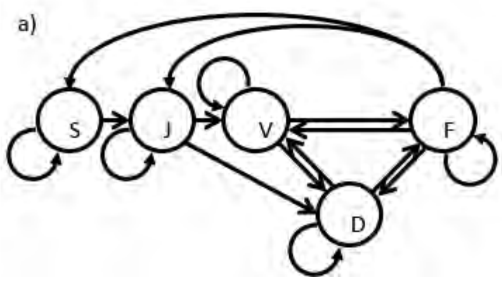
Chapter 4
Raw Matrix Projection Models

Matrix projection models (MPMs) are representations of the dynamics of a population across all life history stages deemed relevant, across the most relevant time interval (typically one year, but sometimes different, and assumed to be consistent within each analysis). In the simplest MPMs, matrix elements (a_{kj}) show either the probability of transition for an individual in stage j at occasion t (along the columns), to stage k at occasion t+1 (along the rows), or the mean rate of production of offspring into stage k at occasion t+1 (along the rows) by adult individuals in reproductive stage j in occasion t (along the columns). Conceptually, each individual is in a particular stage in the instance of monitoring or observation, and then either dies or completes a transition in the interval between that observation occasion and the next. Death is not an explicit life stage and so is not modeled as such, instead becoming a potential endpoint of each transition.

a)



b)

time t (columns); time t+1 (rows)

	From S	From J	From V	From D	From F
To S	S_{SS}	0	0	0	F_{SF}
To J	S_{JS}	S_{JJ}	0	0	F_{JF}
To V	0	S_{VJ}	S_{VV}	S_{VD}	S_{VF}
To D	0	S_{DJ}	S_{DV}	S_{DD}	S_{DF}
To F	0	0	S_{FV}	S_{FD}	S_{FF}

Figure 4.1: MPM for *Cypripedium candidum*, a North American herbaceous plant

Figure 4.1 and equation 4.1 shows a simple matrix projection with a matrix that assumes 5 stages in the *Cypripedium candidum* life cycle. These stages are dormant seed (S), juvenile (J, comprised of protocorms and seedlings), non-flowering but sprouting adult (V), non-sprouting adult (D), and flowering adult (F). We project a column vector of numbers of individuals alive in each stage at some time (e.g., $n_{1,S}$ is the number of individuals in stage S in occasion 1) a single time step forward using standard matrix multiplication with the projection matrix. The product is another column vector showing the predicted numbers of individuals alive in each stage in the next occasion (e.g., $n_{2,S}$ is the number of individuals in stage S in occasion 2).

$$\begin{bmatrix} n_{2,S} \\ n_{2,J} \\ n_{2,V} \\ n_{2,D} \\ n_{2,F} \end{bmatrix} = \begin{bmatrix} S_{SS} & 0 & 0 & 0 & F_{SF} \\ S_{JS} & S_{JJ} & 0 & 0 & F_{JF} \\ 0 & S_{VJ} & S_{VV} & S_{VD} & S_{VF} \\ 0 & S_{DJ} & S_{DV} & S_{DD} & S_{DF} \\ 0 & 0 & S_{FV} & S_{FD} & S_{FF} \end{bmatrix} \begin{bmatrix} n_{1,S} \\ n_{1,J} \\ n_{1,V} \\ n_{1,D} \\ n_{1,F} \end{bmatrix} \tag{4.1}$$

Given this, the total population size in any occasion is the sum of the numbers of individuals in all stages in that occasion, or in other words the sum of the elements in the column vector. The true discrete population growth rate (λ) is calculated as the ratio of the true total population size in occasion t+1 to the true total population size in occasion t. Naturally, projections are estimates, so the estimated population growth rate ($\hat{\lambda}$) can be calculated as either the ratio of projected population size in time t+1 to projected population size in time t, or as the dominant eigenvalue of the projection matrix. In the latter case, estimated $\hat{\lambda}$ is actually the expected population growth rate assuming that the population is at stable stage equilibrium, and so may differ dramatically from the true λ depending on conditions.

How does one actually estimate the elements composing the matrix? First of all, we note that there are two primary sorts of elements - survival-transition elements, and fecundity elements. The former are probabilities denoting the chance of transitioning from one stage in time t to another in stage t+1, and the latter are rates denoting the number of offspring produced per reproductive individual in time t that survive to time t+1 (this is the pre-breeding model as described in Chapter 2, while fecundity in the post-breeding case would equal the survival of the reproductive parent from time t to time t+1 multiplied by the number of offspring produced). In the **raw MPM**, which is the first and still dominant kind of MPM, survival-transition elements are estimated as follows:

$$a_{kj} = \frac{n_{kj}}{\sum_{i=1}^{d} n_{ij}} \tag{4.2}$$

Here, we can refer to matrix elements as a_{kj}, where the element represents the rate at which individuals transition to stage k in occasion t+1 after having been stage j in occasion t. Then, n_{kj} is the number of individuals making this transition, d is the number of stages plus death in the life history model ($d = m + 1$, where m is the number of life history stages), and so the denominator represents the total number of individuals alive in stage j in time t regardless of whether they are alive or dead in time t+1. For example, if 100 individuals are alive in stage D in year 2010, and 20 of these are alive in stage D in year 2011, as are a further 40 in stage V and a further 25 in stage F, then the associated transition probabilities are 0.20, 0.40, and 0.25, respectively. The overall survival probability for stage D is the sum of these transitions, or 0.85, with 15% of individuals alive in 2010 dying by the time of the monitoring occasion in 2011. Fecundity in the pre-breeding model can be estimated as:

