Matrix Population Models for Wildlife Conservation and Management

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Matrix model theory

Hal CASWELL,
showing a matrix model to
a Laysan Albatross
on Midway atoll (Hawaï).

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

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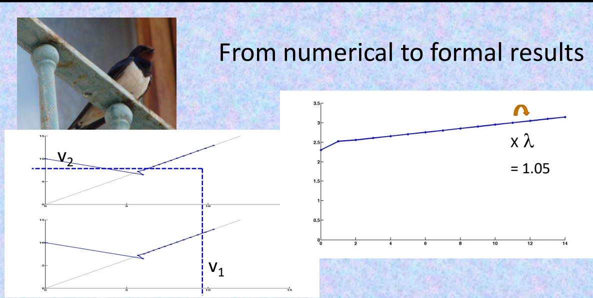
From numerical to formal results



$$V = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$$

$M\,V = \lambda\,V$

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

… in loose notation

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From numerical to formal results

$$
\begin{array}{lllllll}
t = & 1 & 2 & 3 & \dots & 10 & 11\\
M^t = & \begin{pmatrix}0.3000 & 0.6000\\ 0.5000 & 0.6500\end{pmatrix} & \begin{pmatrix}0.3900 & 0.5700\\ 0.4750 & 0.7225\end{pmatrix} & \begin{pmatrix}0.4020 & 0.6045\\ 0.5038 & 0.7546\end{pmatrix} & \dots & \begin{pmatrix}0.5666 & 0.8499\\ 0.7082 & 1.0623\end{pmatrix} & \begin{pmatrix}0.5949 & 0.8924\\ 0.7436 & 1.1154\end{pmatrix}\\
M^t./M^{t-1} = & & \begin{pmatrix}1.3000 & 0.9500\\ 0.9500 & 1.1115\end{pmatrix} & \begin{pmatrix}1.0308 & 1.0605\\ 1.0605 & 1.0445\end{pmatrix} & \dots & \begin{pmatrix}1.0500 & 1.0500\\ 1.0500 & 1.0500\end{pmatrix} & \begin{pmatrix}1.0500 & 1.0500\\ 1.0500 & 1.0500\end{pmatrix}
\end{array}
$$

Termwise division

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\end{array}
$$

Termwise division

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

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

$$M^t \to \lambda^t \begin{pmatrix}u_1V & u_2V\end{pmatrix} = \lambda^t \begin{pmatrix}u_1v_1 & u_2v_1\\ u_1v_2 & u_2v_2\end{pmatrix}$$

... in loose notation

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Transposition and matrix product

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

- $Q = V U' = \begin{pmatrix}v_1\\ v_2\end{pmatrix}\begin{pmatrix}u_1 & u_2\end{pmatrix}$ is a 2 x 2 matrix

- Q_{11} is v_1u_1 (1st row x 1st column)
- Q_{12} is v_1u_2 (1st row x 2nd column)
- Q_{21} is v_2u_1 (2nd row x 1st column)
- Q_{22} is v_2u_2 (2nd row x 2nd column)

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Transposition and matrix product

- Hence $Q = V\,U' = \begin{pmatrix} v_1\,u_1 & v_1\,u_2 \\ v_2\,u_1 & v_2\,u_2 \end{pmatrix}$
- While $U'V = \left(v_1\,u_1 + v_2\,u_2 \right)$ is a 1 x 1 matrix, i.e. a scalar, also denoted as $\Sigma\, u_i\, v_i$

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From numerical to formal results

Hence, $M^t \rightarrow \lambda^t \left(u_1 V \quad u_2 V \right) = \lambda^t\, V\, U'$

Or, equivalently and more rigorously

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

$u_i > 0,\ v_i > 0$

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

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

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

Premutiply by U' and simplify by scalar U'V, to get:

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

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...From formal to numerical results

In our numerical example:

$\lambda^{-t}\, M^t \rightarrow \begin{pmatrix} 0.3478 & 0.5217 \\ 0.4348 & 0.4522 \end{pmatrix}$

- One may choose $U' = \left(0.3478 \quad 0.5217 \right)$, then $V = \begin{pmatrix} 1.0000 \\ 1.2500 \end{pmatrix}$
- or $V = \begin{pmatrix} 0.3478 \\ 0.4348 \end{pmatrix}$, then $U' = \left(1.000 \quad 1.5000 \right)$
- or any other coherent choice.

