# Appendix

Shripad Tuljapurkar*[1], Wenyun Zuo[1], Tim Coulson[2], Carol Horvitz[3], and Jean-Michel Gaillard[4]

[1]Department of Biology, Stanford University, Stanford, CA 94305-5020, USA
[2]Department of Zoology, University of Oxford, Oxford, OX1 3SZ, UK
[3]Department of Biology, University of Miami, Coral Gables, FL 33124-0421 USA.
[4]Laboratoire de Biométrie et Biologie Evolutive, Université Lyon 1, CNRS, UMR 5558, F-69622 Villeurbanne, France

## A.1 Discrete Convolutions and Age structure

Consider an age-structured population with only two age classes. Say that an individual of age class 1 has some number of offspring $i_1 = 0, 1, \ldots, k_m$ with probabilities $\boldsymbol{\kappa}_1 = \{\kappa_1(i_1)\}$, and an individual of age class 2 has $i_2 = 0, 1, \ldots, k_m$ offspring with probabilities $\boldsymbol{\kappa}_2 = \{\kappa_2(i_2)\}$. Now consider an individual who may produce offspring at both ages 1 and 2, and call $\delta(n)$ the probability that such an individual produces $n$ offspring, $n = 0, 1, 2, \ldots, 2k_m$. Given any $n$, some $m_1$ offspring are produced at age 1 and the rest, $k_2 = (n - m_1)$, must be produced at age 2. The number of ways to obtain a given $n$ varies with $n$. For example, there is only one way to obtain $n = 0$ (both

*corresponding author: tulja@stanford.edu

$m_1 = 0$ and $m_2 = 0$). Similarly, there is only one way for $n = 2k_m$ (both $m_1 = k_m$ and $m_2 = k_m$). There are only two ways for $n = 1$ (either $m_1 = 1$ and $m_2 = 0$ or $m_1 = 0$ and $m_2 = 1$). In general, we sum over the probabilities of the different ways we could get a particular $n$

$$\delta(n) = \sum \kappa_1(m_1)\, \kappa_2(n - m_1), \tag{A.1}$$

where the number of terms in the summation varies from 1 to a maximum of $k_m + 1$. The probabilities $\{\delta(n)\}$ are components of a distribution that we write as $\boldsymbol{\delta}$. Also, the fact that the first argument in equation (A.1) is $m_1$ and the second is $(n - m_1)$ means that $\boldsymbol{\delta}$ is what is called a discrete convolution of the distributions $\boldsymbol{\kappa}_1$ and $\boldsymbol{\kappa}_2$, written as

$$\boldsymbol{\delta} = \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2. \tag{A.2}$$

Alternatively we can describe $\boldsymbol{\kappa}_1$ and $\boldsymbol{\kappa}_2$ by the probability generating functions

$$w_1(x) = \sum_{i_1} \kappa_1(i_1) x^{i_1}, \;\; w_2(x) = \sum_{i_2} \kappa_2(i_2) x^{i_2}, \tag{A.3}$$

where $x$ is a dummy variable. Let the probability generating function for $\boldsymbol{\delta}$ be

$$u(x) = \sum_{n} \delta(n) x^n. \tag{A.4}$$

Setting

$$u(x) = w_1(x)\, w_2(x), \tag{A.5}$$

also (algebra!) yields the probabilities in equation (A.1). Thus there is a correspondence between convolutions of distributions (as in equation (A.2)) and products of generating functions (as in equation (A.5)).

Using equation (A.3), we see that the distribution $\boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_1$ has a generating function $[w_1(x)]^2$. As a result, we write $\boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_1$ as $\boldsymbol{\kappa}^2$. Also, $\boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2 = \boldsymbol{\kappa}_2 \star \boldsymbol{\kappa}_1$. Finally, note that convolutions can be rapidly computed (for discrete and continuous functions).

For age structured populations, we can use repeated convolutions to compute the LRS distribution as in the main text. But this method doesn't work for stage structure so we need a different approach that starts with the property discussed next.

## A.2 Fourier transforms

Fourier transforms require complex numbers. Denote

$$\mathbf{i} = \sqrt{-1}. \tag{A.6}$$

For an integer $N$, define the frequencies

$$\theta(z) = \exp\left[\frac{-2\pi z \mathbf{i}}{N}\right], z = 0, 1, \ldots, N-1. \tag{A.7}$$

Then for any integer $q$, define the discrete function $\boldsymbol{\kappa} = \{\kappa(0), \kappa(1), \kappa(2), \ldots, \kappa(q)\}$ (this could be a probability distribution). Then we define the Discrete Fourier Transform (DFT) of $\boldsymbol{\kappa}$ as a function $\widehat{\kappa}$, whose values are given for each frequency in equation (A.7) as,

$$\widehat{\kappa}(\theta(z)) = \sum_{b=0}^{q} \kappa(b)\, \theta(z)^b. \tag{A.8}$$

Now suppose that $\boldsymbol{\psi}$ is another series of numbers, $\boldsymbol{\psi} = \{\psi(0), \psi(1), \ldots, \psi(q)\}$. For frequencies $\theta(z)$, we can use equation (A.8) to find the Fourier transform $\widehat{\psi}(\theta(z))$. It is well known that (James 2002)

the Fourier transform of $\{\boldsymbol{\kappa} \star \boldsymbol{\psi}\}$ is the product $\widehat{\kappa}\,\widehat{\psi}$

