Notes on Matrix Population Analysis

Conservation biologists and wildlife managers use life cycle graphs to characterize the life history of the particular species whose population size they would like either to increase (because it's endangered) or decrease (because it's a pest). An example appears in the diagram below. Each stage-j individual contributes a_{ij} individuals to stage i per period. So, if there are n life-history stages and $x_i(t)$ denotes number of stage-i individuals at time t, we have

$$(1) \qquad x_i(t+1) \; = \; \sum_{j=1}^{n} a_{ij}\, x_j(t)$$

or

$$(2) \qquad \mathbf{x}(t+1) \; = \; A\mathbf{x}(t), \qquad t = 0, 1, \dots ,$$

where A is called the *population projection matrix*.

Suppose, for example, that there are three stage classes, namely,

1. Yearlings
2. Juveniles and young adults
3. Reproductive adults

as in the life cycle graph shown below; the F_i represent fecundities, the G_i represent probabilities of surviving and growing to the next stage within a period, and the P_i represent probabilities of surviving but staying in the same stage (so, e.g., a stage-2 individual has probability $1 - P_2 - G_2$ per period of dying). Then the associated projection matrix is

$$(3) \qquad A \; = \; \begin{bmatrix} 0 & F_2 & F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{bmatrix} .$$

An example of a species with such a life cycle is the killer whale (*Orcinus orca*), for which

$$(4) \qquad A \; = \; \begin{bmatrix} 0 & 0.0043 & 0.1132 \\ 0.9775 & 0.9111 & 0 \\ 0 & 0.0736 & 0.9534 \end{bmatrix} .$$
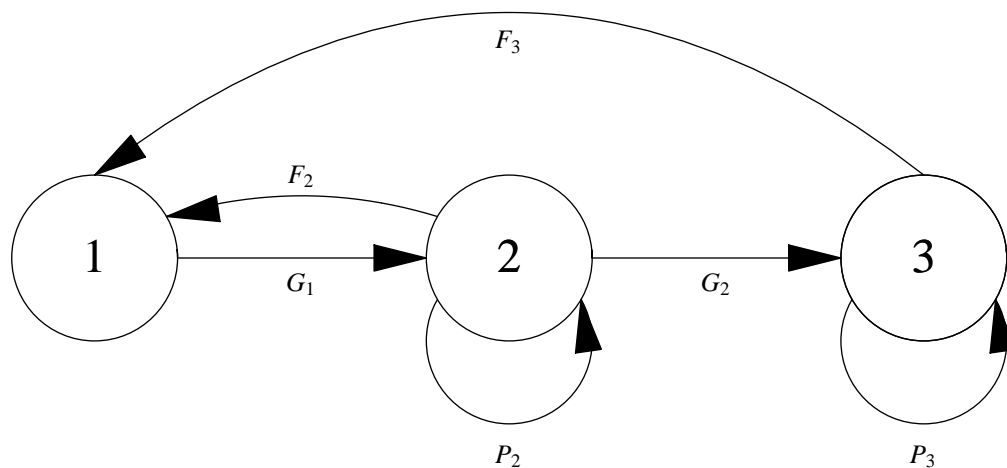
Note that its eigenvalues are

(5) $$\lambda_1 = 1.02544, \lambda_2 = 0.834223, \lambda_3 = 0.0048357.$$

Because they are distinct, A is a simple (diagonalizable) matrix.

