9

Reproductive Value from Matrix Models

The concept of reproductive value is not limited to age-structured populations. It also applies to matrix population models for stage-structured populations, where it appears as an eigenvector of the projection matrix.

9.1 Reproductive Value as an Eigenvector

We begin by returning to the projection equation

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \qquad \mathbf{n}(0) = \mathbf{n}_0 \tag{9.1.1}$$

the solution of which (Section 7.1) can be written

$$\mathbf{n}(t) = \sum_i c_i \lambda_i^t \mathbf{w}_i, \tag{9.1.2}$$

where λ_i and $\mathbf{w}_i$ are the eigenvalues and right eigenvectors of $\mathbf{A}$ and the scalar constants c_i are determined by the initial conditions $\mathbf{n}_0$;

$$\mathbf{c} = \mathbf{W}^{-1}\mathbf{n}_0 \tag{9.1.3}$$
$$= \overline{\mathbf{V}}\mathbf{n}_0. \tag{9.1.4}$$

The matrix $\mathbf{W}$ has the right eigenvectors $\mathbf{w}_i$ as its columns; $\mathbf{W}^{-1}$ has as its rows the complex conjugate transposes of the left eigenvectors $\mathbf{v}_i$. Thus

$$c_i = \mathbf{v}_i^* \mathbf{n}_0 \tag{9.1.5}$$

with $\mathbf{w}_i$ and $\mathbf{v}_i$ scaled so that $\mathbf{v}_i^* \mathbf{w}_i = 1$.

If $\mathbf{A}$ is primitive, then

$$\lim_{t \to \infty} \frac{\mathbf{n}(t)}{\lambda_1^t} = c_1 \mathbf{w}_1. \tag{9.1.6}$$

The growth rate and stable population structure are independent of $\mathbf{n}_0$, but the size of the population at any (large) time t depends on $\mathbf{n}_0$, through the constant c_1. From (9.1.5), c_1 is a weighted sum of the initial population, with weights equal to the elements of $\mathbf{v}_1$.

Thus, if we take "the contribution of stage i to long-term population size" as a reasonable measure of the "value of stage i," the left eigenvector $\mathbf{v}_1$ gives the relative reproductive values of the stages (Goodman 1968, Keyfitz 1968). We must insert the qualifier "relative" because eigenvectors can be scaled by any nonzero constant. The result $c_1 = \mathbf{v}_1^* \mathbf{n}_0$ holds when $\mathbf{v}_1^* \mathbf{w}_1 = 1$, but any other scaling can be accounted for by setting $c_1 = \mathbf{v}_1^* \mathbf{n}_0 / \mathbf{v}_1^* \mathbf{w}_1$, and eventual population size is still proportional to $\mathbf{v}_1^* \mathbf{n}_0$. It is customary to scale $\mathbf{v}_1$ so that its first entry is 1.

Regardless of the scaling imposed on $\mathbf{v}_1$, the total reproductive value of a population, $V(t) = \mathbf{v}_1^* \mathbf{n}(t)$, increases exponentially at the rate λ_1, regardless of the stage distribution:

$$V(t+1) = \mathbf{v}_1^* \mathbf{n}(t+1) \tag{9.1.7}$$
$$= \mathbf{v}_1^* \mathbf{A} \mathbf{n}(t) \tag{9.1.8}$$
$$= \lambda \mathbf{v}_1^* \mathbf{n}(t). \tag{9.1.9}$$

9.1.1 *The Effect of Adding a Single Individual*

Suppose that we add a single individual of stage j to the initial population $\mathbf{n}_0$. Let $\mathbf{e}_j$ be a vector with zeros everywhere except for a 1 in the jth entry. If we drop the subscripts on λ_1, $\mathbf{w}_1$ and $\mathbf{v}_1$, we have

$$\lim_{t \to \infty} \frac{\mathbf{A}^t \left(\mathbf{n}_0 + \mathbf{e}_j \right)}{\lambda^t} = \mathbf{v}^* \left(\mathbf{n}_0 + \mathbf{e}_j \right) \mathbf{w} \tag{9.1.10}$$
$$= \mathbf{v}^* \mathbf{n}_0 \mathbf{w} + v_j \mathbf{w}. \tag{9.1.11}$$

The total population is $\mathbf{v}^* \mathbf{n}_0 \|\mathbf{w}\| + v_j \|\mathbf{w}\|$, which differs from (9.1.6) by $v_j \|\mathbf{w}\|$. That is, adding a single individual in stage j increases asymptotic population size by an amount proportional to the reproductive value of stage j.