In consequence, for any frequency $\theta(z)$ in equation (A.7): for any integer $m \geq 0$,

$$\widehat{\left(\kappa^m\right)}(\theta(z)) = \left(\widehat{\kappa}(\theta(z))\right)^m, \tag{A.9}$$

and for any non-negative integers $m_a, m_b$

$$\left(\widehat{\kappa^{m_a} \star \psi^{m_b}}\right)(\theta(z)) = \widehat{\kappa}(\theta(z))^{m_a}\, \widehat{\psi}(\theta(z))^{m_b}. \tag{A.10}$$

## A.3 Digression: A Generating Function

We consider a general age+stage model following Steiner and Tuljapurkar (2012). Age and stage are used together: given $A$ ages and $S$ discrete stages, there are $(A \times S) = S_1$ unique combinations, so that we can proceed as if we had a stage-only model with $S_1$ stages. Let there be $S_1$ living stages, with transitions between them with probabilities $\mathbf{U}$ (Table 1 in main text). Form the matrix $\mathbf{U}^T = \mathbf{Q}$. The element $q_{ij}$ of matrix $\mathbf{Q}$ is the probability of being in stage $i$ in one time interval and then surviving to reach stage $j$ in the next time interval. The stages that are rows (or columns) of $\mathbf{Q}$ are transient, meaning that an individual starts in any stage then makes transitions to other stages until an eventual but certain death. Starting in a particular stage $i$ let $\tau_j$ be the (random) time spent in stage $j$ before death. (In the main text we use matrix $\mathbf{U}$, but here, we are using the transposed matrix $\mathbf{Q}$ and so reverse rows and columns).

The death probabilities for stages 1 to $S$ are components $d_i$ of a vector $\mathbf{d}$. These death rates are of course simply probabilities of not reaching another transient stage, so e.g.,

$$d_i = 1 - \sum_j q_{ij}.$$

We summarize by defining

$$\mathbf{e} = \text{ a column vector whose every entry is 1,} \tag{A.11}$$

and writing $\mathbf{I}$ for the identity matrix, so that

$$\mathbf{d} = \big(\mathbf{I} - \mathbf{Q}\big)\,\mathbf{e}. \tag{A.12}$$

Consider the possible outcome in which an individual spends a time $m_j$ in stage $j$. In our notation, this outcome means that $\tau_j = m_j$, conditional on starting in stage $i$, and has probability,

$$P_i[m_1, m_2, \ldots, m_S] = \Pr[\tau_1 = m_1, \tau_2 = m_2, \ldots, \tau_S = m_S | \text{ starting stage } i]. \tag{A.13}$$

Let $w_i, i = 1, \ldots, S$ be a set of (dummy) variables, and make a generating function for the above probabilities,

$$V_i = \sum_{m_1, m_2, \ldots, m_S} P_i[m_1, m_2, \ldots, m_S]\, w_1^{m_1}\, w_2^{m_2} \ldots\, w_S^{m_S}. \tag{A.14}$$

Say we start in stage 1, so $i = 1$. Then $V_i = V_1$ is a polynomial, whose first term is $w_1 d_1$ – meaning an individual starts in 1 but dies before making a transition. The second term of $V_1$ is

$$w_1 q_{11} w_1 d_1 + w_1 q_{12} w_2 d_2 + \cdots + w_1 q_{1S} w_S d_S,$$

meaning an individual starts in stage 1, lives one period and reaches some stage $j$, but then dies before making a second transition. And so on.

Following Steiner and Tuljapurkar (2012), form the diagonal matrix

$$\mathbf{W} = \text{diag}\{w_i\}, i = 1, \ldots, S. \tag{A.15}$$

Define the vector function

$$\mathbf{V} = \mathbf{W}\left(\mathbf{I} - \mathbf{Q}\,\mathbf{W}\right)^{-1}\mathbf{d}, \tag{A.16}$$

where $\mathbf{I}$ is the identity matrix and $\mathbf{d}$ is defined in equation (A.12).

Let the components of $\mathbf{V}$ in equation (A.16) be $\{V_i, i = 1, \ldots, S\}$. Then this component $V_i$ is indeed the generating function defined earlier in equation (A.14). The reader can derive this by expanding the inverse in equation (A.16) and seeing, e.g., that the resulting polynomial $V_1$ has the same terms as we describe above.

## A.4 To the LRS

We now combine convolutions, the generating function, and Fourier transforms.

Start by defining frequencies. Choose a number $N$ that is the largest possible number of offspring. This may be approximated by a product like $k_U \leq (\omega \times k_m)$ with $\omega$ being an estimated maximum age, and $k_m$ being the maximum number of offspring per time period. Or a biological upper limit can be used. Either way, we can test the adequacy of our choice by computing $\Gamma$ and then its sum, which should be very close to 1.

Given $N$, for every stage $i$ we pad each offspring probability distribution $\boldsymbol{\kappa}_i$ by adding zeros so that the padded distribution has $N$ elements. For each frequency $\theta(z)$, as in equation (A.7), let the Fourier transforms of the padded distributions $\boldsymbol{\kappa}_i$ be $\widehat{\boldsymbol{\kappa}}_i$, so for example

$$\widehat{\boldsymbol{\kappa}}_i(\theta(z)) = \sum_{k=0}^{N-1} \kappa_i(k)\,\theta(z)^k. \tag{A.17}$$

For any non-reproducing stage $i$ we have $\kappa_i = \{1, 0, \ldots\}$, and so

$$\widehat{\boldsymbol{\kappa}}_i(\theta(z)) = 1, \text{ for all } \theta(z) \text{ for non-reproducing stages.} \tag{A.18}$$

Now as in the previous subsection, say that, starting in stage $i$ an individual spends time $m_j$ in each stage $j$ before death (for stages $j = 1, 2, \ldots$). The total offspring numbers that result have the distribution

$$\boldsymbol{\kappa}_1^{m_1} \star \boldsymbol{\kappa}_2^{m_2} \star \cdots \star \boldsymbol{\kappa}_S^{m_S} = \boldsymbol{\delta}. \tag{A.19}$$

