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Appendix from F. Bienvenu and S. Legendre, "A New Approach to the Generation Time in Matrix Population Models" (Am. Nat., vol. 185, no. 6, p. 000)

Turning Nodes into Arcs: The Line Graph

To compute the return time to transitions rather than stages, we construct an appropriate Markov chain in which we can use equation (4). This new Markov chain should have the following properties: (1) there should be a one-to-one correspondence between its arcs and the nodes of the initial Markov chain; (2) there should be a one-to-one correspondence between paths in both Markov chains; and (3) for every cycle, the weights of the arcs along corresponding cycles in the two Markov chains should be identical. This leads us to define the new Markov chain according to equation (6); that is,

$$\tilde{p}_{[i\to j][k\to l]} = \begin{cases} p_{kl} & \text{if } j = k, \\ 0 & \text{otherwise,} \end{cases}$$

where $[i \to j]$ is the node of $\tilde{\mathbf{P}}$ that corresponds to the arc going from i to j in $\mathbf{P}$. This simply means that the weight of an arc of $\tilde{\mathbf{P}}$ equals the weight of the arc of $\mathbf{P}$ that corresponds to the node of $\tilde{\mathbf{P}}$ to which it points. This is why equation (6) can be extended as we did to mixed transitions by treating them as two distinct transitions. Examples of this construction are given in figure A1.

The intuition for this definition is the following: because of the one-to-one correspondence between the paths in both graphs, it should be possible to go from $[i \to j]$ to $[k \to l]$ in $\tilde{\mathbf{P}}$ if and only if there are paths in $\mathbf{P}$ in which the transition $i \to j$ occurs just before the transition $k \to l$, which clearly is possible if and only if $j = k$. And because of the one-to-one correspondence between the weights of the paths in both graphs, the weights of the arcs of $\tilde{\mathbf{P}}$ should be chosen from the weights of the arcs of $\mathbf{P}$. Here, the weights of the arcs of $\tilde{\mathbf{P}}$ correspond to the weight of the arc of $\mathbf{P}$ to which they point. In graph theory terms, we have built what is known as a line graph (or adjoint graph) of a directed graph (Aigner 1967).

We now show some properties of the line graph that ensure that $\tilde{\mathbf{P}}$ indeed allows us to compute the return time to a set of transitions. We must show that (1) $\tilde{\mathbf{P}}$ is a Markov matrix, (2) $\tilde{\mathbf{P}}$ is primitive (assuming $\mathbf{P}$ is), and (3) the return time to any transition $i \to j$ in $\mathbf{P}$ is the same as the return time to the corresponding node $[i \to j]$ in $\tilde{\mathbf{P}}$.

First, we need to introduce some vocabulary: graphs in which there are more than one arc going from one node to another are called multigraphs. Thus, when mixed transitions are treated as two distinct transitions, the life-cycle graph is a multigraph. By contrast, there is always at most one arc going from one node to another in $\tilde{\mathbf{P}}$ (by construction). Graphs that have this property are called simple graphs to distinguish them from multigraphs.

$\tilde{\mathbf{P}}$ *Is a Markov Matrix*

Clearly, the entries of $\tilde{\mathbf{P}}$ are in the [0, 1] range. So all we have to show is that its rows sum to 1. Let $[i \to j]$ be the index of a row of $\tilde{\mathbf{P}}$. Then, by using equation (6) and the fact that the rows of $\mathbf{P}$ sum to 1 (because $\mathbf{P}$ is a Markov matrix), we have

$$\sum_{[k\to l]} \tilde{p}_{[i\to j],[k\to l]} = \sum_{l} \tilde{p}_{[i\to j],[j\to l]} = \sum_{l} p_{jl} = 1.$$

$\tilde{\mathbf{P}}$ *Is Primitive*

Let $[i \to j]$ and $[k \to l]$ be any two nodes in $\tilde{\mathbf{P}}$. Because $\mathbf{P}$ is irreducible, there exists a path from j to k in $\mathbf{P}$, say $j \to j_1 \to \cdots \to j_m \to k$. Because, by construction of the arcs of $\tilde{\mathbf{P}}$ according to equation (6), all the arcs of the putative path of $\tilde{\mathbf{P}}$ defined by $[i \to j] \to [j \to j_1] \to \cdots \to [j_m \to k] \to [k \to l]$ do exist, we have exhibited a path going from $[i \to j]$ to $[k \to l]$ in $\tilde{\mathbf{P}}$. Therefore, $\tilde{\mathbf{P}}$ is irreducible.