$$a_{kj} = s_k \frac{\sum_{i=1}^{n_{.j}} fec_i}{n_{.j}} \tag{4.3}$$

Here, s_k is the survival of newborns to the first year stage from time t to time t+1, fec_i is the actual fecundity of individual i in time t, $n_{.j}$ is the number of reproductive adults in stage j at time t, and the right-hand term, $\frac{\sum_{i=1}^{n_{.j}} fec_i}{n_{.j}}$, is the average offspring production per reproductive adult.

Developing raw MPMs with `lefko3`

In package `lefko3`, the primary function creating these raw MPMs is `rlefko2()`. In the code below, we use it to create a series of raw matrices for our *Cypripedium candidum* dataset. In our call to `rlefko2()`, we need to provide R at the very least with the dataset that it will use to estimate the matrix with (`data = cypraw_v1`), the stageframe identifying stages (`stageframe = cypframe_raw`), and the names of the variables coding for stage in times t+1 and t (`stages = c("stage3", "stage2")`). Our call also includes a statement that we wish to estimate matrices for all occasions possible (`year = "all"`, which also requires the identification of the monitoring time variable, `yearcol = "year2"`), and we will also specify that we wish matrices to be estimated for all three patches (`patch = "all"`, which also requires the identification of the patch variable, `patchcol = "patchid"`). This function assumes default variable names for most of the status variables in *hfv* datasets, and since we are using size variables other than the defaults, we need to supply those names (`size = c("size3added", "size2added")`). Finally, we will supply our supplement table (`supplement = cypsupp2_raw`), and note the name of the variable coding for individual identity (`indivcol = "individ"`).

```
cypmatrix2rp <- rlefko2(data = cypraw_v1, stageframe = cypframe_raw,
  year = "all", patch = "all", stages = c("stage3", "stage2"),
  size = c("size3added", "size2added"), supplement = cypsupp2_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ")

cypmatrix2rp
> $A
> $A$`1`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]  [,8]         [,9] [,10]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 500.0 1666.6666667     0
```

```
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 500.0 1666.6666667     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000   0.0    0.0000000     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000   0.0    0.0000000     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000   0.0    0.0000000     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.0    0.0000000     0
>  [7,] 0.00  0.0  0.0  0.0 0.6363636    0 0.6363636   0.2    0.0000000     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.2727273   0.6    0.6666667     1
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.2    0.3333333     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.0    0.0000000     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.0    0.0000000     0
>       [,11]
>  [1,]     0
>  [2,]     0
>  [3,]     0
>  [4,]     0
>  [5,]     0
>  [6,]     0
>  [7,]     0
>  [8,]     0
>  [9,]     0
> [10,]     0
> [11,]     0
> 
> $A$`2`
>       [,1] [,2] [,3] [,4]  [,5] [,6]    [,7]         [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.000    0 312.500 1111.1111111 1250     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.000    0 312.500 1111.1111111 1250     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.000    0   0.000    0.0000000    0     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.000    0   0.000    0.0000000    0     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.050    0   0.000    0.0000000    0     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.125    0   0.125    0.0000000    0     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.750    0   0.750    0.3333333    0     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.000    0   0.000    0.4444444    0     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.000    0   0.000    0.2222222    1     0     0
> [10,] 0.00  0.0  0.0  0.0 0.000    0   0.000    0.0000000    0     0     0
> [11,] 0.00  0.0  0.0  0.0 0.000    0   0.000    0.0000000    0     0     0
> 
> $A$`3`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7] [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000    0 0.00     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.6666667    0 0.6666667    0 0.00     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    1 0.3333333    1 0.25     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.75     0     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
> 
> $A$`4`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]      [,8]      [,9] [,10]
```

```
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000 0.0000000 0.0000000     0
>  [6,] 0.00  0.0  0.0  0.0 0.1666667    0 0.1666667 0.2222222 0.0000000     0
>  [7,] 0.00  0.0  0.0  0.0 0.5000000    0 0.5000000 0.4444444 0.3333333     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.3333333 0.3333333     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.3333333     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>       [,11]
>  [1,]     0
>  [2,]     0
>  [3,]     0
>  [4,]     0
>  [5,]     0
>  [6,]     0
>  [7,]     0
>  [8,]     0
>  [9,]     0
> [10,]     0
> [11,]     0
>
> $A$`5`
>       [,1] [,2] [,3] [,4]      [,5]      [,6]      [,7]  [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000 500.0 5000     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000 500.0 5000     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000 0.0000000 0.0000000   0.0    0     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000 0.0000000 0.0000000   0.0    0     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000 0.0000000 0.0000000   0.0    0     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000   0.0    0     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.4444444 0.3333333 0.4444444   0.0    0     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000 0.6666667 0.4444444   0.6    0     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000   0.0    0     0     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000   0.0    1     0     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000   0.0    0     0     0