We will invariably assume that A has distinct eigenvalues, because the empirical evidence in favor of this assumption is overwhelming. We will also assume that there is a *dominant* real eigenvalue associated with a strictly positive eigenvector[1]—largely because the empirical evidence for this assumption again is overwhelming, though more can be said on purely theoretical grounds (see the remark at the very end). Let the eigenvalues be ordered so that the dominant one is first, as in the example above. Then

(6) $$\lambda_1 > \left| \lambda_i \right|, \qquad i = 2, \dots, n.$$

Also, if the eigenvectors of A are the columns of W, then all entries of $\mathbf{w}_1$ are strictly positive; for example, for the killer whale,

(7) $$W = \begin{bmatrix} 0.0815501 & 0.0667654 & 0.678783 \\ 0.697169 & -0.848929 & -0.732138 \\ 0.712253 & 0.524272 & 0.0568073 \end{bmatrix},$$

so that $\mathbf{w}_1 = \begin{bmatrix} 0.0815501 & 0.697169 & 0.712253 \end{bmatrix}^T$. Because W forms a basis for R^n, the initial stage distribution vector can be written

(8) $$\mathbf{x}(0) = \sum_{k=1}^{n} c_k \mathbf{w}_k,$$

implying

(9) $$\mathbf{x}(t) = A^t \mathbf{x}(0) = A^t \sum_{k=1}^{n} c_k \mathbf{w}_k$$

(10) $$= \sum_{k=1}^{n} c_k A^t \mathbf{w}_k = \sum_{k=1}^{n} c_k \lambda_k^t \mathbf{w}_k$$

(11) $$\approx c_1 \lambda_1^t \mathbf{w}_1$$

if t is large. More precisely,

(12) $$\lim_{t \to \infty} \lambda_1^{-t} \mathbf{x}(t) = c_1 \mathbf{w}_1.$$

So $\mathbf{w}_1$ yields the asymptotic stage distribution. For example, after many years, if the so-called *vital rates*—i.e., the entries of A—don't change, about 5.5% of killer whales will be yearlings, about 47.8% will be reproductive adults and the remaining 46.7% or so will be juveniles.

Because A is simple, we have $AW = WD$ with $D = \text{diag}(\lambda_1, \dots, \lambda_n)$. Defining

(13) $$U = W^{-1},$$

we easily deduce that $UA = DU$, and hence that if $\mathbf{u}^i$ denotes the i-th *row* of U then

(14) $$\mathbf{u}^i A = \lambda_i \mathbf{u}^i.$$

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[1]More precisely, a nonzero eigenvector whose entries all have the same sign, so that they can all be made positive without loss of generality

We could call $\mathbf{u}^i$ the i-th *left* eigenvector of A to distinguish it from $\mathbf{w}_j$, which would then become the j-th *right* eigenvector. Because $UW = I$ (the $n \times n$ identity matrix) implying

$$(15) \qquad \sum_{k=1}^{n} u_{ik} w_{kj} = \begin{cases} 0 \text{ if } i \neq j \\ 1 \text{ if } i = j, \end{cases}$$

if A had real eigenvalues and hence real eigenvectors (as in all of the cases we deal with here), then (15) would make left and right eigenvectors associated with different eigen-values orthogonal. If some eigenvalues and eigenvectors were complex, however, there would arise the complication that (15) would no longer be a statement about orthogonal-ity in the sense of vectors $\mathbf{u}$ and $\mathbf{z}$ being orthogonal if $\mathbf{u}^H \mathbf{z} = 0$ (where $\mathbf{u}^H = \overline{\mathbf{u}}^T$ denotes the complex-conjugate transpose of $\mathbf{u}$). To circumvent this potential complication, we instead define

$$(16) \qquad V = \left(\overline{W^{-1}} \right)^T,$$

so that $V^H = W^{-1}$, and say that $\mathbf{v}$ is a left eigenvector associated with eigenvalue λ if

$$(17) \qquad \mathbf{v}^H A = \lambda \mathbf{v}^H.$$

In this way both left and right eigenvectors are always column vectors, and a left eigen-vector of A associated with eigenvalue λ is the same thing as a right eigenvector of A^H ($= A^T$ in population demography) associated with $\overline{\lambda}$, because (17) implies $A^H \mathbf{v} = \overline{\lambda} \mathbf{v}$. Moreover, $V^H W = I$, so that left and right eigenvectors associated with different eigen-values are orthogonal.