Reproductive Value and Extinction.

Any population is subject to stochastic fluctuations because the vital rates are probabilities applied to discrete individuals (demographic stochasticity). These fluctuations lead to a nonzero probability of extinction, even when $\lambda > 1$. This probability can be calculated for unstructured populations from the Galton–Watson branching process (see Section 16.4). The corresponding probability for structured population is calculated from the

multi-type branching process (Pollard 1973, MPM Chapter 15). In several empirical examples (MPM Section 15.4.5), it has been shown that the probability of non-extinction of a population descended from a single founder is directly proportional to the reproductive value of that founder. This suggests, though it does not prove, that the reproductive value of an individual influences not only long-term population size but also short-term risk of extinction.

9.1.2 Age-Specific Reproductive Value

We can write down the reproductive value for the age-classified case directly from the equations defining the eigenvector:

$$\mathbf{v}^\mathsf{T}\mathbf{A} = \lambda\mathbf{v}^\mathsf{T},$$

where we have dropped the subscript, and are assuming that $\mathbf{v}$ is real. Suppose there are four age classes, as in Figure 3.9a, and set $v_1 = 1$. Then

$$\begin{pmatrix} 1 & v_2 & v_3 & v_4 \end{pmatrix} \begin{pmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix} = \lambda \begin{pmatrix} 1 & v_2 & v_3 & v_4 \end{pmatrix} \tag{9.1.12}$$

or, writing each equation out

$$F_1 + v_2 P_1 = \lambda \tag{9.1.13}$$

$$F_2 + v_3 P_2 = \lambda v_2 \tag{9.1.14}$$

$$F_3 + v_4 P_3 = \lambda v_3 \tag{9.1.15}$$

$$F_4 = \lambda v_4. \tag{9.1.16}$$

From the last equation

$$v_4 = F_4 \lambda^{-1}. \tag{9.1.17}$$

Substituting this into the next-to-last equation gives

$$v_3 = F_3 \lambda^{-1} + P_3 F_4 \lambda^{-2} \tag{9.1.18}$$

and then

$$v_2 = F_2 \lambda^{-1} + P_2 F_3 \lambda^{-2} + P_2 P_3 F_4 \lambda^{-3}. \tag{9.1.19}$$

Finally, substituting this into the first equation gives

$$1 = F_1 \lambda^{-1} + P_1 F_2 \lambda^{-2} + P_1 P_2 F_3 \lambda^{-3} + P_1 P_2 P_3 F_4 \lambda^{-4} \tag{9.1.20}$$

which is the characteristic equation (see Example 7.1). In general the age-specific reproductive value is

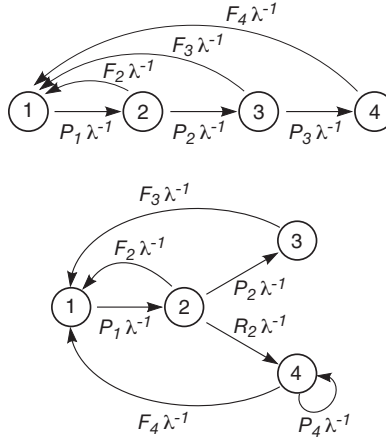$$v_i = \sum_{j=i}^{s} \left(\prod_{h=i}^{j-1} P_h \right) F_j \lambda^{i-j-1}, \tag{9.1.21}$$

Figure 9.1. The transformed graphs for two life cycles. Above: an age-structured model with four age classes. Below: a hypothetical life cycle in which individuals of stage $\mathcal{N}_2$ have two developmental choices, in one of which ($\mathcal{N}_3$) they reproduce only once and in the other of which ($\mathcal{N}_4$) they survive with probability P_4 and reproduce repeatedly.

which is the discrete version of Fisher's formula (8.1.1).

9.1.3 Stage-Specific Reproductive Value and the Life Cycle Graph

We can understand the correspondence of the left eigenvector and reproductive value in stage-structured models by writing down the eigenvector directly from the life cycle graph (Caswell 1982a; see Chapter 7 of MPM for details). Begin by transforming the life cycle graph by replacing each coefficient a_{ij} with $a_{ij}\lambda^{-1}$. (This is known as the z-transform of the graph; in our context, however, the variable usually denoted by z will be the eigenvalue of $\mathbf{A}$, so we denote it as λ.)