>
> $A$`6`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]        [,8]   [,9]   [,10]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 166.6666667 625.00 1875.00
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 166.6666667 625.00 1875.00
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000   0.0000000   0.00    0.00
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000   0.0000000   0.00    0.00
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000   0.0000000   0.00    0.00
>  [6,] 0.00  0.0  0.0  0.0 0.1111111    0 0.1111111   0.0000000   0.00    0.00
>  [7,] 0.00  0.0  0.0  0.0 0.6666667    0 0.6666667   0.2666667   0.00    0.00
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.1111111   0.6000000   0.50    0.00
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.1333333   0.25    0.25
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.1111111   0.0000000   0.25    0.50
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.0000000   0.00    0.25
>       [,11]
>  [1,]     0
```

```
>  [2,]     0
>  [3,]     0
>  [4,]     0
>  [5,]     0
>  [6,]     0
>  [7,]     0
>  [8,]     0
>  [9,]     0
> [10,]     0
> [11,]     0
>
> $A$`7`
>       [,1] [,2] [,3] [,4]       [,5] [,6]       [,7]         [,8]    [,9]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000    0 0.00000000 1.666667e+03 4375.00
>  [2,] 0.15  0.0  0.0  0.0 0.00000000    0 0.00000000 1.666667e+03 4375.00
>  [3,] 0.00  0.1  0.0  0.0 0.00000000    0 0.00000000 0.000000e+00    0.00
>  [4,] 0.00  0.0  0.1  0.0 0.00000000    0 0.00000000 0.000000e+00    0.00
>  [5,] 0.00  0.0  0.0  0.1 0.05000000    0 0.00000000 0.000000e+00    0.00
>  [6,] 0.00  0.0  0.0  0.0 0.09090909    0 0.09090909 8.333333e-02    0.00
>  [7,] 0.00  0.0  0.0  0.0 0.45454545    0 0.45454545 2.500000e-01    0.25
>  [8,] 0.00  0.0  0.0  0.0 0.00000000    1 0.36363636 5.833333e-01    0.50
>  [9,] 0.00  0.0  0.0  0.0 0.00000000    0 0.00000000 0.000000e+00    0.25
> [10,] 0.00  0.0  0.0  0.0 0.00000000    0 0.00000000 0.000000e+00    0.00
> [11,] 0.00  0.0  0.0  0.0 0.00000000    0 0.00000000 0.000000e+00    0.00
>         [,10] [,11]
>  [1,] 5000.00 17500
>  [2,] 5000.00 17500
>  [3,]    0.00     0
>  [4,]    0.00     0
>  [5,]    0.00     0
>  [6,]    0.00     0
>  [7,]    0.00     0
>  [8,]    0.50     0
>  [9,]    0.25     0
> [10,]    0.25     0
> [11,]    0.00     1
>
> $A$`8`
>       [,1] [,2] [,3] [,4]      [,5] [,6]        [,7]     [,8]   [,9] [,10]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 277.7777778 781.2500 6250.0  5000
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 277.7777778 781.2500 6250.0  5000
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0   0.0000000   0.0000    0.0     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0   0.0000000   0.0000    0.0     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0   0.0000000   0.0000    0.0     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000    0   0.0000000   0.1875    0.0     0
>  [7,] 0.00  0.0  0.0  0.0 0.3333333    1   0.3333333   0.3125    0.0     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0   0.3333333   0.3750    0.5     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0   0.1111111   0.0625    0.0     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0   0.0000000   0.0625    0.5     1
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0   0.0000000   0.0000    0.0     0
>       [,11]
>  [1,] 10000
>  [2,] 10000
```

```
> [3,]      0
> [4,]      0
> [5,]      0
> [6,]      0
> [7,]      0
> [8,]      0
> [9,]      0
> [10,]     1
> [11,]     0
>
> $A$`9`
>       [,1] [,2] [,3] [,4]      [,5]      [,6]      [,7]  [,8] [,9]   [,10]
> [1,]  0.03  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000 250.0  0.0 1250.00
> [2,]  0.15  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000 250.0  0.0 1250.00
> [3,]  0.00  0.1  0.0  0.0 0.0000000 0.0000000 0.0000000   0.0  0.0    0.00
> [4,]  0.00  0.0  0.1  0.0 0.0000000 0.0000000 0.0000000   0.0  0.0    0.00
> [5,]  0.00  0.0  0.0  0.1 0.0500000 0.0000000 0.0000000   0.0  0.0    0.00
> [6,]  0.00  0.0  0.0  0.0 0.1818182 0.3333333 0.1818182   0.0  0.0    0.00
> [7,]  0.00  0.0  0.0  0.0 0.2727273 0.3333333 0.2727273   0.2  0.0    0.00
> [8,]  0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.4545455   0.2  0.5    0.00
> [9,]  0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000   0.4  0.5    0.50
> [10,] 0.00  0.0  0.0  0.0 0.0000000 0.3333333 0.0000000   0.0  0.0    0.25
> [11,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000   0.0  0.0    0.25
>       [,11]
> [1,]      0
> [2,]      0
> [3,]      0
> [4,]      0
> [5,]      0
> [6,]      0
> [7,]      0
> [8,]      0
> [9,]      0
> [10,]     0
> [11,]     0
>
> $A$`10`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]  [,8]        [,9] [,10]
> [1,]  0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000 714.2857143  1250
> [2,]  0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000 714.2857143  1250
> [3,]  0.00  0.1  0.0  0.0 0.0000000    0 0.0000000 0.000   0.0000000     0
> [4,]  0.00  0.0  0.1  0.0 0.0000000    0 0.0000000 0.000   0.0000000     0
> [5,]  0.00  0.0  0.0  0.1 0.0500000    0 0.0000000 0.000   0.0000000     0
> [6,]  0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000   0.0000000     0
> [7,]  0.00  0.0  0.0  0.0 0.5714286    1 0.5714286 0.125   0.0000000     0
> [8,]  0.00  0.0  0.0  0.0 0.0000000    0 0.2857143 0.750   0.0000000     0
> [9,]  0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.125   0.7142857     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000   0.2857143     1