Although we are basically digressing, the effect of the above can be understood most easily in terms of a simple example (that is completely irrelevant to any real-world population). Suppose that

$$(18) \qquad A = \begin{bmatrix} 1 & -1 \\ 1 & 1 \end{bmatrix}$$

with eigenvalues $\lambda_1 = 1 + i$, $\lambda_2 = 1 - i = \overline{\lambda}_1$ and associated eigenvectors $\mathbf{w}_1 = [i, 1]^T$, $\mathbf{w}_2 = [-i, 1]^T = \overline{\mathbf{w}}_1$. Then

$$(19) \qquad U = \frac{1}{2} \begin{bmatrix} -i & 1 \\ i & 1 \end{bmatrix}, \qquad W = \begin{bmatrix} i & -i \\ 1 & 1 \end{bmatrix}$$

satisfy $UW = I$, but $\mathbf{u}^1 = \begin{bmatrix} -i & 1 \end{bmatrix}/2$, although orthogonal to $\mathbf{w}_2 = \begin{bmatrix} -i & 1 \end{bmatrix}^T$ in the sense that $\mathbf{u}^1 \mathbf{w}_2 = 0$, is not orthogonal in the Hermitian sense because $\overline{\mathbf{u}}^1 \mathbf{w}_2 = 1$. But with

$$(20) \qquad V = \frac{1}{2} \begin{bmatrix} i & -i \\ 1 & 1 \end{bmatrix}, \qquad V^H = \begin{bmatrix} -i & 1 \\ i & 1 \end{bmatrix}$$

we have $\overline{\mathbf{v}}_1^H \mathbf{w}_2 = 0$, as required (also $\overline{\mathbf{v}}_2^H \mathbf{w}_1 = 0$ and $\overline{\mathbf{v}}_1^H \mathbf{w}_1 = 1 = \overline{\mathbf{v}}_2^H \mathbf{w}_2$). End of digression.

Now, from (8), we have $\mathbf{x}(0) = W\mathbf{c}$ or $\mathbf{c} = V\mathbf{x}(0)$, from which it follows that

$$(21) \qquad c_1 = \sum_{k=1}^{n} v_{1k} x_k(0).$$

So the asymptotic contribution to the population of an individual currently in stage i will be v_{1i}/v_{1j} times as great as that of an individual currently in stage j. In other words, the vector $\mathbf{v}_1^T$ records the relative asymptotic contributions of the different stages. For that

reason, $\mathbf{v}_1$ is known as the *stage-specific reproductive value.* For example, for killer whales we have

(22)
$$V^H = V^T = W^{-1} = \begin{bmatrix} 0.517574 & 0.542959 & 0.813275 \\ -0.865268 & -0.738442 & 0.821873 \\ 1.49615 & 0.00740146 & -0.178548 \end{bmatrix},$$

so that the stage-specific reproductive value is

(23)
$$\mathbf{v}_1 = \begin{bmatrix} 0.517574 & 0.542959 & 0.813275 \end{bmatrix}^T.$$

So juveniles are almost 5% more valuable than yearlings in terms of long-term reproduction, and adults in turn are almost 50% more valuable than juveniles.

In practice, wildlife biologists are often most interested in how changes in vital rates affect population growth rate. The *sensitivity* of λ_1 to a change in flux along the life-cycle arc from node j to node i is measured by the relevant partial derivative. Because we are now interested solely in the dominant eigenvalue and its associated left and right eigenvectors, however, it greatly simplifies notation to denote them by $\lambda, \mathbf{v}$ and $\mathbf{w}$, respectively (as opposed to $\lambda_1, \mathbf{v}_1$ and $\mathbf{w}_1$). Then the sensitivity of the asymptotic growth rate to changes in the rate of transition from stage j to stage i of the life cycle is

