

## Appendix

In an age-based demography, the information about the life cycle can be represented by a Leslie matrix such as:

$$\begin{array}{ccccc}
 0 & F_2 & F_3 & F_4 & F_5 \\
 p_1 & 0 & 0 & 0 & 0 \\
 0 & p_2 & 0 & 0 & 0 \\
 0 & 0 & p_3 & 0 & 0 \\
 0 & 0 & 0 & p_4 & 0
 \end{array} = \mathbf{L}.$$

The entries refer to transitions between one state (the columns) and another state (the rows). The F values are the age-specific fecundity of the population, while the p's are the age specific probability of survival to the next age class. Individuals of age 1 have a probability of  $p_1$  of surviving to age 2. An individual of age 4 will produce  $F_4$  individuals of age 1. The number of individuals, at some time  $t$ , in each of the year cohorts is:  $(N_0 \ N_1 \ N_2 \ N_3 \ N_4)^T = \mathbf{n}_t$ . {Note: This is actually a column vector, but representing the column vector takes a lot of space. Instead I will use T to indicate the transpose.} Post-multiplying the Leslie matrix by the population vector gives the number of individuals in each of the age groups in the next year  $\mathbf{n}_2 = \mathbf{L}\mathbf{n}_1$ . If this process is repeated the age distribution is  $\mathbf{n}_3 = \mathbf{L}\mathbf{n}_2$ . If this process continues to be repeated (using the assumption that the age related patterns of mortality and fecundity are consistent) it will rapidly converge on the stable age distribution. There is a scalar value,  $\lambda$ , for which the following is true:  $\lambda\mathbf{n} = \mathbf{L}\mathbf{n}$ . Multiplying the Leslie matrix by a particular vector is equal to multiplying the same vector by a constant. The vector is the stable age distribution of the population represented by the Leslie matrix and the  $\lambda$  is the growth 'rate' of the population (it is actually a multiplicative constant). These values are the dominant eigenvector and eigenvalue of the Leslie matrix and can be obtained from standard mathematical packages.

This procedure is easily generalized to size or stage-based demography. These life cycles are more flexible. As for age, it may be impossible for stages to reverse. For example, stages may be queen, incipient colony, immature colony, mature colony. However, colonies that are categorized by size can become larger, smaller or remain the same size. In the matrix below colonies can stay the same size (the entries on the diagonal), increase in size (below the diagonal) or contribute to size categories that are smaller (above the diagonal).

$$\begin{matrix}
 F_1 & F_2 & F_3 & F_4 & F_5 \\
 p_{11} & p_{12} & p_{13} & 0 & 0 \\
 0 & p_{22} & p_{23} & p_{24} & 0 \\
 0 & 0 & p_{33} & p_{34} & p_{35} \\
 0 & 0 & 0 & p_{44} & p_{45}
 \end{matrix} = \mathbf{S}.$$

There is a corresponding vector for the size or stage distribution, which we can still call  $\mathbf{n}$ . Either by repeatedly post-multiplying the stage transition matrix until it reaches stable values, or by extracting the dominant eigenvalues and eigenvectors of the matrix  $\mathbf{S}$  we can again find the growth ‘rate’ of the population and the stable size or stage distribution. A major difference between the stable age and size distribution is that the entries of the stable age distribution are a non-increasing function of age. The proportion of the population in successively older age categories must decline. If the age distribution is not declining, then the stable age distribution has not been achieved. The same is not true for the stable size distribution. If colonies rapidly grow to a mature size and then remain at that size for a relatively long time, they will build up in this category which will be the most common size. This means that it is possible for there to be a modal size or stage in a population.

**Getting age information from stage-based data.** It is often very useful to obtain information about age-related patterns of demography from data that are not based on age. For example, a study may have information about the size distribution of colonies or the distribution of life cycle stages (e.g. queens, incipient colonies, reproductive colonies, etc.) and not have information about the age of the colonies. It is still possible to extract certain age-related information from these data (see Cochran & Ellner 1992 and Caswell 2002 for description). If we are using age or stage-based transition matrices to represent the demography this is the same as the assumption that the life cycle of an organism can be represented as a Markov chain with an absorbing state (death). The reason that I say “we can often make this assumption,” is because colonies that bud or swarm (hesmosis) can potentially be of unlimited lifespan. In this case we must limit our consideration