So in this case

$$\Pr[\text{number of offspring is } k|\text{ starting stage } i]$$

is given by the $k$th element of the convolution $\delta$ in equation (A.19)

The lifetime probability of having $k$ offspring is the $k$th element $\gamma(k)$ of

$$\Gamma = \sum_{m_1, m_2, \ldots, m_S} P[m_1, m_2, \ldots, m_S|\text{ starting stage } i]\, \boldsymbol{\kappa}_1^{m_1} \star \boldsymbol{\kappa}_2^{m_2} \star \cdots \star \boldsymbol{\kappa}_S^{m_S}. \tag{A.20}$$

Here $\Gamma$ can be thought of as a function of the discrete argument $k = 0, 1, \ldots$ with values $\gamma(0), \gamma(1), \ldots$. This is reminiscent of equation (A.14), but unfortunately here we have convolutions and not products of numbers. This is where Fourier transforms come in.

We denote the Fourier transform of this function by $\widehat{\Gamma}$. Note that this latter transformed function is defined for each discrete frequency; so if the frequencies are $\theta(0), \theta(1), \ldots$, the Fourier transform is the set of (scalar) values $\widehat{\Gamma}(\theta(0)), \widehat{\Gamma}(\theta(1)), \ldots$.

Using the facts about Fourier transforms and equation (A.20) we conclude that

$$\widehat{\Gamma}(\theta) = \sum_{m_1, m_2, \ldots, m_S} P[m_1, m_2, \ldots, m_S|\text{ starting stage } i]\, \widehat{\boldsymbol{\kappa}_1}(\theta)^{m_1} \ldots \widehat{\boldsymbol{\kappa}_S}(\theta)^{m_S}. \tag{A.21}$$

Now this is indeed similar to equation (A.14), so the sum here can be exactly computed using the generating function equation (A.16).

## A.5 Method for Stages

Start with choosing a large number $N$, fix the starting stage $i$, then find the frequencies as in equation (A.7). For each frequency $\theta(z)$ and every stage $j$, compute the Fourier transforms $\widehat{\boldsymbol{\kappa}_j}(\theta(z))$, and then make the matrix

$$\widetilde{\mathbf{W}} = \begin{pmatrix} \widehat{\boldsymbol{\kappa}_1}(\theta(z)) & 0 & 0 & \ldots \\ 0 & \widehat{\boldsymbol{\kappa}_2}(\theta(z)) & 0 & \ldots \\ \vdots & \vdots & \vdots & \vdots \end{pmatrix}. \tag{A.22}$$

Remembering the generating function, use equations (A.21) and (A.22) to compute the quantity

$$\mathbf{V} = \widetilde{\mathbf{W}}\left(\mathbf{I} - \mathbf{Q}\,\widetilde{\mathbf{W}}\right)^{-1} \mathbf{d} \text{ with components } \{V_i\}.$$

Then use equation (A.21) to conclude that

$$\widehat{\Gamma}(\theta(z)) = V_i. \tag{A.23}$$

Repeat for all frequencies. Thus one computes the set of (scalar) values $\widehat{\Gamma}(\theta(0)), \widehat{\Gamma}(\theta(1)), \ldots$ and hence the function $\widehat{\Gamma}$.

Final step: use the Inverse FFT to find $\Gamma$.

Note: since every age+stage model can be cast as a stage-only model, this method can also be used for age-only or age+stage models. But the age-structured analysis in the main text explains the basic logic that the general method does not. The age-based method is often computationally useless for stage based or age+stage models when we have a large number of stages, or when individuals can stay in a stage for a long time. In such cases, the method here is essential.

## A.6 Block method for age+stage

An age+stage model has ages $a = 1, 2, \ldots, \omega$, stages $s = 1, 2, \ldots, S$. A unique age+stage combination is written $a, s$, and there are $A \times S$ such combinations. In some cases, the general method of the preceding section may be computationally lengthy and the method described below is faster.

### A.6.1 Inverse

To make it efficient to find the generating function, start by computing the inverse of the matrix

$$\mathbf{H} = \left(\mathbf{I} - \mathbf{Q}\,\widetilde{\mathbf{W}}\right), \tag{A.24}$$

in which $\mathbf{Q} = \mathbf{U}^T$. Here $\widetilde{\mathbf{W}}$ is a diagonal matrix as in equation (A.22). Suppose that we have $S$ stages at each age, and that ages $a = 1, 2, \ldots, A-1$ have corresponding and distinct $S \times S$ transition matrices $\mathbf{U}_a = \mathbf{Q}_a^T$. The transition matrix $\mathbf{U}_A = \mathbf{Q}_A^T$ for age $A$ is repeating, and applies at age $A+1, A+2, \ldots$ until death. Note that for this case, there are total $A * S$ stages. Write the diagonal elements of $\widetilde{\mathbf{W}}$ for a given frequency, $\theta(z)$,as

$$\widetilde{\mathbf{W}} = (\widetilde{\mathbf{W}}_1, \widetilde{\mathbf{W}}_2, \ldots, \widetilde{\mathbf{W}}_A), \tag{A.25}$$

$$\widetilde{\mathbf{W}}_a = (\widehat{\boldsymbol{\kappa}_{a,1}}(\theta(z)), \widehat{\boldsymbol{\kappa}_{a,2}}(\theta(z)), \ldots, \widehat{\boldsymbol{\kappa}_{a,S}}(\theta(z))), \tag{A.26}$$

and the matrix of transition probabilities as

$$\mathbf{Q} = \begin{pmatrix} \mathbf{0} & \mathbf{Q}_1 & \mathbf{0} & \dots \\ \mathbf{0} & \mathbf{0} & \mathbf{Q}_2 & \dots \\ \vdots & \vdots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \dots & \mathbf{Q}_{A-1} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{Q}_A \end{pmatrix}. \tag{A.27}$$