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000   0.0000000     0
>       [,11]
> [1,]   2500
> [2,]   2500
> [3,]      0
```

```
>  [4,]     0
>  [5,]     0
>  [6,]     0
>  [7,]     0
>  [8,]     0
>  [9,]     0
> [10,]     0
> [11,]     1
>
> $A$`11`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]   [,8]        [,9] [,10]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 625.00 833.3333333     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 625.00 833.3333333     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000   0.00   0.0000000     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000   0.00   0.0000000     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000   0.00   0.0000000     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.00   0.0000000     0
>  [7,] 0.00  0.0  0.0  0.0 0.6666667    0 0.6666667   0.25   0.0000000     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.3333333   0.50   0.3333333     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.25   0.6666667     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.00   0.0000000     1
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.00   0.0000000     0
>       [,11]
>  [1,]  7500
>  [2,]  7500
>  [3,]     0
>  [4,]     0
>  [5,]     0
>  [6,]     0
>  [7,]     0
>  [8,]     0
>  [9,]     0
> [10,]     0
> [11,]     1
>
> $A$`12`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]      [,8]         [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.00    0 0.00 0.0000000 4166.6666667  1250  5000
>  [2,] 0.15  0.0  0.0  0.0 0.00    0 0.00 0.0000000 4166.6666667  1250  5000
>  [3,] 0.00  0.1  0.0  0.0 0.00    0 0.00 0.0000000    0.0000000     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.00    0 0.00 0.0000000    0.0000000     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.05    0 0.00 0.0000000    0.0000000     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000    0.0000000     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.75    0 0.75 0.1666667    0.0000000     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.8333333    0.6666667     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000    0.3333333     1     0
> [10,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000    0.0000000     0     1
> [11,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000    0.0000000     0     0
>
> $A$`13`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]         [,8]         [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.00    0 0.00 1071.4285714 2500.0000000  2500     0
>  [2,] 0.15  0.0  0.0  0.0 0.00    0 0.00 1071.4285714 2500.0000000  2500     0
```

```
>  [3,] 0.00  0.1  0.0  0.0 0.00    0 0.00    0.0000000    0.0000000     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.00    0 0.00    0.0000000    0.0000000     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.05    0 0.00    0.0000000    0.0000000     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.00    0 0.00    0.0000000    0.0000000     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.50    0 0.50    0.0000000    0.3333333     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.00    0 0.25    0.5714286    0.3333333     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.00    0 0.00    0.2857143    0.3333333     0     0
> [10,] 0.00  0.0  0.0  0.0 0.00    0 0.00    0.1428571    0.0000000     1     0
> [11,] 0.00  0.0  0.0  0.0 0.00    0 0.00    0.0000000    0.0000000     0     0
>
> $A$`14`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]        [,8]      [,9] [,10]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 416.6666667 0.0000000   0.0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 416.6666667 0.0000000   0.0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000   0.0000000 0.0000000   0.0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000   0.0000000 0.0000000   0.0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000   0.0000000 0.0000000   0.0
>  [6,] 0.00  0.0  0.0  0.0 0.3333333    0 0.3333333   0.1666667 0.0000000   0.0
>  [7,] 0.00  0.0  0.0  0.0 0.3333333    0 0.3333333   0.1666667 0.3333333   0.0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.3333333 0.3333333   0.5
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.3333333   0.3333333 0.3333333   0.0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.0000000 0.0000000   0.0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000   0.0000000 0.0000000   0.5
>       [,11]
>  [1,]     0
>  [2,]     0
>  [3,]     0
>  [4,]     0
>  [5,]     0
>  [6,]     0
>  [7,]     0
>  [8,]     0
>  [9,]     0
> [10,]     0
> [11,]     0
>
> $A$`15`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.00  0.0 0.00 0.00  625     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.00  0.0 0.00 0.00  625     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.00  0.0 0.00 0.00    0     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.00  0.0 0.00 0.00    0     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.05  0.0 0.00 0.00    0     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.00  0.0 0.00 0.00    0     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.25  0.5 0.25 0.00    0     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.00  0.5 0.75 0.50    0     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.00  0.0 0.00 0.25    1     0     0
> [10,] 0.00  0.0  0.0  0.0 0.00  0.0 0.00 0.25    0     0     0
> [11,] 0.00  0.0  0.0  0.0 0.00  0.0 0.00 0.00    0     0     1
>
>
> $U
> $U$`1`
```

```