(24)
$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}}.$$

Sensitivity, however, is an absolute measure of influence. For many purposes one is much more interested in a relative measure: roughly, by what percentage will λ change in response to a 1% change in a_{ij}? If the absolute change in both quantities is small, say δa_{ij} for the change in a_{ij} and $\delta\lambda$ for the corresponding change in λ, then a $100\delta a_{ij}/a_{ij}\%$ change in vital rate yields—all other things being equal— a $100\delta\lambda/\lambda\%$ change in population growth rate. The ratio of these two quantities in the limit as $\delta a_{ij} \to 0$ (and $\delta\lambda \to 0$) is the *elasticity* of λ with respect to a_{ij} and is denoted by e_{ij}. That is,

(25)
$$e_{ij} = \lim_{\delta a_{ij}\to 0} \frac{a_{ij}\delta\lambda}{\lambda\delta a_{ij}} = \frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}} = \frac{a_{ij}s_{ij}}{\lambda}.$$

Note that this limit does not exist if a_{ij} is identically zero.

A useful formula for s_{ij} (and hence a_{ij}) can be obtained as follows. First, because $\mathbf{v}^T\mathbf{w} = 1$ (both vectors being real) and $A\mathbf{w} = \lambda\mathbf{w}$, we have

(26)
$$\lambda = \mathbf{v}^T A\mathbf{w} = \sum_{k=1}^{n} v_k \sum_{m=1}^{n} a_{km}w_m = \sum_{k=1}^{n}\sum_{m=1}^{n} a_{km}v_k w_m$$

because the order of summation is irrelevant; here v_k and w_m denote, respectively, the k-th element of $\mathbf{v}$ and the m-th element of $\mathbf{w}$. Alternatively, λ is defined implicitly by the equation $|A - \lambda I| = 0$, where I is the $n \times n$ identity matrix. Either way, λ is a function of at most n^2 variables. But some a_{ij}, say r in all, are identically zero because they correspond to impossible arcs of the life cycle graph. So in practice λ is a function of $n^2 - r$ variables; more precisely, λ is a function of the a_{ij} corresponding to arcs for which a_{ij} is

not identically zero. Now

$$
(27) \qquad
\begin{aligned}
\frac{\partial \lambda}{\partial a_{ij}} &= \sum_{k=1}^{n} \sum_{m=1}^{n} \frac{\partial a_{km}}{\partial a_{ij}} v_k w_m + \sum_{k=1}^{n} \sum_{m=1}^{n} a_{km} \frac{\partial v_k}{\partial a_{ij}} w_m + \sum_{k=1}^{n} \sum_{m=1}^{n} a_{km} v_k \frac{\partial w_m}{\partial a_{ij}} \\
&= \sum_{k=1}^{n} \sum_{m=1}^{n} \frac{\partial a_{km}}{\partial a_{ij}} v_k w_m + \sum_{k=1}^{n} \frac{\partial v_k}{\partial a_{ij}} \sum_{m=1}^{n} a_{km} w_m + \sum_{m=1}^{n} \frac{\partial w_m}{\partial a_{ij}} \sum_{k=1}^{n} v_k a_{km} \\
&= \sum_{k=1}^{n} \sum_{m=1}^{n} \frac{\partial a_{km}}{\partial a_{ij}} v_k w_m + \sum_{k=1}^{n} \frac{\partial v_k}{\partial a_{ij}} \lambda\, w_k + \sum_{m=1}^{n} \frac{\partial w_m}{\partial a_{ij}} \lambda\, v_m
\end{aligned}
$$

by the definitions for left and right eigenvector. Because summation indices are interchangeable, it follows that

