

Supplementary material to:

Chapter 10: Dynamics of Class-Structured Populations

From:

A Biologist's Guide to Mathematical Modeling in Ecology and Evolution

S. P. Otto and T. Day (2005)

Princeton University Press

Supplementary Material 10.1: A precise definition and derivation of reproductive value

In the text, we derived an equation for reproductive value (i.e., the left eigenvector equation) without first providing a precise definition of reproductive value. Here, we present a formal definition of the reproductive value and illustrate how this definition is tied to the left eigenvectors of a transition matrix. For simplicity we will work with model (10.1) but an analogous derivation is possible for other models as well. Importantly, the definition (and analogous derivations) can be applied to continuous-time models as well.

The reproductive value of a juvenile, $\rho_J(t)$, is defined as the total number of its descendants (both adults and juveniles) at some time, t , in the future. Similarly, the reproductive value of an adult, $\rho_A(t)$, is defined as the total number of its descendants (both adults and juveniles) at time, t . Thus, $\rho_J(t)$ and $\rho_A(t)$ are measures of a juvenile's and an adult's contribution to the population at some future point in time, t . As time passes, the number of descendants changes, so let's derive recursion equations for both $\rho_J(t)$ and $\rho_A(t)$.

Let's begin by focusing on the descendants of a juvenile. With probability p_j the juvenile becomes an adult, and with probability $1 - p_j$ it dies. Consequently, the total number of descendants of this juvenile t time steps in the future is just p_j multiplied by the total number of descendants that an adult individual leaves in the remaining $t - 1$ time steps. This quantity is given by $\rho_A(t - 1)$. Thus the recursion for $\rho_J(t)$ is $\rho_J(t) = p_j \rho_A(t - 1)$.

Next, let's focus on the descendants of an adult. With probability p_a this adult survives and then has a total of $\rho_A(t - 1)$ descendants by time step, t . This adult also produces a total of b juvenile offspring in the first time step, and these go on to leave a total of $\rho_J(t - 1)$ descendants

by time t . Thus, the recursion equation for $\rho_A(t)$ is $\rho_A(t) = b\rho_J(t-1) + p_a\rho_A(t-1)$. Putting this together with the recursion equation for $\rho_J(t)$ and writing these recursions in matrix notation yields

$$\begin{pmatrix} \rho_J(t) & \rho_A(t) \end{pmatrix} = \begin{pmatrix} \rho_J(t-1) & \rho_A(t-1) \end{pmatrix} \begin{pmatrix} 0 & b \\ p_j & p_a \end{pmatrix} \quad (\text{S10.1.1a})$$

or

$$\bar{\rho}(t) = \bar{\rho}(t-1)\mathbf{M}. \quad (\text{S10.1.1b})$$

Equation (S10.1.1) is a linear system of recursion equations that can be solved using the methods of Chapter 9. Its general solution is given by $\bar{\rho}(t) = \bar{\rho}_0\mathbf{M}^t$, but typically we are interested in the value of $\bar{\rho}(t)$ for large t (i.e., the contribution of a juvenile versus an adult to the ‘distant’ future). In this case, supposing that the long-term growth rate of the population is given by the leading eigenvalue, λ_1 , we can follow the approach of Box 9.1 to obtain the approximation

$$\bar{\rho}(t) \approx \lambda_1^t c \bar{v}_1, \quad (\text{S10.1.2})$$

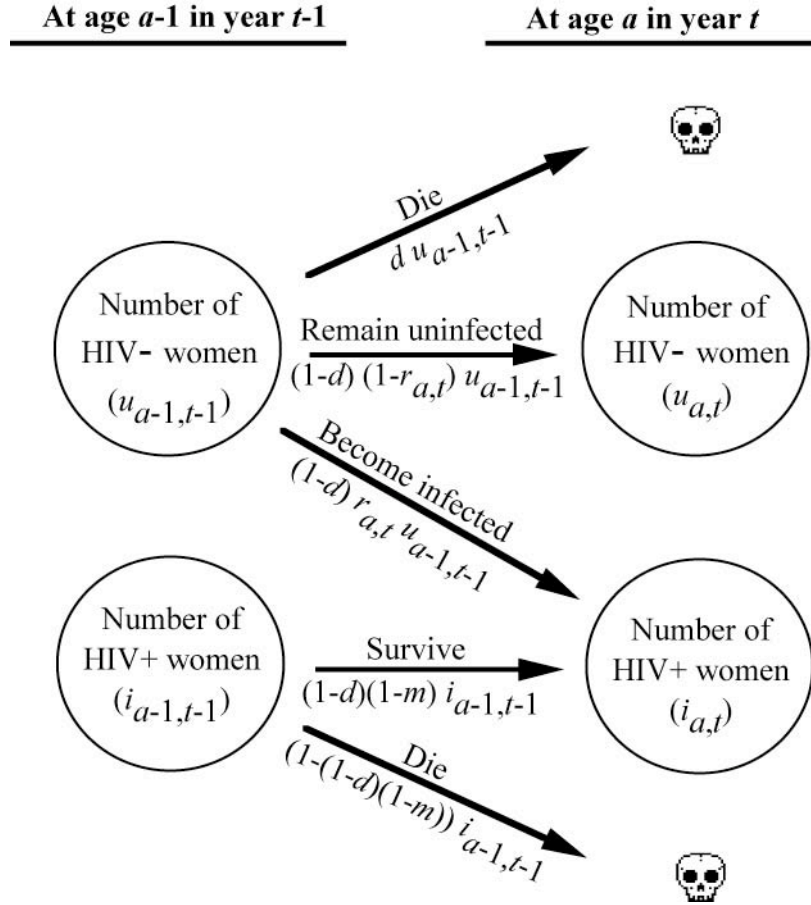
where c is the constant, $c = \rho_J(0)u_{11} + \rho_A(0)u_{21}$, \bar{v}_1 is the left eigenvector associated with λ_1 , and u_{11} and u_{21} are the first and second elements of the right eigenvector associated with λ_1 . Notice that the only vector on the right-hand side of (S10.1.2) is \bar{v}_1 , which does not change over time. We thus obtain a key result: the elements of $\bar{\rho}(t)$, the reproductive value of a juvenile and the reproductive value of an adult, are proportional to the entries of the left eigenvector associated with the leading eigenvalue.