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7] [,8]      [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000  0.0 0.0000000     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000  0.0 0.0000000     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000  0.0 0.0000000     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000  0.0 0.0000000     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000  0.0 0.0000000     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000  0.0 0.0000000     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.6363636    0 0.6363636  0.2 0.0000000     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.2727273  0.6 0.6666667     1     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000  0.2 0.3333333     0     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000  0.0 0.0000000     0     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000  0.0 0.0000000     0     0
>
> $U$`2`
>       [,1] [,2] [,3] [,4]  [,5] [,6]  [,7]      [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.000    0 0.000 0.0000000    0     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.000    0 0.000 0.0000000    0     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.000    0 0.000 0.0000000    0     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.000    0 0.000 0.0000000    0     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.050    0 0.000 0.0000000    0     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.125    0 0.125 0.0000000    0     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.750    0 0.750 0.3333333    0     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.000    0 0.000 0.4444444    0     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.000    0 0.000 0.2222222    1     0     0
> [10,] 0.00  0.0  0.0  0.0 0.000    0 0.000 0.0000000    0     0     0
> [11,] 0.00  0.0  0.0  0.0 0.000    0 0.000 0.0000000    0     0     0
>
> $U$`3`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7] [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000    0 0.00     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.6666667    0 0.6666667    0 0.00     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    1 0.3333333    1 0.25     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.75     0     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000    0 0.00     0     0
>
> $U$`4`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]      [,8]      [,9] [,10]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000 0.0000000 0.0000000     0
>  [6,] 0.00  0.0  0.0  0.0 0.1666667    0 0.1666667 0.2222222 0.0000000     0
>  [7,] 0.00  0.0  0.0  0.0 0.5000000    0 0.5000000 0.4444444 0.3333333     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.3333333 0.3333333     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.3333333     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
```

```
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000     0
>       [,11]
>  [1,]     0
>  [2,]     0
>  [3,]     0
>  [4,]     0
>  [5,]     0
>  [6,]     0
>  [7,]     0
>  [8,]     0
>  [9,]     0
> [10,]     0
> [11,]     0
>
> $U$`5`
>       [,1] [,2] [,3] [,4]      [,5]      [,6]      [,7] [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0    0     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0    0     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0    0     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000 0.0000000 0.0000000  0.0    0     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000 0.0000000 0.0000000  0.0    0     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0    0     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.4444444 0.3333333 0.4444444  0.0    0     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000 0.6666667 0.4444444  0.6    0     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0    0     0     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0    1     0     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0    0     0     0
>
> $U$`6`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]      [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.00  0.00     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.00  0.00     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.00  0.00     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000 0.0000000 0.00  0.00     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000 0.0000000 0.00  0.00     0
>  [6,] 0.00  0.0  0.0  0.0 0.1111111    0 0.1111111 0.0000000 0.00  0.00     0
>  [7,] 0.00  0.0  0.0  0.0 0.6666667    0 0.6666667 0.2666667 0.00  0.00     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.1111111 0.6000000 0.50  0.00     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.1333333 0.25  0.25     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.1111111 0.0000000 0.25  0.50     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.00  0.25     0
>
> $U$`7`
>       [,1] [,2] [,3] [,4]       [,5] [,6]       [,7]       [,8] [,9] [,10]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000    0 0.00000000 0.00000000 0.00  0.00
>  [2,] 0.15  0.0  0.0  0.0 0.00000000    0 0.00000000 0.00000000 0.00  0.00
>  [3,] 0.00  0.1  0.0  0.0 0.00000000    0 0.00000000 0.00000000 0.00  0.00
>  [4,] 0.00  0.0  0.1  0.0 0.00000000    0 0.00000000 0.00000000 0.00  0.00
>  [5,] 0.00  0.0  0.0  0.1 0.05000000    0 0.00000000 0.00000000 0.00  0.00
>  [6,] 0.00  0.0  0.0  0.0 0.09090909    0 0.09090909 0.08333333 0.00  0.00
>  [7,] 0.00  0.0  0.0  0.0 0.45454545    0 0.45454545 0.25000000 0.25  0.00
>  [8,] 0.00  0.0  0.0  0.0 0.00000000    1 0.36363636 0.58333333 0.50  0.50
>  [9,] 0.00  0.0  0.0  0.0 0.00000000    0 0.00000000 0.00000000 0.25  0.25
```

```
> [10,] 0.00  0.0  0.0  0.0 0.00000000    0 0.00000000 0.00000000 0.00  0.25
> [11,] 0.00  0.0  0.0  0.0 0.00000000    0 0.00000000 0.00000000 0.00  0.00
>       [,11]
>  [1,]     0
>  [2,]     0
>  [3,]     0
>  [4,]     0
>  [5,]     0
>  [6,]     0
>  [7,]     0
>  [8,]     0
>  [9,]     0
> [10,]     0
> [11,]     1
>