We can write the matrix of equation (A.24) in block form as

$$\mathbf{H} = \begin{pmatrix} \mathbf{I} & \mathbf{B}_1 & \mathbf{0} & \dots & \mathbf{0} \\ \mathbf{0} & \mathbf{I} & \mathbf{B}_2 & \dots & \mathbf{0} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \mathbf{I} & \dots & \mathbf{B}_{A-1} \\ \mathbf{0} & \mathbf{0} & \dots & & \mathbf{C} \end{pmatrix}, \tag{A.28}$$

where

$$\mathbf{B}_a = -\mathbf{Q}_a \widetilde{\mathbf{W}}_{a+1}, (a < A), \tag{A.29}$$

$$\mathbf{C} = \mathbf{I} - \mathbf{Q}_A \widetilde{\mathbf{W}}_A. \tag{A.30}$$

Now use the result in Singh (1979) applied to block matrices. It is best to write this first in cases and then in general. First, say that $A = 5$ so that

$$\mathbf{H} = \begin{pmatrix} \mathbf{I} & \mathbf{B}_1 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I} & \mathbf{B}_2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I} & \mathbf{B}_3 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I} & \mathbf{B}_4 \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{C} \end{pmatrix}, \tag{A.31}$$

where

$$\mathbf{C} = \mathbf{I} - \mathbf{Q}_5 \widetilde{\mathbf{W}}_5. \tag{A.32}$$

Then

$$\mathbf{H}^{-1} = \begin{pmatrix} \mathbf{I} & -\mathbf{B}_1 & \mathbf{B}_1\mathbf{B}_2 & -\mathbf{B}_1\mathbf{B}_2\mathbf{B}_3 & \mathbf{B}_1\mathbf{B}_2\mathbf{B}_3\mathbf{B}_4\mathbf{C}^{-1} \\ \mathbf{0} & \mathbf{I} & -\mathbf{B}_2 & \mathbf{B}_2\mathbf{B}_3 & -\mathbf{B}_2\mathbf{B}_3\mathbf{B}_4\mathbf{C}^{-1} \\ \mathbf{0} & \mathbf{0} & \mathbf{I} & -\mathbf{B}_3 & \mathbf{B}_3\mathbf{B}_4\mathbf{C}^{-1} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I} & -\mathbf{B}_4\mathbf{C}^{-1} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{C}^{-1} \end{pmatrix}, \tag{A.33}$$

In general, the inverse matrix for equation (A.28) has the form

$$\mathbf{H}^{-1} = \begin{pmatrix} \mathbf{I} & \mathbf{J}_{1,2} & \mathbf{J}_{1,3} & \dots & \mathbf{J}_{1,A} \\ \mathbf{0} & \mathbf{I} & \mathbf{J}_{2,3} & \dots & \mathbf{J}_{2,A} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \mathbf{I} & \mathbf{I} & \mathbf{J}_{A-1,A} \\ \mathbf{0} & \mathbf{0} & \dots & \mathbf{0} & \mathbf{C}^{-1} \end{pmatrix}, \tag{A.34}$$

Here,

$$\mathbf{J}_{i,j} = \big(-1\big)^{i+j} \left\{ \prod_{k=i}^{j-1} \mathbf{B}_k \right\}, \text{ for } i < j \leq (A-1), \tag{A.35}$$

$$\mathbf{J}_{i,A} = \big(-1\big)^{i+j} \left\{ \prod_{k=i}^{A-1} \mathbf{B}_k \right\} \mathbf{C}^{-1}, \text{ for } j = A. \tag{A.36}$$

### A.6.2 The Generating Function

Fix a starting stage $i$ out of all $A \times S$ combinations, where $S$ is the number of stages in a given age and $A$ is the age where the transition matrix $\mathbf{U}_A$ starts repeating for following age. Death rates by age+stage are elements (there are $A \times S$ elements) of the vector

$$\mathbf{d} = \begin{pmatrix} \mathbf{d}_1 \\ \mathbf{d}_2 \\ \vdots \\ \mathbf{d}_A \end{pmatrix}, \qquad \mathbf{d}_a = \begin{pmatrix} \mathbf{d}_{a,1} \\ \mathbf{d}_{a,2} \\ \vdots \\ \mathbf{d}_{a,S} \end{pmatrix}. \tag{A.37}$$

The generating function is

$$\mathbf{V} = \widetilde{\mathbf{W}}\, \mathbf{H}^{-1}\, \mathbf{d}, \tag{A.38}$$

We start with the product

$$\mathbf{H}^{-1}\, \mathbf{d}, \tag{A.39}$$

which is a vector of $A$ blocks, each $S$-long.