Figure 9.1 shows the transformation of the life cycle graph for the age-classified model. Comparing this graph with (9.1.17)–(9.1.20), we see that v_i is the sum, over all pathways from $\mathcal{N}_i$ to $\mathcal{N}_1$, of the product over each pathway of the transformed life cycle graph coefficients. There are, for example, two pathways from $\mathcal{N}_3$ to $\mathcal{N}_1$. The products of the transformed coefficients on these pathways are $F_3\lambda^{-1}$ and $P_3F_4\lambda^{-2}$; the sum of these is v_3 in (9.1.18).

In other words, v_i measures the expected future reproductive contribution from stage $\mathcal{N}_i$, discounted by the population growth rate and the time

required for the contribution; e.g.,

$$v_2 = \underbrace{F_2\lambda^{-1}}_{\text{1 step}} + \underbrace{P_2F_3\lambda^{-2}}_{\text{2 steps}} + \underbrace{P_2P_3F_4\lambda^{-3}}_{\text{3 steps}}. \tag{9.1.22}$$

This algorithm gives the left eigenvector for a wide class of life cycles.[*]

In the (imaginary) stage-classified life cycle of Figure 9.1b, an individual in $\mathcal{N}_2$ may proceed to a stage ($\mathcal{N}_3$) in which it only reproduces once or to a stage ($\mathcal{N}_4$) in which it survives indefinitely with a probability P_4. The resulting reproductive value vector, obtained by summing contributions from each stage back to the first, is

$$v_1 = 1 \tag{9.1.23}$$

$$v_2 = F_2\lambda^{-1} + P_2F_3\lambda^{-2} + \frac{R_2F_4\lambda^{-2}}{1 - P_4\lambda^{-1}} \tag{9.1.24}$$

$$v_3 = F_3\lambda^{-1} \tag{9.1.25}$$

$$v_4 = \frac{F_4\lambda^{-1}}{1 - P_4\lambda^{-1}}. \tag{9.1.26}$$

Each of these values is clearly a measure of future contribution to births, discounted by the population growth rate.[†]

Residual Reproductive Value.

Equation (8.9.1) decomposed reproductive value at age x into two components, one from reproduction at age x and the other from survival to, and reproduction at, later ages. These components were called *current reproduction* and *residual reproductive value* by Williams (1966). In the age-classified case (9.1.12), e.g.,

$$v_2 = F_2\lambda^{-1} + P_2\lambda^{-1}v_3, \tag{9.1.27}$$

where the first term is current reproduction and the second is residual reproductive value. In the stage-classified example, an individual in $\mathcal{N}_2$ has two possible fates, so

$$v_2 = F_2\lambda-1 + P_2\lambda^{-1}v_3 + R_2\lambda^{-1}v_4. \tag{9.1.28}$$

The first term is current reproduction and the second two terms together constitute residual reproductive value.

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[*]Including any life cycle in which all loops other than self-loops pass through $\mathcal{N}_1$. If there are more complicated loop structures, additional terms are required (Caswell 1982a, MPM Chapter 7).

[†]The terms

$$\frac{1}{1 - P_4\lambda^1} = 1 + P_4\lambda^{-1} + P_4^2\lambda^{-2} + \ldots$$

created by the self-loop on $\mathcal{N}_4$ reflect the probability that the individual will remain in $\mathcal{N}_4$ for $1, 2, \ldots$ time steps.

9.2   The Stable Equivalent Population

The stable equivalent population of Section 8.8 applies to any classification of individuals (Keyfitz 1969). An initial population $\mathbf{n}_0$ with an arbitrary stage distribution will asymptotically produce an exponentially growing population of the same size as an initial population of size Q with the stable stage distribution.

To calculate Q, we scale $\mathbf{w}$ so that $\|\mathbf{w}\| = 1$, and $\mathbf{v}$ so that $\mathbf{v}^*\mathbf{w} = 1$. The population starting at $\mathbf{n}_0$ will eventually grow as

$$\lim_{t\to\infty} \frac{\mathbf{n}(t)}{\lambda^t} = \mathbf{v}^*\mathbf{n}_0\mathbf{w} \tag{9.2.1}$$

while that starting from $\mathbf{n}(0) = Q\mathbf{w}$ will grow as

$$\lim_{t\to\infty} \frac{\mathbf{n}(t)}{\lambda^t} = Q\left(\mathbf{v}^*\mathbf{w}\right)\mathbf{w}. \tag{9.2.2}$$

Equating the two gives

$$Q = \mathbf{v}^*\mathbf{n}_0. \tag{9.2.3}$$

That is, the stable equivalent is just the total reproductive value of the initial population, when scaled so that $\|\mathbf{w}\| = 1$ and $\mathbf{v}^*\mathbf{w} = 1$.