Now, let $i \to j \to \cdots \to k \to i$ be a cycle of $\mathbf{P}$. Clearly, the corresponding cycle in $\tilde{\mathbf{P}}$ is $[i \to j] \to [j \to \cdots] \to \cdots \to [\cdots \to k] \to [k \to i]$, and both cycles have the same length. Thus, the lengths of the cycles of $\mathbf{P}$ are also the lengths of the corresponding cycles in $\tilde{\mathbf{P}}$. With $\mathbf{P}$ being aperiodic, the greatest common divisor of the lengths of its cycles is 1, and as a result, so is that of $\tilde{\mathbf{P}}$. Note that this proof is easily generalized to multigraphs. Indeed, in a multigraph, a cycle is defined by its arcs. As a result, to a cycle of $\mathbf{P}$, defined by its arcs, corresponds a cycle in $\tilde{\mathbf{P}}$, unambiguously defined by its nodes because $\tilde{\mathbf{P}}$ is a simple graph. With $\tilde{\mathbf{P}}$ being irreducible and aperiodic, it is primitive.

The Return Time to Any Transition $\mathrm{i}\rightarrow\mathrm{j}$ *in* $\boldsymbol{P}$ *Is the Same as the Return Time to the Corresponding Node* $[\mathrm{i}\rightarrow\mathrm{j}]$ *in* $\tilde{\boldsymbol{P}}$

We have just shown that to every cycle of $\mathbf{P}$ corresponds a unique cycle of $\tilde{\mathbf{P}}$. In fact, this is a one-to-one correspondence; indeed, as we have just mentioned, with $\tilde{\mathbf{P}}$ being a simple graph, any of its cycles is unambiguously defined by its nodes. To this list of nodes corresponds a list of arcs in $\mathbf{P}$, which uniquely define a cycle. Thus, because there is a one-to-one correspondence between the cycles of both Markov chains and because the weights composing these cycles are the same, the return times are going to be identically distributed in both Markov chains.

Simplification of Cochran and Ellner's Formula

We show that the formula of Cochran and Ellner (1992) is equivalent to our equation (12), $T = \lambda\mathbf{vw}/\mathbf{vFw}$. Indeed, Cochran and Ellner's formula is

$$T = \frac{\sum_{i=1}^{m} y_i w_i \gamma_i}{\sum_{i=1}^{m} w_i \gamma_i}, \text{ with}$$

$$\begin{cases} y_i = \dfrac{\sum_{j=1}^{m} [(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-2}]_{ij} b_j}{\sum_{j=1}^{m} [(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-1}]_{ij} b_j} & \text{where } b_j = \dfrac{(\mathbf{Fw})_j}{\sum_{i=1}^{m} (\mathbf{Fw})_i}, \\[2ex] \gamma_i = \dfrac{(\mathbf{vF})_i}{v_{\mathrm{ref}}} & \text{where } v_{\mathrm{ref}} \text{ is a newborn stage of reference.} \end{cases}$$

After substituting γ_i and simplifying the v_{ref}, we can write this formula as

$$T = \frac{\sum_{i=1}^{m} y_i w_i (\mathbf{vF})_i}{\sum_{i=1}^{m} w_i (\mathbf{vF})_i}, \tag{A1}$$

which makes it clear that, as in our formula, the denominator is equal to $\mathbf{vFw}$ and allows us to focus on the numerator, $\sum_{i=1}^{m} y_i w_i (\mathbf{vF})_i$. We start by looking at

$$y_i = \frac{\sum_{j=1}^{m} [(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-2}]_{ij} b_j}{\sum_{j=1}^{m} [(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-1}]_{ij} b_j}, \text{ where } b_j = \frac{(\mathbf{Fw})_j}{\sum_{i=1}^{m} (\mathbf{Fw})_i}.$$

Because b_j is in both the numerator and the denominator, its denominator $\sum_{i=1}^{m} (\mathbf{Fw})_i$, which is independent of j, can be simplified. Taking advantage of matrix notation, we have

$$y_i = \frac{[(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-2}(\mathbf{Fw})]_i}{[(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-1}(\mathbf{Fw})]_i}. \tag{A2}$$

Now, we note that $(\mathbf{S} + \mathbf{F})\mathbf{w} = \lambda\mathbf{w}$, so that we also have $\mathbf{Fw} = \lambda(\mathbf{I} - \lambda^{-1}\mathbf{S})\mathbf{w}$. But because $\lambda^{-1}\mathbf{S}$ is a convergent matrix (a proof of this can be found in appendix 4 of Cochran and Ellner 1992), we know that $(\mathbf{I} - \lambda^{-1}\mathbf{S})$ is inversible. Therefore,

$$(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-1}\mathbf{Fw} = \lambda\mathbf{w}. \tag{A3}$$