Using the pattern in eqations (A.33 – A.36), we define a sequence:

$$\widehat{\mathbf{d}}_A = \mathbf{C}^{-1}\mathbf{d}_A, \tag{A.40}$$

$$\widehat{\mathbf{d}}_{A-1} = \mathbf{d}_{A-1} - \mathbf{B}_{A-1}\widehat{\mathbf{d}}_A, \tag{A.41}$$

$$\widehat{\mathbf{d}}_{A-2} = \mathbf{d}_{A-2} - \mathbf{B}_{A-2}\widehat{\mathbf{d}}_{A-1}, \tag{A.42}$$

$$\widehat{\mathbf{d}}_a = \mathbf{d}_a - \mathbf{B}_a\widehat{\mathbf{d}}_{a+1},\ 1 \le a \le (A-1). \tag{A.43}$$

Then set

$$\widehat{\mathbf{d}} = (\widehat{\mathbf{d}}_1, \widehat{\mathbf{d}}_2, \ldots, \widehat{\mathbf{d}}_A)^T, \tag{A.44}$$

so finally

$$\mathbf{H}^{-1}\,\mathbf{d} = \widehat{\mathbf{d}}. \tag{A.45}$$

Therefore the generating function is

$$\mathbf{V} = \{V_1, V_2, \ldots, V_{A\times S}\} = \widetilde{\widetilde{\mathbf{W}}}\widehat{\mathbf{d}}. \tag{A.46}$$

This quantity gives us the Fourier Transform $\widehat{\Gamma}$ of the LRS distribution $\Gamma$ – which is the distribution we want. So at the given frequency $\theta(k)$ we have found that

$$\widehat{\Gamma}(\theta(k)) = V_i. \tag{A.47}$$

Repeat for all frequencies. Thus one computes the set of (scalar) values $\widehat{\Gamma}(\theta(0)), \widehat{\Gamma}(\theta(1)), \ldots$ and hence the function $\widehat{\Gamma}$. The inverse Fourier transform then yields $\Gamma$.

## A.7 Special probabilities: Ages only

To compute Pr[LRS = 0], observe that an individual has 0 offspring if it either (a) dies before reaching reproductive age $\alpha$ or (b) survives through the pre-reproductive period, but has 0 offspring thereafter. At reproductive ages $a$ the probability of having 0 offspring is $\kappa_a(0)$. Assuming survival, the cumulative probability of having had no offspring by age $a$ is

$$p'_a = \kappa_1(0)\,\kappa_2(0)\ldots\kappa_a(0). \tag{A.48}$$

Thus,

$$\begin{aligned}\Pr[\text{LRS} = 0] = \big(1 - l_\alpha\big) + \\ + \sum_{a \geq \alpha}^{\beta-1} \phi_a \, p'_a + \\ + l_\beta \, p'_\beta. \end{aligned} \tag{A.49}$$

The first line gives us (a) above, the second line adds in reproduction at intermediate ages weighted by the odds of death, and the third line gives us the final contribution to childlessness.

## A.8 Special probabilities: Stages

To compute Pr[LRS = 0], we need a different method. Each stage $i$ has a corresponding probability that an individual in that stage produces 0 offspring. This probability is 1 for non-reproducing stages, and $\kappa_i(0)$ for all other stages $i$. Define $\mathbf{W}_{\text{zero}}$ to be a diagonal matrix whose elements are

$$\begin{aligned}\mathbf{W}_{\text{zero}}(i,i) &= 1, \text{ non-reproductive stage } i, \\ \mathbf{W}_{\text{zero}}(i,i) &= \kappa_i(0), \text{ reproductive stage } i. \end{aligned} \tag{A.50}$$

Use the definitions of the preceding section and compute

$$\mathbf{V}_{\text{zero}} = \mathbf{W}_{\text{zero}} \Big(\mathbf{I} - \mathbf{Q}\,\mathbf{W}_{\text{zero}}\Big)^{-1} \mathbf{d}. \tag{A.51}$$

Then the $i$th component of $\mathbf{V}_{\text{zero}}$ is

$$\Pr[\text{LRS} = 0 | \text{ initial stage } i].$$

Since every age+stage model can be cast as a stage-only model, this answer can be used for any model.

For some life cycles we can also compute

$$\Pr[\text{LRS} = 0 | \text{ die without reaching a stage capable of reproduction}]$$

Suppose we start in a non-reproductive stage. In suitable lifecycles, every individual eventually makes an irreversible transition to one or more reproducing stages, or dies. Here it makes sense to treat the reproducing stages as "absorbing" and then (1 - the absorption probability) is just what we want. See Caswell (2001) or Kemeny and Snell (1976) for details on how to do this.

## A.9 Special distributions

### A.9.1 Poisson

Here the average fertility is $f_i$ for stage $i$, and $\boldsymbol{\kappa}_i$ is a Poisson distribution. So $\boldsymbol{\kappa}_i$ has the probability generating function

$$\kappa_i(x) = \exp\big[f_i\,(x-1)\big], \tag{A.52}$$

for $x$ a dummy variable.

So for stage $j$, and any frequency $\theta(k)$ as defined in equation (A.7), the Fourier transform is

$$\widehat{\kappa_j}(\theta(z)) = \exp\big[f_j\,(\theta(z)-1)\big]. \tag{A.53}$$

### A.9.2 Binomial

Here the average fertility is $f_i$ for stage $i$, and $\boldsymbol{\kappa}_i$ is a Binomial (with 1 trial, also known as a Bernoulli) distribution. So $\boldsymbol{\kappa}_i$ has the probability generating function

$$\kappa_i(x) = \kappa_i(0) + (1-\kappa_i(0))x, \tag{A.54}$$

where $\kappa_i(0)$ is the probability that an individual in stage $i$ has 0 offspring and $x$ is a dummy variable.

So for stage $i$, and any frequency $\theta(k)$ as defined in equation (A.7), the Fourier transform is

$$\widehat{\kappa_i}(\theta(z)) = \kappa_i(0) + (1-\kappa_i(0))\theta(z). \tag{A.55}$$

## A.10 Roe deer plots

Small offspring have a high mode at 0, and thus the highest probability of leaving no offspring. Neither the average LRS nor the standard deviation seem to be useful descriptors of the LRS distribution for the smallest yearlings (Fig. A.1). For the full spectrum of size classes, Fig. A.2 shows 41 initial stages spread over size class 1 to 200; thus there is a 5 size class interval between each adjacent pair of curves. Fig. A.3 shows the Pr[LRS = 0] declines with increasing birth mass.