We note in passing that the models considered here and in Chapter 8 describe constant environments. Tuljapurkar and Lee (1997) have extended the stable equivalent concept to models in which the vital rates fluctuate stochastically in time.

Example 9.1 Stable equivalent for the killer whale

Killer whales (*Orcinus orca*) live in stable social groups called pods. A life cycle is shown in Figure 3.10, and a set of vital rates estimated from an intensively studied population of 18 pods in coastal waters of Washington and British Columbia is shown in Example 11.1. The right and left eigenvectors, appropriately scaled, are

$$\mathbf{w} = \begin{pmatrix} 0.037 \\ 0.316 \\ 0.323 \\ 0.324 \end{pmatrix} \quad \mathbf{v} = \begin{pmatrix} 1.142 \\ 1.198 \\ 1.794 \\ 0 \end{pmatrix}. \tag{9.2.4}$$

Each pod has its own observed structure, and Table 9.1 compares the stable equivalent and the observed population of each. In contrast to the comparison of the stable and observed population sizes of 12 countries in Table 8.8, which were within a few percent of each other, among killer whale pods the stable equivalent ranges from 22 percent smaller to 71 percent larger than the observed population. When $Q < N$, the population is biased toward individuals of low reproductive value, and vice versa.

Table 9.1. The observed female population ($N = \|\mathbf{n}\|$) and the stable equivalent population Q for each of 18 pods of resident killer whales (*Orcinus orca*) in Washington and British Columbia.

N	Q	$\frac{Q}{N}$
12.93	10.59	0.82
10.30	8.05	0.78
26.23	28.10	1.07
5.77	5.77	1.00
4.20	6.33	1.51
7.73	9.48	1.23
1.23	2.11	1.71
5.10	4.74	0.93
5.63	6.69	1.19
11.53	12.27	1.06
5.13	7.33	1.43
3.07	4.82	1.57
2.50	3.78	1.51
2.30	1.99	0.87
6.37	9.12	1.43
6.13	9.00	1.47
2.93	4.22	1.44
8.47	11.71	1.38

The influence of $\mathbf{n}_0$ on eventual population size (and probability of extinction) is of more than academic interest in conservation biology. Invasions of introduced animals and plants create huge environmental and economic problems around the world. Studies of the determinants of invasion success of birds and mammals in New Zealand (which, because of its isolation, has been particularly vulnerable to invasions) have shown a correlation between the size of the introduced population and the success of the invasion (Veltman et al. 1996, Forsyth and Duncan 2001). The stable equivalent of the introduced population might be even more relevant.

The effect of initial population also arises in attempts to reintroduce threatened species to areas from which they have been exterminated. This is an increasingly frequent task; at this writing, 132 such projects involving 63 species are underway in New Zealand alone. Many of these involve introductions of individuals to offshore islands from which introduced predators have been eliminated. All else being equal, it might be useful to try to maximize the stable equivalent population size in such introductions.

9.2.1   Other Scalings of the Eigenvectors

Since the time of Fisher (1930) it has been customary to scale reproductive value so that $v_1 = 1$, as was done in Section 8.8. But if $\mathbf{w}$ is also scaled to sum to 1, this means that Q must be modified to

$$Q = \frac{\mathbf{v}^*\mathbf{n}_0}{\mathbf{v}^*\mathbf{w}}. \qquad (9.2.5)$$

For age-classified matrix models, it can be shown that, with this scaling of $\mathbf{v}$ and $\mathbf{w}$, the denominator

$$\mathbf{v}^*\mathbf{w} = \lambda^{-1} B\overline{A}, \qquad (9.2.6)$$

where B is the finite birth rate and $\overline{A}$ is the mean age of childbearing in the stable population [the equivalent of κ in (8.1.2)]. Thus (9.2.5) is the analogue of the continuous-time result (8.8.5); see also Goodman (1968).

It does not appear that the interpretation of $\mathbf{v}^*\mathbf{w}$ in terms of birth rate and generation time holds for general stage classifications, so in the general case it is easier to compute Q by scaling $\|\mathbf{w}\| = 1$ and $\mathbf{v}^*\mathbf{w} = 1$ and sacrificing $v_1 = 1$.