Supplementary Material 10.2: Calculating the risk of infection with HIV using an age-structured model.

Williams *et al.* (2001) developed a model to estimate the risk that an uninfected woman in the Hlabisa district of South Africa becomes newly infected with HIV. The goal of the study was to estimate the probability per year of infection per uninfected woman as a function of her age (this probability is known as the *incidence* of HIV infection). Although this probability can be measured directly by tracking women over time, such a study takes time. Quicker estimates can be obtained by using a model to estimate the incidence of HIV infection from the fraction of infected women, for which data already exists.

To understand their model, it is worth thinking about all of the possible events that might happen over the course of a year. For each age class a and time t (both measured in years), there are a number of uninfected (HIV-) and infected (HIV+) women within the Hlabisa population; we'll label these numbers $u_{a,t}$ and $i_{a,t}$, respectively. We will measure the incidence of HIV as the fraction of women aged a that are HIV+ at time t but were HIV- in the previous year, and we will call this fraction $r_{a,t}$, for "risk". This is the parameter that we wish to infer. Each year, there will also be a fraction, d , of women who die due to causes unrelated to HIV/AIDS. This makes the simplifying assumption that background mortality does not depend on a woman's age or on the year. The fraction of HIV- women that survive each year is thus $(1-d)$. As a result of HIV/AIDS-related complications, HIV+ women have a higher risk of dying. Let m equal the fraction by which the probability of survival is reduced by HIV infection, so that the overall survival probability of HIV+ women is $(1-d)(1-m)$. Data for the median survival rate of HIV infected individuals in Africa indicates that HIV infection causes about a 9.4% reduction in survival (see references in Williams *et al.*, 2001). That is, m is approximately 0.094, regardless of age. To keep everything straight, we draw all of these possible events in a flow diagram (Figure S10.2.1).

Figure S10.2.1: Estimating the risk of acquiring HIV. Model for estimating the risk of acquiring HIV ($r_{a,t}$) from data on the prevalence of HIV (Williams *et al.* 2001). The circles represent the number of uninfected ($u_{a,t}$) and infected ($i_{a,t}$) women within the Hlabisa population of South Africa for each age class a at time t . The arrows connect these numbers from one year to the next and represent the fraction of individuals that die, become newly infected ($r_{a,t}$), or retain the same HIV status over the year.



From Figure S10.2.1, we can write down how the numbers of HIV- and HIV+ women of age a change from one year ($t-1$) to the next (t):

$$\begin{aligned} u_{a,t} &= u_{a-1,t-1}(1-d)(1-r_{a,t}) \\ i_{a,t} &= u_{a-1,t-1}(1-d)r_{a,t} + i_{a-1,t-1}(1-d)(1-m) \end{aligned} \quad (\text{S10.2.1})$$

□

(Check that these equations make sense by comparing them to Figure S10.2.1.)

