Matrix Population Models for Wildlife Conservation and Management

27 February - 5 March 2016

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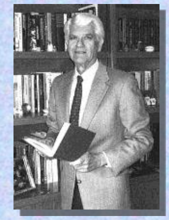
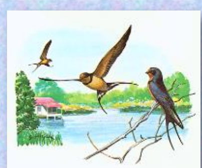
Lecture 5
Multistate matrix models

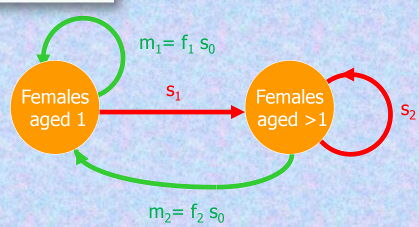
Hervé LE BRAS and Andrei ROGERS, who developed a generalization of the Euler-Lotka equation for multistate matrix models

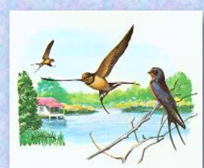




A simple age-classified model

LIFE CYCLE graph in a barn swallow population





A simple age-classified model

QUANTITATIVE CYCLE in a barn swallow population

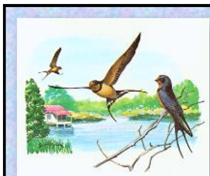
Two linear Equations

$$N_1(t+1) = m_1\, N_1(t) + m_2\, N_2(t)$$
$$N_2(t+1) = s_1\, N_1(t) + s_2\, N_2(t)$$

One matrix Equation

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

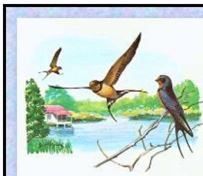
$$N_{t+1} = M\, N_t$$



Expanding over age-classes

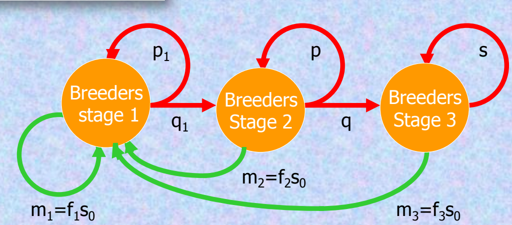
INFINITELY MANY AGE CLASSES

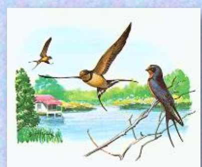
$$M(\infty) = \begin{pmatrix} m_1 & m_2 & m_2 & m_2 & m_2 & \dots \\ s_1 & 0 & 0 & 0 & 0 & \dots \\ 0 & s_2 & 0 & 0 & 0 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 0 & \dots & s_2 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{pmatrix}$$



A simple stage-classified model

LIFE CYCLE GRAPH





A simple stage-classified model

MATRIX EQUATION

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

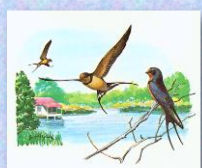
m_1, m_2, m_3 = 0.3, 0.6, 1.0
p_1, q_1 = 0.25, 0.25
p, q = 0.25, 0.40
s = 0.65

λ_1 = 1.05, λ_2 & $\lambda_3 \in \mathbb{C}$
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

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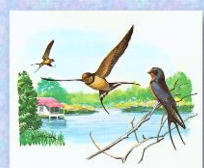
$$\begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}_{t+1} = \begin{pmatrix} m_1 + p_1 & m_2 & m_3 \\ q_1 & p & 0 \\ 0 & q & s \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_3 \end{pmatrix}_t$$

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

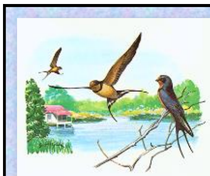


A simple stage-classified model

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

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

$$M = F+T$$

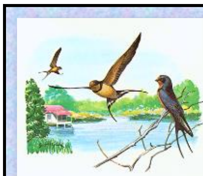


Expanding over age-classes

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

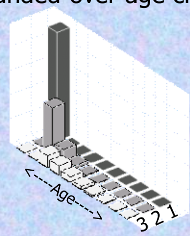
- The Le Bras-Rogers equation, a multistate generalization of the Euler-Lotka equation

$$\det(F\lambda^{-1} + F\,T\lambda^{-2} + \dots + F\,T^{i-1}\lambda^{-i} + \dots - I) = 0$$

- Largest root = dominant eigenvalue of M, as the equation reduces to det (F+T- λ 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”
  - body weight classes….

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

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

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 $a < b$

Leslie Matrices

2 age classes, 2 *non-connected* sites

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

Coupling Leslie Matrices

2 age classes, 2 sites

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

Coupling Leslie Matrices

2 age classes, 2 sites

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

Coupling by first-year dispersal

Coupling Leslie Matrices

2 age classes, 2 sites: SITE ⊂ AGE

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

Coupling Leslie Matrices

2 age classes, 2 sites: SITE ⊂ AGE

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

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

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

Coupling Leslie Matrices

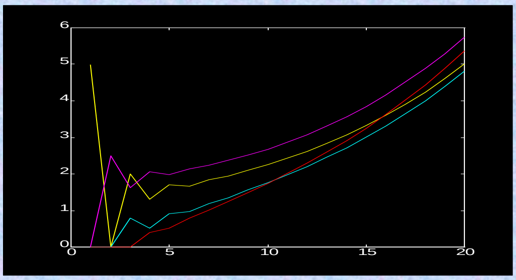
2 age classes, 2 sites: SITE ⊂ AGE

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

ULM recognizes multistate Leslie matrices if states ⊂ ages

Asymptotically exponential Growth

2 age classes, 2 sites



Asymptotically exponential Growth

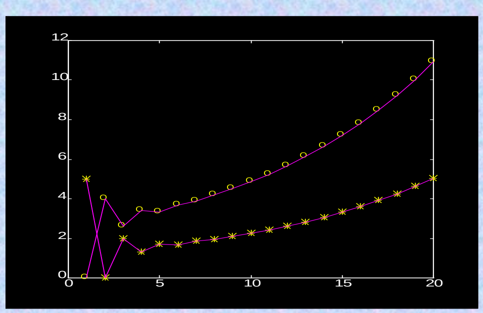
$$N_{t+1} = M\,N_t$$

$$N_t \dashrightarrow c\,\lambda^t\,V$$

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

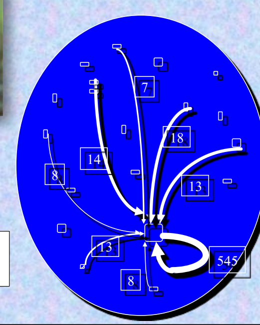
Spatial reproductive value

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



Dispersal and Recruitment

Black-headed gull
(Forez, central France)



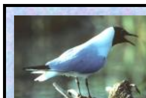
resightings as breeders of gulls ringed as chicks

Coupling Leslie Matrices

5 age classes, 2 sites

Black-Headed Gull Population

AGE	SITE	1	1	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



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

Sensivity results easily generalized:

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

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