Similarly, we can show that

$$\mathbf{vF}(\mathbf{I} - \mathbf{l}^{-1}\mathbf{S})^{-1} = \lambda\mathbf{v}. \tag{A4}$$

We can now substitute equation (A3) into equation (A2). After simplifying the λ's, this yields $y_i = [(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-1}\mathbf{w}]_i / w_i$, which we can in turn substitute in $\sum_{i=1}^{m} y_i w_i (\mathbf{vF})_i$. After this, we get that the denominator of equation (A1) is equal to

$$\sum_{i=1}^{m} [(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-1}\mathbf{w}]_i (\mathbf{vF})_i = \mathbf{vF}(\mathbf{I} - \lambda^{-1}\mathbf{S})^{-1}\mathbf{w}.$$

Using equation (A4), we obtain that this is also $\lambda\mathbf{vw}$. Therefore, Cochran and Ellner's formula for the mean age of mothers at birth can be rewritten as

$$T = \frac{\lambda\mathbf{vw}}{\mathbf{vFw}},$$

which is identical to our equation (12).

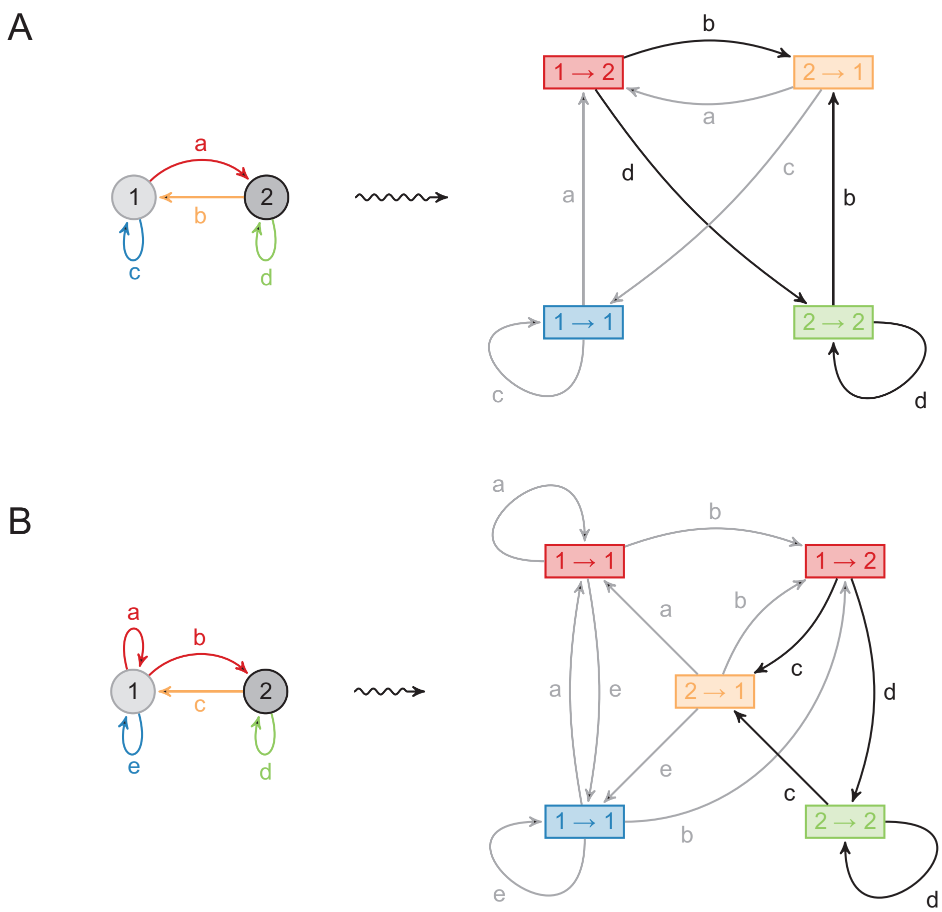

Figure A1: Examples of line graphs. The initial graphs (*left*) could correspond to the markovized graph of a model with two size classes. *A* does not include mixed transitions, while *B* does (small individuals are fertile), illustrating how mixed transitions are dealt with. In both cases, each arc of the initial graph corresponds to a unique node of the line graph. The labels on the arcs of both graphs indicate their weight, and the colors only aim at easing the identification of the correspondence between the elements of each graph.