Instead of describing how the numbers of each type of woman changed over time, Williams *et al.* (2001) performed a transformation. They described a new set of variables, equal

to the proportion of women of age a that were infected at time t , $P_{a,t}$. These proportions are related to the original variables by:

$$P_{a,t} = \frac{i_{a,t}}{u_{a,t} + i_{a,t}}.$$

The age-specific proportion of HIV+ women in any year can be related to the numbers of uninfected and infected individuals in the previous year as well as the model parameters by plugging equations (S10.2.1) into (S10.2.2):

$$P_{a,t} = \frac{u_{a-1,t-1}(1-d)r_{a,t} + i_{a-1,t-1}(1-d)(1-m)}{u_{a-1,t-1}(1-d)(1-r_{a,t}) + u_{a-1,t-1}(1-d)r_{a,t} + i_{a-1,t-1}(1-d)(1-m)}. \quad (\text{S10.2.3})$$

We can simplify (S10.2.3) by factoring out $(1-d)$ and adding together the first two terms in the denominator to get:

$$P_{a,t} = \frac{u_{a-1,t-1} r_{a,t} + i_{a-1,t-1} (1-m)}{u_{a-1,t-1} + i_{a-1,t-1} (1-m)}. \quad (\text{S10.2.4})$$

This simplification provides some insight: as long as both HIV- and HIV+ women are subject to the same background mortality rate (d), these deaths do not influence the relative proportions of HIV- and HIV+ women.

At this point, we have an equation in terms of proportions (on the left) and in terms of numbers (on the right). To obtain an equation only in terms of proportions, we have to transform the right-hand side as well. To do this, we need the "reverse" of equation (S10.2.2), that is, we need an equation that tells us how to write the number of infected individuals in terms of the proportion of infected individuals. To get this reverse equation for $i_{a,t}$, rearrange (S10.2.2) until you get $i_{a,t} = \frac{P_{a,t}}{1 - P_{a,t}} u_{a,t}$. This equation holds for all ages and all years, so it is also true that

$i_{a-1,t-1} = \frac{P_{a-1,t-1}}{1 - P_{a-1,t-1}} u_{a-1,t-1}$. Next use this formula for $i_{a-1,t-1}$ in (S10.2.4) to get:

$$P_{a,t} = \frac{u_{a-1,t-1} r_{a,t} + \frac{P_{a-1,t-1}}{(1 - P_{a-1,t-1})} u_{a-1,t-1} (1 - m)}{u_{a-1,t-1} + \frac{P_{a-1,t-1}}{(1 - P_{a-1,t-1})} u_{a-1,t-1} (1 - m)}. \quad (\text{S10.2.5})$$

Multiplying through by $(1 - P_{a-1,t-1})$ to get rid of the fractions within fractions and dividing by $u_{a-1,t-1}$, we get an equation relating the risk of contracting HIV ($r_{a,t}$) to the proportion of infected women in each age class:

$$\square \quad P_{a,t} = \frac{(1 - P_{a-1,t-1}) r_{a,t} + P_{a-1,t-1} (1 - m)}{1 - m P_{a-1,t-1}}. \quad (\text{S10.2.6})$$

Equation (S10.2.6) allows us to infer the age-specific risk ($r_{a,t}$) from observed data on the proportion of HIV infected women ($P_{a,t}$) in the Hlabisa population. This goal is made easier if we rearrange equation (S10.2.6) to give us an equation directly for $r_{a,t}$:

$$\square \quad r_{a,t} = \frac{P_{a,t} (1 - m P_{a-1,t-1}) - P_{a-1,t-1} (1 - m)}{(1 - P_{a-1,t-1})}. \quad (\text{S10.2.7})$$

Unfortunately, prevalence data were only available for 1998. In other words, Williams *et al.* (2001) had data for all age classes in a year ($P_{a,1998}$) but no data for the previous year ($P_{a,1997}$). Because the overall prevalence of HIV increased by a factor 1.45 between 1997 and 1998, Williams *et al.* (2001) assumed that this was also true for each age class, so that $P_{a-1,t} \approx 1.45 P_{a-1,t-1}$. With this assumption, we can estimate the probability that a woman of age a at time t has contracted HIV during the past year:

$$r_{a,t} \approx \frac{P_{a,t} \left(1 - m \frac{P_{a-1,t}}{1.45} \right) - \frac{P_{a-1,t}}{1.45} (1 - m)}{\left(1 - \frac{P_{a-1,t}}{1.45} \right)}. \quad (\text{S10.2.8})$$

Given mortality estimates for HIV (m), prevalence data ($P_{a,1998}$), and equation (S10.2.8), we can estimate the risk of contracting HIV for women as a function of their age ($r_{a,1998}$, see Figure 1.7a).

This example illustrates how age-structured models can be used to infer parameters of interest from data. As an aside, our results differ slightly from those presented by Williams *et al.* (2001). Rather than performing an explicit transformation, they developed a recursion for the proportion of HIV infected women ($P_{a,t}$) that effectively assumed that the term $\left(1 - m \frac{P_{a-1,t}}{1.45}\right)$ in equation (S10.2.8) was one. This approximation would be reasonable if m and $P_{a-1,t}$ were both small. In South Africa, however, the prevalence of HIV has reached high levels (Figure 1.7a). Thus, it is safer to use the more accurate result, (S10.2.8), without further approximation. Plus, it's a good rule of thumb not to make approximations unless necessary. In this case, the approximations used by Williams *et al.* (2001) lead to the same overall picture but generate slightly different estimates of risk (comparing Figure 1.7a to their Figure 3).