In all cases $U'V = \Sigma\, u_i\, v_i = 1$

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Of eigenvalues and eigenvectors

Demographic ergodicity

$M\,V = \lambda\,V$ 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 = « reproductive values »

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Of eigenvalues and eigenvectors

Demographic ergodicity

λ, U, V are dispositional properties

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Of eigenvalues and eigenvectors

Usually, no formulas, but easy to get numerically

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Scalar, weighting the components of N_0 by the u_i = « reproductive values »

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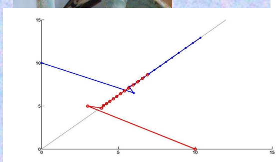
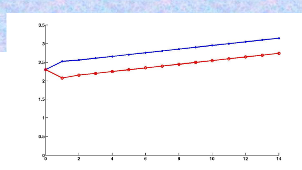
Reproductive values





lue 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 = « reproductive values »

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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

(a sufficient condition, not a necessary one)

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Why is it so?

n x n Matrices have (in general) n eigenvalues which are complex numbers

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

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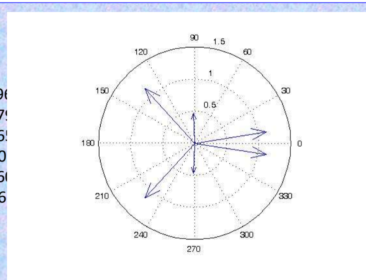
Why is it so?

n x n Matrices have (in general) n eigenvalues which are complex numbers

$$M = \begin{pmatrix} -0.6579 & -0.096 \\ 0.8771 & 0.67 \\ 0.1810 & 0.06 \\ -0.1187 & 0.10 \\ 0.8838 & 0.36 \\ 0.3118 & -0.26 \end{pmatrix}$$



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Why is it so?

However, positive, nonnegative irreducible matrices …

$$M = \begin{pmatrix} 0.0842 & 0.0954 & 0.9969 & 0.0710 & 0.6135 & 0.8979 \\ 0.1639 & 0.1465 & 0.5535 & 0.8877 & 0.8186 & 0.5934 \\ 0.3242 & 0.6311 & 0.5155 & 0.0646 & 0.8862 & 0.5038 \\ 0.3017 & 0.8593 & 0.3307 & 0.4362 & 0.9311 & 0.6128 \\ 0.0117 & 0.9742 & 0.4300 & 0.8266 & 0.1908 & 0.8194 \\ 0.5399 & 0.5708 & 0.4918 & 0.3945 & 0.2586 & 0.5319 \end{pmatrix}$$

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Why is it so?

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

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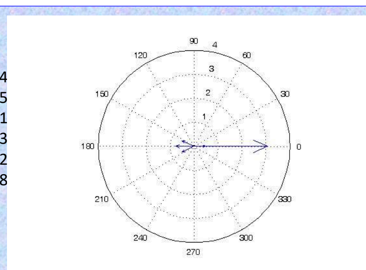

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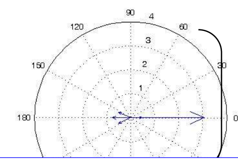

In products such as M^t, this "dominant eigenvalue" tends to outweigh the influence of other eigenvalues.

i.e., when $t \rightarrow \infty$ $M^t N(0) \rightarrow \alpha(0)\lambda^t V$

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Of eigenvalues and eigenvectors

Usually, no formulas,
but easy to get numerically

Eigenvalues are the roots of $\det\left(M - \lambda \begin{pmatrix} 1\,0 \ldots 0\,0 \\ 0\,1 \ldots 0\,0 \\ \ldots \\ 0\,0 \ldots 1\,0 \\ 0\,0 \ldots 0\,1 \end{pmatrix}\right) = 0$

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

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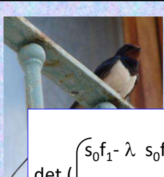