|   |      |      |      |      |      |      |      |      |     |
|---|------|------|------|------|------|------|------|------|-----|
| 0 | 0.81 | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0   |
| 0 | 0    | 0.87 | 0    | 0    | 0    | 0    | 0    | 0    | 0   |
| 0 | 0    | 0    | 0.91 | 0    | 0    | 0    | 0    | 0    | 0   |
| 0 | 0    | 0    | 0    | 0.96 | 0    | 0    | 0    | 0    | 0   |
| 0 | 0    | 0    | 0    | 0    | 0.94 | 0    | 0    | 0    | 0   |
| 0 | 0    | 0    | 0    | 0    | 0    | 0.93 | 0    | 0    | 0   |
| 0 | 0    | 0    | 0    | 0    | 0    | 0    | 0.84 | 0    | 0   |
| 0 | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0.83 | 0.9 |

As an example, we can consider the age based transition matrix for *P. occidentalis* shown here. The matrix represents the probability that a colony survives from one age to the next. The only difference is the last entry in the matrix which gives the probability that a colony in the largest age class will continue to survive. This is the solution to the problem that the maximum lifespan of the colonies is not just 10 years, even if the data do not extend beyond 10 years, but it makes the matrix a hybrid of strictly age-related terms and stage-related terms (the last value in the analysis will then refer to colonies of ten or more years of age). If we find  $(\mathbf{I}-\mathbf{T})^{-1}$ , then we obtain the number of time units, years in this case, that a colony is expected to spend in each age category  $j$ , given it is currently in age category  $i$ .

|      |      |      |      |      |   |   |   |   |   |
|------|------|------|------|------|---|---|---|---|---|
| 1    | 0    | 0    | 0    | 0    | 0 | 0 | 0 | 0 | 0 |
| 0.72 | 1    | 0    | 0    | 0    | 0 | 0 | 0 | 0 | 0 |
| 0.58 | 0.81 | 1    | 0    | 0    | 0 | 0 | 0 | 0 | 0 |
| 0.51 | 0.71 | 0.87 | 1    | 0    | 0 | 0 | 0 | 0 | 0 |
| 0.46 | 0.64 | 0.79 | 0.91 | 1    | 0 | 0 | 0 | 0 | 0 |
| 0.44 | 0.62 | 0.76 | 0.87 | 0.96 | 1 | 0 | 0 | 0 | 0 |

|      |      |      |      |      |      |      |      |     |    |
|------|------|------|------|------|------|------|------|-----|----|
| 0.42 | 0.58 | 0.71 | 0.82 | 0.90 | 0.94 | 1    | 0    | 0   | 0  |
| 0.39 | 0.54 | 0.66 | 0.76 | 0.84 | 0.87 | 0.93 | 1    | 0   | 0  |
| 0.33 | 0.45 | 0.56 | 0.64 | 0.71 | 0.73 | 0.78 | 0.84 | 1   | 0  |
| 2.7  | 3.75 | 4.63 | 5.32 | 5.85 | 6.09 | 6.48 | 6.97 | 8.3 | 10 |

For this matrix the entries refer to the amount of time that a colony of a given age is expected to spend in each subsequent age. For example, colonies spend 1 year in each age that they are in, while colonies of age 10 or more, which are given a probability of death of 0.1, spend 10 years in the last stage. Colonies that are currently 5 years old are expected to spend 0.84 years as 8 year old colonies. The expectation is less than one year because some of the colonies will die before reaching their eighth year. The sum across rows is the life expectancy, (7.6 9.1 10.0 10.3 10.3 9.6 9.2 8.8 9.3 10).

In addition to the life expectancy, one can obtain an estimate of the age-specific survival to time  $t$ , given a particular starting stage by finding  $T^t$ . This is done by iteratively multiplying the matrix. The sum across rows is the probability that the colony is in one of the activity/size stages and therefore not dead. Scherba's data (1963) can be used to form this transition matrix where the entries refer to his activity categories 0-4. Calculating  $(I-T)^{-1}$  gives the life expectancy for a colony, given that it is currently in a particular stage shown in the text. By finding  $T^t$  for increasing  $t$ , we get the age-specific survival, conditioned on the assumption that colonies start in category 1 shown in Figure 2.