> $U$`8`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]   [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000  0.0     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000  0.0     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000 0.0000  0.0     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000 0.0000  0.0     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000 0.0000  0.0     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.1875  0.0     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.3333333    1 0.3333333 0.3125  0.0     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.3333333 0.3750  0.5     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.1111111 0.0625  0.0     0     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0625  0.5     1     1
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000  0.0     0     0
>
> $U$`9`
>       [,1] [,2] [,3] [,4]      [,5]      [,6]      [,7] [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0  0.0  0.00     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0  0.0  0.00     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0  0.0  0.00     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000 0.0000000 0.0000000  0.0  0.0  0.00     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000 0.0000000 0.0000000  0.0  0.0  0.00     0
>  [6,] 0.00  0.0  0.0  0.0 0.1818182 0.3333333 0.1818182  0.0  0.0  0.00     0
>  [7,] 0.00  0.0  0.0  0.0 0.2727273 0.3333333 0.2727273  0.2  0.0  0.00     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.4545455  0.2  0.5  0.00     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.4  0.5  0.50     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000 0.3333333 0.0000000  0.0  0.0  0.25     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000 0.0000000 0.0000000  0.0  0.0  0.25     0
>
> $U$`10`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]  [,8]      [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000 0.0000000     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000 0.0000000     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000 0.000 0.0000000     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000 0.000 0.0000000     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000 0.000 0.0000000     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000 0.0000000     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.5714286    1 0.5714286 0.125 0.0000000     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.2857143 0.750 0.0000000     0     0
```

```
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.125 0.7142857     0     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000 0.2857143     1     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.000 0.0000000     0     1
>
> $U$`11`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7] [,8]      [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 0.00 0.0000000     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 0.00 0.0000000     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000 0.00 0.0000000     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000 0.00 0.0000000     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000 0.00 0.0000000     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.00 0.0000000     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.6666667    0 0.6666667 0.25 0.0000000     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.3333333 0.50 0.3333333     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.25 0.6666667     0     0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.00 0.0000000     1     0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.00 0.0000000     0     1
>
> $U$`12`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]      [,8]      [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.05    0 0.00 0.0000000 0.0000000     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.75    0 0.75 0.1666667 0.0000000     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.8333333 0.6666667     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.3333333     1     0
> [10,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     1
> [11,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>
> $U$`13`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]      [,8]      [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.05    0 0.00 0.0000000 0.0000000     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.50    0 0.50 0.0000000 0.3333333     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.00    0 0.25 0.5714286 0.3333333     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.2857143 0.3333333     0     0
> [10,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.1428571 0.0000000     1     0
> [11,] 0.00  0.0  0.0  0.0 0.00    0 0.00 0.0000000 0.0000000     0     0
>
> $U$`14`
>       [,1] [,2] [,3] [,4]      [,5] [,6]      [,7]      [,8]      [,9] [,10]
>  [1,] 0.03  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000   0.0
>  [2,] 0.15  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000   0.0
>  [3,] 0.00  0.1  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000   0.0
>  [4,] 0.00  0.0  0.1  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000   0.0
>  [5,] 0.00  0.0  0.0  0.1 0.0500000    0 0.0000000 0.0000000 0.0000000   0.0
```

```
>  [6,] 0.00  0.0  0.0  0.0 0.3333333    0 0.3333333 0.1666667 0.0000000   0.0
>  [7,] 0.00  0.0  0.0  0.0 0.3333333    0 0.3333333 0.1666667 0.3333333   0.0
>  [8,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.3333333 0.3333333   0.5
>  [9,] 0.00  0.0  0.0  0.0 0.0000000    0 0.3333333 0.3333333 0.3333333   0.0
> [10,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000   0.0
> [11,] 0.00  0.0  0.0  0.0 0.0000000    0 0.0000000 0.0000000 0.0000000   0.5
>       [,11]
>  [1,]     0
>  [2,]     0
>  [3,]     0
>  [4,]     0
>  [5,]     0
>  [6,]     0
>  [7,]     0
>  [8,]     0
>  [9,]     0
> [10,]     0
> [11,]     0
>
> $U$`15`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10] [,11]
>  [1,] 0.03  0.0  0.0  0.0 0.00  0.0 0.00 0.00    0     0     0
>  [2,] 0.15  0.0  0.0  0.0 0.00  0.0 0.00 0.00    0     0     0
>  [3,] 0.00  0.1  0.0  0.0 0.00  0.0 0.00 0.00    0     0     0