Of eigenvalues and eigenvectors

The largest root of

$$\det\begin{pmatrix} s_0f_1 - \lambda & s_0f_2 \\ s_1 & s_2 - \lambda \end{pmatrix} = \lambda^2 - (s_0f_1+s_2)\lambda + s_0f_1 s_2 - s_0f_2 s_1 = 0$$

is

$$\frac{s_0f_1 + s_2 + \sqrt{(s_0f_1+s_2)^2 - 4(s_0f_1 s_2 - s_0f_2 s_1)}}{2}$$

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Of eigenvalues and eigenvectors

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

$$\frac{s_0 f_1 + s_2 + \sqrt{(s_0 f_1 + s_2)^2 - 4\,(s_0 f_1\, s_2 - s_0 f_2\, s_1)}}{2}$$

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Of eigenvalues and eigenvectors

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

$$\frac{s_0 f_1 + s_2 + \sqrt{(s_0 f_1 + s_2)^2 - 4\,(s_0 f_1\, s_2 - s_0 f_2\, s_1)}}{2}$$

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

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Sensitivity analysis

What if swallows were not nesting at age 1 ?

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

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

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

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

If you harvest each year 30 % of a roe deer population whose growth rate is 40 % (λ=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

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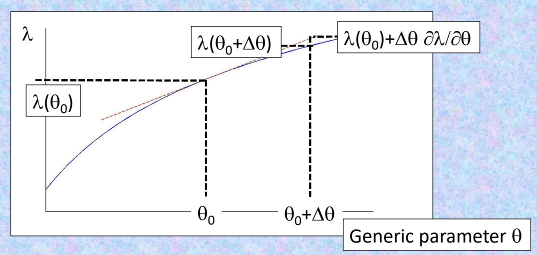
Sensitivity Analysis

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



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Sensitivity Analysis

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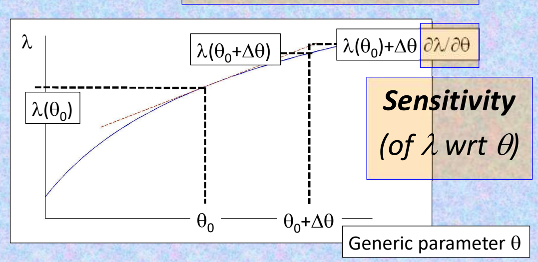

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Sensitivity and Elasticity

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

Elasticity

$\partial \text{ Log } \lambda / \partial \text{ Log } \theta = (\theta / \lambda) \, \partial\lambda / \partial\theta = (\partial\lambda / \lambda) / (\partial\theta / \theta)$

Relative change in λ vs relative change in θ

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

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Sensitivity to matrix element: perturbation analysis

a beautiful result due to Hal Caswell (1978)

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

$\partial\text{Log}\lambda / \partial \text{ Log } m_{ij} = m_{ij} / \lambda \times u_i v_j / \Sigma u_i v_i$
$= m_{ij} u_i v_j / \lambda \Sigma u_i v_i$

Under $\Sigma u_i v_i = 1$,
$\partial\text{Log}\lambda / \partial \text{ Log } m_{ij} = m_{ij} u_i v_j / \lambda$

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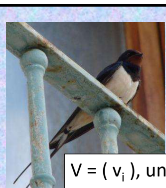

Sensitivity to matrix element: perturbation analysis

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

$(u_i v_i)$ under $\Sigma u_i v_i = 1$, is the stable structure,
expressed with reproductive value as the currency.

At next time step, it becomes $(\lambda u_i v_i)$, summing up to λ
i.e., since $MV = \lambda V$: $(u_i \Sigma_j m_{ij} v_j)$

…or, once normalized by λ, $(u_i \Sigma_j m_{ij} v_j) / \lambda$

Hence $(\Sigma_i \Sigma_j m_{ij} u_i v_j) / \lambda = 1$

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Sensitivity to matrix element: perturbation analysis

$m_{ij}\, u_i\, v_j / \lambda$, under $\Sigma\, u_i\, v_i = 1$, is thus the next time ***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 often use $\Sigma\, u_i\, v_i = 1$

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

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Sensitivity to lower-level parameters: the chain rule

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

$\partial\lambda / \partial\theta = \Sigma_i\, \Sigma_j\, (\partial\lambda / \partial m_{ij} \times \partial m_{ij} / \partial\theta)$

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 :

$s_0 / \lambda \times \partial\lambda / \partial\, s_0 = u_1\, v_1$

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