$$
(28) \qquad
\begin{aligned}
\frac{\partial \lambda}{\partial a_{ij}} &= \sum_{k=1}^{n} \sum_{m=1}^{n} \frac{\partial a_{km}}{\partial a_{ij}} v_k w_m + \lambda \sum_{k=1}^{n} \frac{\partial v_k}{\partial a_{ij}} w_k + \lambda \sum_{m=1}^{n} \frac{\partial w_m}{\partial a_{ij}} v_m \\
&= \sum_{k=1}^{n} \sum_{m=1}^{n} \frac{\partial a_{km}}{\partial a_{ij}} v_k w_m + \lambda \sum_{k=1}^{n} \frac{\partial v_k}{\partial a_{ij}} w_k + \lambda \sum_{k=1}^{n} \frac{\partial w_k}{\partial a_{ij}} v_k \\
&= \sum_{k=1}^{n} \sum_{m=1}^{n} \frac{\partial a_{km}}{\partial a_{ij}} v_k w_m + \lambda \sum_{k=1}^{n} \frac{\partial (v_k w_k)}{\partial a_{ij}} \\
&= \sum_{k=1}^{n} \sum_{m=1}^{n} \frac{\partial a_{km}}{\partial a_{ij}} v_k w_m + \lambda \frac{\partial}{\partial a_{ij}} \sum_{k=1}^{n} v_k w_k.
\end{aligned}
$$

But $\sum_{k=1}^{n} v_k w_k = \mathbf{v}^T \mathbf{w} = 1$, so that the last term of (28) is identically zero, and

$$
(29) \qquad \frac{\partial a_{km}}{\partial a_{ij}} = \begin{cases} 1 & \text{if } i = k \quad \text{AND} \quad j = m \quad \text{AND} \quad a_{km} \text{ is not identically zero} \\ 0 & \text{otherwise.} \end{cases}
$$

Alternatively, we can say that the above expression for $\partial \lambda / \partial a_{ij}$ applies only to the a_{ij} that might be nonzero; in the other r cases, $\partial \lambda / \partial a_{ij} = 0$ because λ is a function of only $n^2 - r$ variables. Either way, it follows from (24), (25) and (28) that

$$
(30) \qquad s_{ij} = \begin{cases} v_i w_j & \text{if } a_{ij} \not\equiv 0 \\ 0 & \text{if } a_{ij} \equiv 0 \end{cases}
$$

and

$$
(31) \qquad e_{ij} = \frac{a_{ij} v_i w_j}{\lambda}.
$$

For example, for killer whales it follows from above that the sensitivity matrix is

$$
(32) \qquad S = \begin{bmatrix} 0 & 0.3608 & 0.3686 \\ 0.0443 & 0.3785 & 0 \\ 0 & 0.5670 & 0.5793 \end{bmatrix}
$$

and the elasticity matrix is

$$(33) \qquad E \;=\; \begin{bmatrix} 0 & 0.0015 & 0.0407 \\ 0.0422 & 0.3363 & 0 \\ 0 & 0.0407 & 0.5386 \end{bmatrix}.$$

The most important arc in the life cycle graph appears to be adult survival.

All of the above depends, of course, on A having a dominant eigenvalue associated with positive left and right eigenvectors, for which a sufficient condition is that A (given that it's nonnegative) be *primitive*, i.e., that K exist such that A^K is positive (in which case, K cannot exceed $(n-1)(n-2)$). For example, A defined by (3) is primitive because A^2 is positive.[2]

FURTHER READING

Benton, T.G. & Grant, A. 1999: Elasticity analysis as an important tool in evolutionary and population ecology *Trends in Ecology and Evolution* **14**, 467-471.

Caswell, H. 1997: Matrix Methods for Population Analysis. In *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems* (ed. S. Tuljapurkar & H. Caswell), pp. 19-58. New York: Chapman & Hall

Horvitz, C., Schemke, D.W. & Caswell, H. 1997: The Relative "Importance" of Life-History Stages to Population Growth: Prospective and Retrospective Analyses. In *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems* (ed. S. Tuljapurkar & H. Caswell), pp. 247-271. New York: Chapman & Hall

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[2] A primitive matrix is invariably also *irreducible*, which means that its graph is strongly connected; i.e., there exists a path from any node to any other node (there are no black holes).