>  [4,] 0.00  0.0  0.1  0.0 0.00  0.0 0.00 0.00    0     0     0
>  [5,] 0.00  0.0  0.0  0.1 0.05  0.0 0.00 0.00    0     0     0
>  [6,] 0.00  0.0  0.0  0.0 0.00  0.0 0.00 0.00    0     0     0
>  [7,] 0.00  0.0  0.0  0.0 0.25  0.5 0.25 0.00    0     0     0
>  [8,] 0.00  0.0  0.0  0.0 0.00  0.5 0.75 0.50    0     0     0
>  [9,] 0.00  0.0  0.0  0.0 0.00  0.0 0.00 0.25    1     0     0
> [10,] 0.00  0.0  0.0  0.0 0.00  0.0 0.00 0.25    0     0     0
> [11,] 0.00  0.0  0.0  0.0 0.00  0.0 0.00 0.00    0     0     1
>
>
> $F
> $F$`1`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8]     [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0  500 1666.667     0     0
>  [2,]    0    0    0    0    0    0    0  500 1666.667     0     0
>  [3,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [4,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [5,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [6,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [7,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [8,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [9,]    0    0    0    0    0    0    0    0    0.000     0     0
> [10,]    0    0    0    0    0    0    0    0    0.000     0     0
> [11,]    0    0    0    0    0    0    0    0    0.000     0     0
>
> $F$`2`
>       [,1] [,2] [,3] [,4] [,5] [,6]  [,7]     [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0 312.5 1111.111 1250     0     0
>  [2,]    0    0    0    0    0    0 312.5 1111.111 1250     0     0
```

```
>  [3,]    0    0    0    0    0    0  0.0    0.000    0     0     0
>  [4,]    0    0    0    0    0    0  0.0    0.000    0     0     0
>  [5,]    0    0    0    0    0    0  0.0    0.000    0     0     0
>  [6,]    0    0    0    0    0    0  0.0    0.000    0     0     0
>  [7,]    0    0    0    0    0    0  0.0    0.000    0     0     0
>  [8,]    0    0    0    0    0    0  0.0    0.000    0     0     0
>  [9,]    0    0    0    0    0    0  0.0    0.000    0     0     0
> [10,]    0    0    0    0    0    0  0.0    0.000    0     0     0
> [11,]    0    0    0    0    0    0  0.0    0.000    0     0     0
>
> $F$`3`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0    0    0     0     0
>  [2,]    0    0    0    0    0    0    0    0    0     0     0
>  [3,]    0    0    0    0    0    0    0    0    0     0     0
>  [4,]    0    0    0    0    0    0    0    0    0     0     0
>  [5,]    0    0    0    0    0    0    0    0    0     0     0
>  [6,]    0    0    0    0    0    0    0    0    0     0     0
>  [7,]    0    0    0    0    0    0    0    0    0     0     0
>  [8,]    0    0    0    0    0    0    0    0    0     0     0
>  [9,]    0    0    0    0    0    0    0    0    0     0     0
> [10,]    0    0    0    0    0    0    0    0    0     0     0
> [11,]    0    0    0    0    0    0    0    0    0     0     0
>
> $F$`4`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0    0    0     0     0
>  [2,]    0    0    0    0    0    0    0    0    0     0     0
>  [3,]    0    0    0    0    0    0    0    0    0     0     0
>  [4,]    0    0    0    0    0    0    0    0    0     0     0
>  [5,]    0    0    0    0    0    0    0    0    0     0     0
>  [6,]    0    0    0    0    0    0    0    0    0     0     0
>  [7,]    0    0    0    0    0    0    0    0    0     0     0
>  [8,]    0    0    0    0    0    0    0    0    0     0     0
>  [9,]    0    0    0    0    0    0    0    0    0     0     0
> [10,]    0    0    0    0    0    0    0    0    0     0     0
> [11,]    0    0    0    0    0    0    0    0    0     0     0
>
> $F$`5`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0  500 5000     0     0
>  [2,]    0    0    0    0    0    0    0  500 5000     0     0
>  [3,]    0    0    0    0    0    0    0    0    0     0     0
>  [4,]    0    0    0    0    0    0    0    0    0     0     0
>  [5,]    0    0    0    0    0    0    0    0    0     0     0
>  [6,]    0    0    0    0    0    0    0    0    0     0     0
>  [7,]    0    0    0    0    0    0    0    0    0     0     0
>  [8,]    0    0    0    0    0    0    0    0    0     0     0
>  [9,]    0    0    0    0    0    0    0    0    0     0     0
> [10,]    0    0    0    0    0    0    0    0    0     0     0
> [11,]    0    0    0    0    0    0    0    0    0     0     0
>
> $F$`6`
```

```
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]     [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0 166.6667  625  1875     0
>  [2,]    0    0    0    0    0    0    0 166.6667  625  1875     0
>  [3,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [4,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [5,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [6,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [7,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [8,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [9,]    0    0    0    0    0    0    0   0.0000    0     0     0
> [10,]    0    0    0    0    0    0    0   0.0000    0     0     0
> [11,]    0    0    0    0    0    0    0   0.0000    0     0     0
>
> $F$`7`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]     [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0 1666.667 4375  5000 17500
>  [2,]    0    0    0    0    0    0    0 1666.667 4375  5000 17500
>  [3,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [4,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [5,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [6,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [7,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [8,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [9,]    0    0    0    0    0    0    0    0.000    0     0     0
> [10,]    0    0    0    0    0    0    0    0.000    0     0     0
> [11,]    0    0    0    0    0    0    0    0.000    0     0     0
>
> $F$`8`
>       [,1] [,2] [,3] [,4] [,5] [,6]     [,7]   [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0 277.7778 781.25 6250  5000 10000