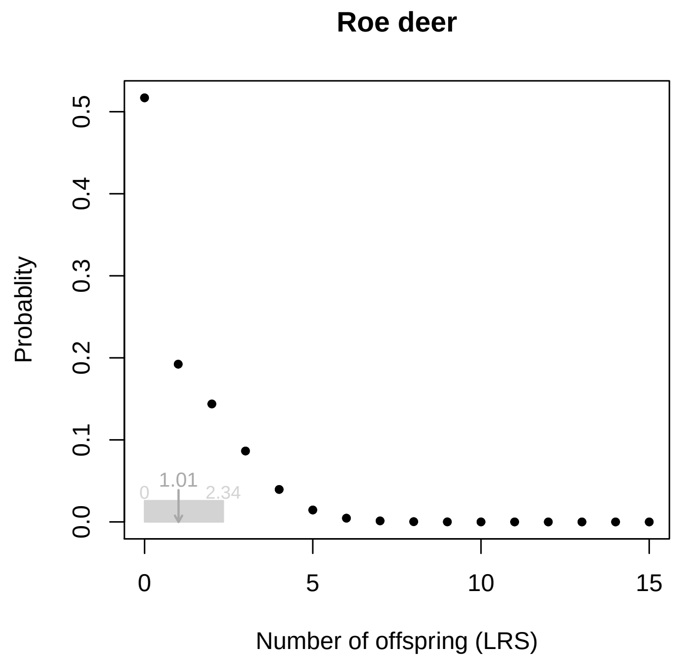


Figure A.1: The LRS distribution of Roe deer *Capreolus capreolus*. Mean LRS = 1.01 and the standard deviation is 1.34.

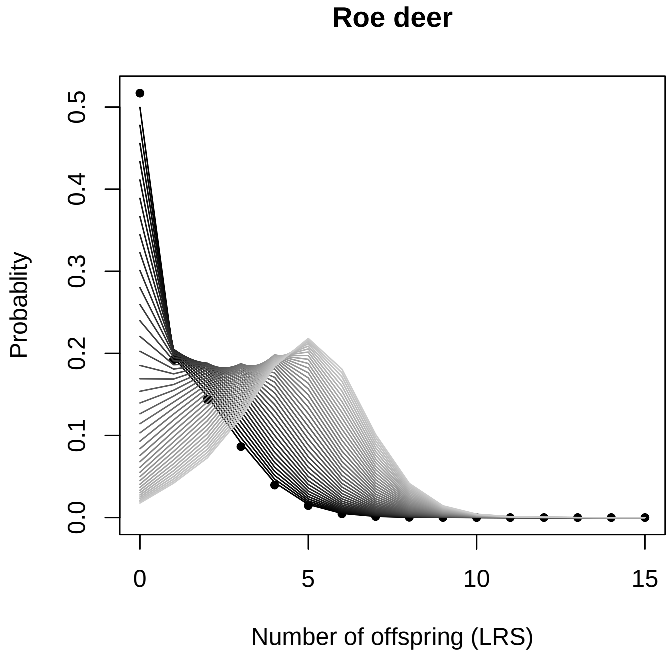


Figure A.2: The LRS distribution of Roe deer *Capreolus capreolus*. Solid points are for yearlings born into size class 1. The lines are for size classes 5 to 200 shown at an interval of 5.

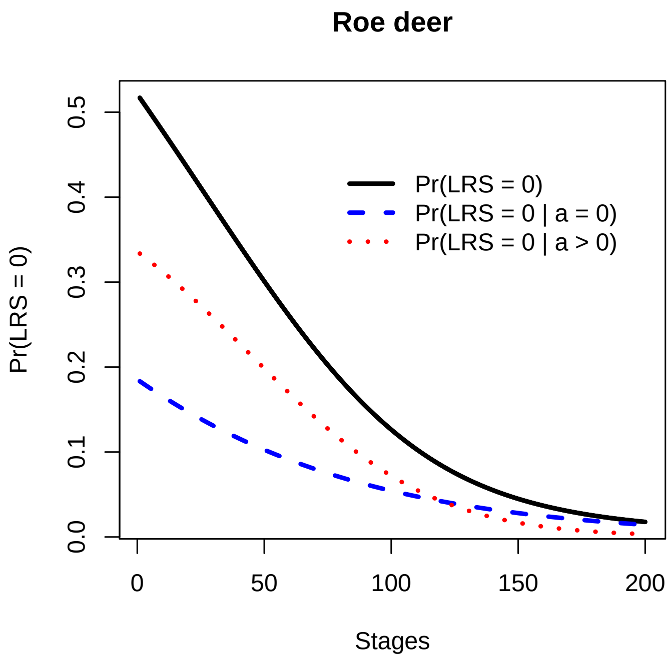


Figure A.3: The probability that LRS = 0 for different initial size classes for yearlings of Roe deer *Capreolus capreolus*. The blue dashed line shows the yearling death probability. The red dotted line shows the probability of having no offspring if you live to later ages.

