pmatrix} F & F & F & \ldots & F & \ldots \\ P & 0 & 0 & \ldots & 0 & \ldots \\ 0 & P & 0 & \ldots & 0 & \ldots \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & \ldots & 0 & \ldots & P & \ldots \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \end{pmatrix}$$

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Age x Stage classified models

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

$$M(\infty) = \begin{pmatrix} F_1 & F_2 & F_3 & \dots & F_n & \dots \\ P_2 & 0 & 0 & \dots & 0 & \dots \\ 0 & P_3 & 0 & \dots & 0 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 0 & \dots & P_n & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{pmatrix}$$

…and, again, the multistate stable population theory

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Multistate models

• Stages = a set of mutually exclusive states

• Think of "states" rather than "stages"

• States can be sites:
  ➢ "multisite models",
  ➢ "regional population models"
  ➢ body weight classes….

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Multisite models

2 sites

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

REACTION - DIFFUSION

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

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Multisite models
2 sites

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

Independent sites with growth rates a and b, respectively

REACTION - DIFFUSION

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

Common growth rate λ, with $a < \lambda < b$ if $a < b$

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Leslie Matrices
2 age classes, 2 *non-connected* sites

site		1	1	2	2
age		1	2	1	2
site	age				
1	1	0	f_1	0	0
1	2	s_1	s_1	0	0
2	1	0	0	0	f_2
2	2	0	0	s_2	s_2

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Coupling Leslie Matrices
2 age classes, 2 sites

site		1	1	2	2
age		1	2	1	2
site	age				
1	1	0	f_{11}	0	f_{21}
1	2	s_1	s_1	0	0
2	1	0	f_{12}	0	f_{22}
2	2	0	0	s_2	s_2

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Coupling Leslie Matrices
2 age classes, 2 sites

site		1	1	2	2
	age	1	2	1	2
site	age				
1	1	0	f_{11}	0	f_{21}
1	2	s_1	s_1	0	0
2	1	0	f_{12}	0	f_{22}
2	2	0	0	s_2	s_2

Coupling by first-year dispersal

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Coupling Leslie Matrices
2 age classes, 2 sites: SITE ⊂ AGE

age		1	1	2	2
	site	1	2	1	2
age	site				
1	1	0	0	f_{11}	f_{21}
1	2	0	0	f_{12}	f_{22}
2	1	s_1	0	s_1	0
2	2	0	s_2	0	s_2

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Coupling Leslie Matrices
2 age classes, 2 sites: SITE ⊂ AGE

age		1	1	2	2
	Site	1	2	1	2
age	site				
1	1	0	0	f_{11}	f_{21}
1	2	0	0	f_{12}	f_{22}

$$M = \begin{pmatrix} F_1 & F_2 \\ P & P \end{pmatrix}$$

fecundity and survival parameters appear as 2 x 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

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Asymptotically exponential Growth
2 age classes, 2 sites
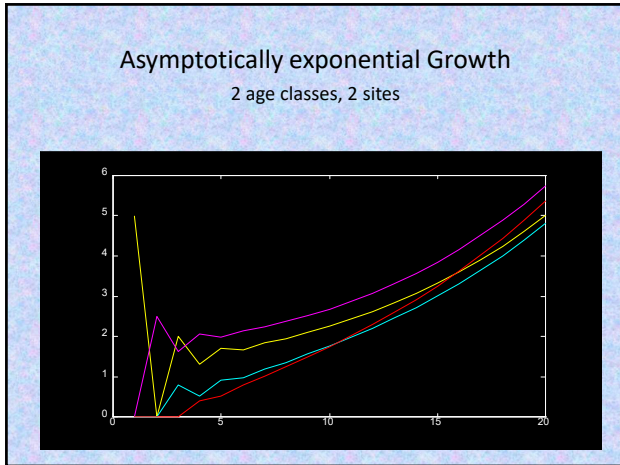
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Asymptotically exponential Growth

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

$$N_t \longrightarrow c \lambda^t V$$

QUANTITY	MEANING	FORMAL NATURE
V	stable structure by age and site	right eigenvector
λ	asymptotic multiplication rate	largest eigenvalue
$c = \Sigma u_i N_i(0)$	function of initial values	U : left eigenvector

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Spatial reproductive value
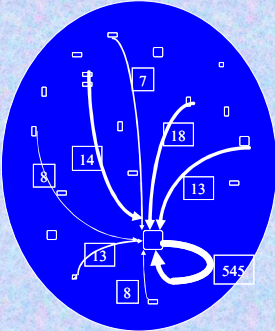### effect of initial values, via $c = \Sigma u_i N_i(0)$
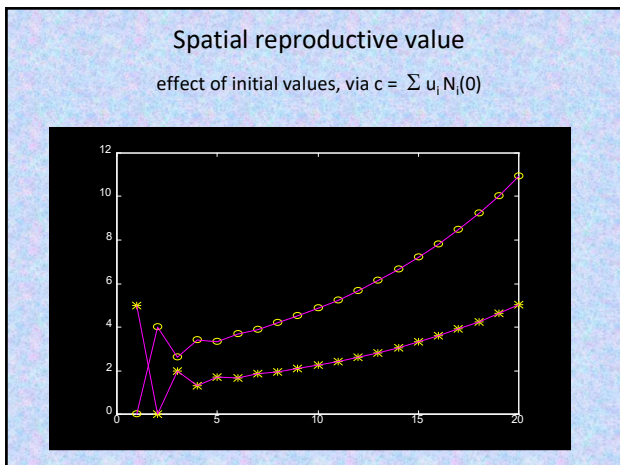
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Dispersal and Recruitment
Black-headed gull
(Forez, central France)

resightings as breeders of
gulls ringed as chicks

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Coupling Leslie Matrices
5 age classes, 2 sites
Black-Headed Gull Population

AGE	1	1	2	2	3	3	4	4	5	5
SITE	1	2	1	2	1	2	1	2	1	2

AGE	SITE										
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

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Coupling Leslie Matrices
5 age classes, 2 sites
Black-Headed Gull Population

Common growth rate (0.997), but ≠ reproductive values

Stable structure (by age and site)

Multisite generation time T

Sensitivity results easily generalized:

e.g., elasticity(fecundities) = 1/T = .130

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