|      |       |       |       |       |
|------|-------|-------|-------|-------|
| 0.16 | 0.131 | 0.018 | 0     | 0     |
| 0.16 | 0.278 | 0.16  | 0.034 | 0     |
| 0.15 | 0.16  | 0.51  | 0.21  | 0.022 |
| 0    | 0.045 | 0.21  | 0.29  | 0.34  |
| 0    | 0     | 0.012 | 0.11  | 0.64  |

For harvester ants a size specific transition matrix for one year showing the probability of a colony changing from one size to another is given below:

|  | Size = 5 | 6    | 7    | 8    | 9    | 10    | 11+   |
|--|----------|------|------|------|------|-------|-------|
|  | 0.18     | 0.07 | 0.04 | 0.01 | 0    | 0     | 0     |
|  | 0.18     | 0.18 | 0.12 | 0.05 | 0    | 0     | 0.003 |
|  | 0.2      | 0.24 | 0.13 | 0.14 | 0.02 | 0.004 | 0.003 |
|  | 0.18     | 0.19 | 0.26 | 0.21 | 0.05 | 0.004 | 0     |
|  | 0        | 0.06 | 0.19 | 0.28 | 0.34 | 0.07  | 0.003 |
|  | 0        | 0    | 0.07 | 0.14 | 0.41 | 0.53  | 0.07  |
|  | 0        | 0    | 0    | 0.01 | 0.07 | 0.39  | 0.9   |

One obtains the size-specific life expectancy, as above ( $= (\mathbf{I}-\mathbf{T})^{-1}$ ): (10.9 12.1 16.4 19.4 26.2 33.1 34.8), and an estimate of the age-specific survival by iterating the matrix (Figure 2).

The fertility matrix for the age-based survival of *P. occidentalis* is just a matrix with (0 0 0 0 .05 .3 .38 .5 .66 .66) in the top row and zeroes in all other cells. This gives the probability that a colony reproduces as a function of age. The amount of reproduction per reproductive event is unrelated to age or size. To change the total number of offspring per event requires that these values are all multiplied by a constant. Including this constant does not have an effect on the analyses of age/stage structure, ages-within stage or reproductive value (see below). The Leslie matrix is simply the sum of the **F** and the **T** matrix Similarly the **F** matrix for sizes is:

|   |   |   |   |   |       |       |
|---|---|---|---|---|-------|-------|
| 0 | 0 | 0 | 0 | 0 | 0.05  | 0.125 |
| 0 | 0 | 0 | 0 | 0 | 0.072 | 0.18  |
| 0 | 0 | 0 | 0 | 0 | 0.05  | 0.125 |
| 0 | 0 | 0 | 0 | 0 | 0.026 | 0.065 |
| 0 | 0 | 0 | 0 | 0 | 0.001 | 0.003 |
| 0 | 0 | 0 | 0 | 0 | 0     | 0     |
| 0 | 0 | 0 | 0 | 0 | 0     | 0     |

This is the probability that colonies of a given size (row) will be produced by the reproductive colonies (the columns). Remember that it is possible for colonies to enter the population at sizes that are larger than the smallest size.

The age-specific reproductive value,  $v$ , can be calculated directly from the Leslie matrix as the dominant eigenvector of  $L^T$  (Caswell 2002). We can obtain the stage-specific ‘reproductive value’ by finding the dominant eigenvector of the transpose of the stage transition matrix. It is

difficult to say what relationship this value has to reproductive value in the sense of Fisher. We could convert this to age specific reproductive value if we could associate an age with a particular stage. However, colonies of many different ages can be in a particular size class—they may have grown directly to this size or they may have once been larger and have decreased to this size class. We can determine the distribution of ages within any particular stage and thus the mean age of individuals within a given stage.

To compute the age within-stage distribution relies on manipulating the stable stage distribution (see Boucher 1997 and, again Caswell 2002 for a discussion). The number of new colonies at a given time is proportional to the stage distribution (the dominant eigenvector of the  $\mathbf{S}$  matrix) times  $\mathbf{F}$ , the fertility matrix. The number of new colonies last year is proportional to this product divided by the growth rate of the population, the dominant eigenvalue of the  $\mathbf{S}$  matrix. They are currently in stages that are determined by the transition matrix,  $\mathbf{T}$ . To determine the current fate of individuals born two years ago requires dividing by growth rate of the population squared and requires two passages through the transition matrix to determine the current stage. Similar reasoning applies for times into the past, with the result that it is possible to estimate the frequency distribution of ages in a given stage and compute the mean age of individuals in any stage.