## A.11 The flow chart of decisions

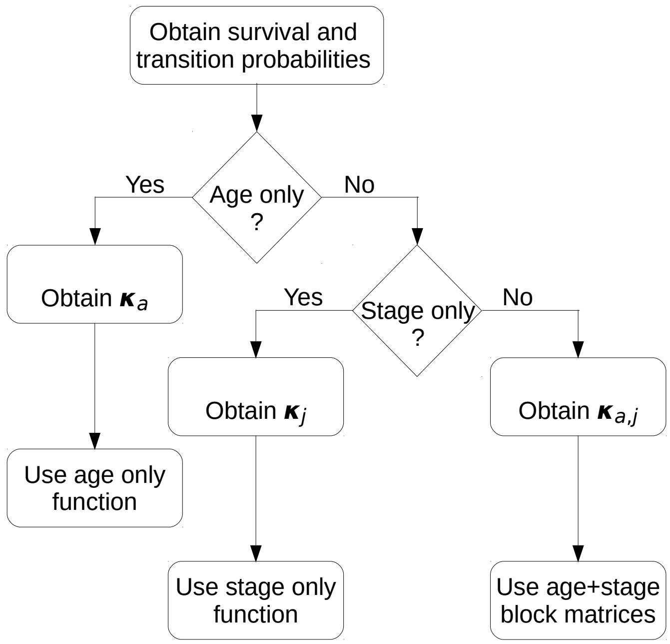


Figure A.4: The flow chart of decisions. Survival probabilities (Table 1) and/or survival-transition matrices (Table 1); Reproduction distributions $\boldsymbol{\kappa_a}$, $\boldsymbol{\kappa_j}$, $\boldsymbol{\kappa_{a,j}}$ (Table 1).

## A.12 Step-by-step example via *Tsuga canadensis*

For the evergreen tree, *Tsuga canadensis*, survival, stage-transition and reproduction during a time interval depends only on stage. The unconditional transition probability matrix $\boldsymbol{U}$ is

$$\boldsymbol{U} = \begin{pmatrix} 0.9030 & 0 & 0 & 0 & 0 & 0 \\ 0.0038 & 0.96070 & 0 & 0 & 0 & 0 \\ 0 & 0.01225 & 0.96545 & 0 & 0 & 0 \\ 0 & 0 & 0.01735 & 0.97595 & 0 & 0 \\ 0 & 0 & 0 & 0.01205 & 0.96335 & 0 \\ 0 & 0 & 0 & 0 & 0.01835 & 0.9903 \end{pmatrix}.$$

The fertility matrix $\boldsymbol{F}$ is

$$\boldsymbol{F} = \begin{pmatrix} 0 & 0 & 0.299 & 0.77415 & 1.9573 & 6.0251 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}.$$

The fertility of each stage in fertility matrix $\boldsymbol{F}$ is the mean fertility of the given stage. Assume the distribution of offspring at each stage, $\boldsymbol{\kappa_j}$ follow Poisson distribution with the mean listed in $\boldsymbol{F}$. Choose $N = 2^{14}$ as the largest possible number of offspring. Truncate the Poisson distribution at $N$ and add sum of the rest of probability to $\boldsymbol{\kappa_j}(N)$, so that we have $\boldsymbol{\kappa_1}$, $\boldsymbol{\kappa_2}$, $\boldsymbol{\kappa_3}$, $\boldsymbol{\kappa_4}$, $\boldsymbol{\kappa_5}$ and $\boldsymbol{\kappa_6}$. Fix the starting stage at 1, the frequencies as in equation (A.7) are

$$\theta(z) = \exp\left[\frac{-2\pi z\mathbf{i}}{2^{14}+1}\right], z = 0, 1, \ldots, 2^{14}. \tag{A.56}$$

For each frequency $\theta(z)$ and every stage $j$, computer the Fourier transforms $\widehat{\boldsymbol{\kappa}_j}(\theta(z))$, and then make the matrix as in equation (A.22). For example, for

$\theta(0)$, the matrix is

$$\widetilde{\mathbf{W}} = \begin{pmatrix} \widehat{\boldsymbol{\kappa}_1}(\theta(0)) & 0 & 0 & 0 & 0 & 0 \\ 0 & \widehat{\boldsymbol{\kappa}_2}(\theta(0)) & 0 & 0 & 0 & 0 \\ 0 & 0 & \widehat{\boldsymbol{\kappa}_3}(\theta(0)) & 0 & 0 & 0 \\ 0 & 0 & 0 & \widehat{\boldsymbol{\kappa}_4}(\theta(0)) & 0 & 0 \\ 0 & 0 & 0 & 0 & \widehat{\boldsymbol{\kappa}_5}(\theta(0)) & 0 \\ 0 & 0 & 0 & 0 & 0 & \widehat{\boldsymbol{\kappa}_6}(\theta(0)) \end{pmatrix}$$

$$= \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix},$$

for $\theta(1)$, the matrix is

$$\widetilde{\mathbf{W}} = \begin{pmatrix} \widehat{\boldsymbol{\kappa}_1}(\theta(1)) & 0 & 0 & 0 & 0 & 0 \\ 0 & \widehat{\boldsymbol{\kappa}_2}(\theta(1)) & 0 & 0 & 0 & 0 \\ 0 & 0 & \widehat{\boldsymbol{\kappa}_3}(\theta(1)) & 0 & 0 & 0 \\ 0 & 0 & 0 & \widehat{\boldsymbol{\kappa}_4}(\theta(1)) & 0 & 0 \\ 0 & 0 & 0 & 0 & \widehat{\boldsymbol{\kappa}_5}(\theta(1)) & 0 \\ 0 & 0 & 0 & 0 & 0 & \widehat{\boldsymbol{\kappa}_6}(\theta(1)) \end{pmatrix}$$

$$= \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.9999999 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.9999996 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.9999969 \end{pmatrix}$$

$$+ \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -0.0001147 & 0 & 0 & 0 \\ 0 & 0 & 0 & -0.0002969 & 0 & 0 \\ 0 & 0 & 0 & 0 & -0.0007506 & 0 \\ 0 & 0 & 0 & 0 & 0 & -0.0023105 \end{pmatrix} i,$$

for $\theta(2^{14})$, the matrix is

$$\widetilde{\mathbf{W}} = \begin{pmatrix} \widehat{\boldsymbol{\kappa}_1}(\theta(2^{14})) & 0 & 0 & 0 & 0 & 0 \\ 0 & \widehat{\boldsymbol{\kappa}_2}(\theta(2^{14})) & 0 & 0 & 0 & 0 \\ 0 & 0 & \widehat{\boldsymbol{\kappa}_3}(\theta(2^{14})) & 0 & 0 & 0 \\ 0 & 0 & 0 & \widehat{\boldsymbol{\kappa}_4}(\theta(2^{14})) & 0 & 0 \\ 0 & 0 & 0 & 0 & \widehat{\boldsymbol{\kappa}_5}(\theta(2^{14})) & 0 \\ 0 & 0 & 0 & 0 & 0 & \widehat{\boldsymbol{\kappa}_6}(\theta(2^{14})) \end{pmatrix}$$

$$= \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.9999999 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.9999996 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.9999969 \end{pmatrix}$$

$$+ \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.0001147 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.0002969 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.0007506 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.0023105 \end{pmatrix} i.$$

Remembering the generating function, use equations (A.16) and (A.22) to compute the quantity

$$\mathbf{V} = \widetilde{\mathbf{W}}\Big(\mathbf{I} - \mathbf{Q}\,\widetilde{\mathbf{W}}\Big)^{-1}\mathbf{d} \text{ with components } \{V_1\},$$

where $\mathbf{Q} = \boldsymbol{U}^T$ and vector $\mathbf{d}$ has components as the death probabilities for stages 1 to 6 which is the 1 minus column sum of $\boldsymbol{U}$.

$$\mathbf{d} = \begin{pmatrix} 0.09320 \\ 0.02705 \\ 0.01720 \\ 0.01200 \\ 0.01830 \\ 0.00970 \end{pmatrix}.$$

For $\theta(0)$,

$$\boldsymbol{V} = \begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \end{pmatrix},$$

for $\theta(1)$,

$$\boldsymbol{V} = \begin{pmatrix} 0.9999017 - 0.0005227i \\ 0.9974899 - 0.0133414i \\ 0.9919472 - 0.0428013i \\ 0.9842478 - 0.0786772i \\ 0.9705003 - 0.1327800i \\ 0.9465049 - 0.2255009i \end{pmatrix},$$

for $\theta(2^{14})$,

$$\boldsymbol{V} = \begin{pmatrix} 0.9999017 + 0.0005227i \\ 0.9974899 + 0.0133414i \\ 0.9919472 + 0.0428013i \\ 0.9842478 + 0.0786772i \\ 0.9705003 + 0.1327800i \\ 0.9465049 + 0.2255009i \end{pmatrix}.$$

Then use equation (A.21) to conclude that

$$\widehat{\Gamma}(\theta(z)) = V_1.$$

because the initial stage is set as 1. Continue to use $z = 0$, $z = 1$ and $z = 2^{14}$ as examples, then

$$\begin{aligned} \widehat{\Gamma}(\theta(0)) &= 1 \\ \widehat{\Gamma}(\theta(1)) &= 0.9999017 - 0.0005227i \\ &\dots \\ \widehat{\Gamma}(\theta(2^{14})) &= 0.9999017 + 0.0005227i \end{aligned}$$

Repeat for all frequencies. Thus one computes the set of (scalar) values $\widehat{\Gamma}(\theta(0)), \widehat{\Gamma}(\theta(1)), \dots, \widehat{\Gamma}(\theta(2^{14} - 1))$ and hence the function $\widehat{\Gamma}$.

Final step: the real part of the Inverse FFT is Γ,

$$\Gamma = \begin{pmatrix} 9.883428 \times 10^{-1} \\ 5.909013 \times 10^{-4} \\ \dots \\ 1.550632 \times 10^{-17} \end{pmatrix},$$

which is plotted in Fig 2 (only plotted to 800 offspring not to $2^{14}$).

## A.13 Definitions for Convolutions

| | |
|---|---|
| $f_a$, $0 \le f_a \le k_m$ | Mean number offspring produced by individuals in age interval $a$. $f_a = \sum_k k\, \boldsymbol{\kappa}_a(k)$, $f_a = 0$ for $a < \alpha$ and $a > \beta$. |
| $f_j$, $0 \le f_j \le k_m$ | Mean number offspring produced during one time interval by individuals in stage $j$. $f_a = \sum_k k\, \boldsymbol{\kappa}_j(k)$, $f_j = 0$ for non-reproductive stages. |
| $R_0 = \sum_a l_a\, f_a$, $a = 1, 2, \dots, \omega$ | Net Reproductive Rate, mean life time reproductive success. |
| $k_m$ | Maximum number of offspring that can be produced by an individual during one time interval. |
| $k_m + 1$ | Number of elements in a vector where each element references one possible number of offspring produced by an individual during one time interval. |
| $2k_m + 1$ | Number of elements in a vector representing number of offspring produced cumulatively during two time intervals. |
| $\boldsymbol{\delta}$ | Vector of probabilities that an individual produces a total of $k$ offspring after reproducing at 2 different ages, $\delta(k)$, conditional on being alive at each of these ages. $\boldsymbol{\delta} = \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2$, Convolution of $\boldsymbol{\kappa}_1$ and $\boldsymbol{\kappa}_2$ (see main text Method:Age-only Model for computation) |

Table A.1: Convolutions

# References


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