>  [2,]    0    0    0    0    0    0 277.7778 781.25 6250  5000 10000
>  [3,]    0    0    0    0    0    0   0.0000   0.00    0     0     0
>  [4,]    0    0    0    0    0    0   0.0000   0.00    0     0     0
>  [5,]    0    0    0    0    0    0   0.0000   0.00    0     0     0
>  [6,]    0    0    0    0    0    0   0.0000   0.00    0     0     0
>  [7,]    0    0    0    0    0    0   0.0000   0.00    0     0     0
>  [8,]    0    0    0    0    0    0   0.0000   0.00    0     0     0
>  [9,]    0    0    0    0    0    0   0.0000   0.00    0     0     0
> [10,]    0    0    0    0    0    0   0.0000   0.00    0     0     0
> [11,]    0    0    0    0    0    0   0.0000   0.00    0     0     0
>
> $F$`9`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0  250    0  1250     0
>  [2,]    0    0    0    0    0    0    0  250    0  1250     0
>  [3,]    0    0    0    0    0    0    0    0    0     0     0
>  [4,]    0    0    0    0    0    0    0    0    0     0     0
>  [5,]    0    0    0    0    0    0    0    0    0     0     0
>  [6,]    0    0    0    0    0    0    0    0    0     0     0
>  [7,]    0    0    0    0    0    0    0    0    0     0     0
>  [8,]    0    0    0    0    0    0    0    0    0     0     0
>  [9,]    0    0    0    0    0    0    0    0    0     0     0
> [10,]    0    0    0    0    0    0    0    0    0     0     0
```



```
> [11,]    0    0    0    0    0    0    0    0    0     0     0
>
> $F$`10`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8]      [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0    0 714.2857  1250  2500
>  [2,]    0    0    0    0    0    0    0    0 714.2857  1250  2500
>  [3,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [4,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [5,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [6,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [7,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [8,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [9,]    0    0    0    0    0    0    0    0   0.0000     0     0
> [10,]    0    0    0    0    0    0    0    0   0.0000     0     0
> [11,]    0    0    0    0    0    0    0    0   0.0000     0     0
>
> $F$`11`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8]      [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0  625 833.3333     0  7500
>  [2,]    0    0    0    0    0    0    0  625 833.3333     0  7500
>  [3,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [4,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [5,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [6,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [7,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [8,]    0    0    0    0    0    0    0    0   0.0000     0     0
>  [9,]    0    0    0    0    0    0    0    0   0.0000     0     0
> [10,]    0    0    0    0    0    0    0    0   0.0000     0     0
> [11,]    0    0    0    0    0    0    0    0   0.0000     0     0
>
> $F$`12`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8]      [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0    0 4166.667  1250  5000
>  [2,]    0    0    0    0    0    0    0    0 4166.667  1250  5000
>  [3,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [4,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [5,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [6,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [7,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [8,]    0    0    0    0    0    0    0    0    0.000     0     0
>  [9,]    0    0    0    0    0    0    0    0    0.000     0     0
> [10,]    0    0    0    0    0    0    0    0    0.000     0     0
> [11,]    0    0    0    0    0    0    0    0    0.000     0     0
>
> $F$`13`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]     [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0 1071.429 2500  2500     0
>  [2,]    0    0    0    0    0    0    0 1071.429 2500  2500     0
>  [3,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [4,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [5,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [6,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [7,]    0    0    0    0    0    0    0    0.000    0     0     0
```

```
>  [8,]    0    0    0    0    0    0    0    0.000    0     0     0
>  [9,]    0    0    0    0    0    0    0    0.000    0     0     0
> [10,]    0    0    0    0    0    0    0    0.000    0     0     0
> [11,]    0    0    0    0    0    0    0    0.000    0     0     0
>
> $F$`14`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]     [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0 416.6667    0     0     0
>  [2,]    0    0    0    0    0    0    0 416.6667    0     0     0
>  [3,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [4,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [5,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [6,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [7,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [8,]    0    0    0    0    0    0    0   0.0000    0     0     0
>  [9,]    0    0    0    0    0    0    0   0.0000    0     0     0
> [10,]    0    0    0    0    0    0    0   0.0000    0     0     0
> [11,]    0    0    0    0    0    0    0   0.0000    0     0     0
>
> $F$`15`
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0    0  625     0     0
>  [2,]    0    0    0    0    0    0    0    0  625     0     0
>  [3,]    0    0    0    0    0    0    0    0    0     0     0
>  [4,]    0    0    0    0    0    0    0    0    0     0     0
>  [5,]    0    0    0    0    0    0    0    0    0     0     0
>  [6,]    0    0    0    0    0    0    0    0    0     0     0
>  [7,]    0    0    0    0    0    0    0    0    0     0     0
>  [8,]    0    0    0    0    0    0    0    0    0     0     0
>  [9,]    0    0    0    0    0    0    0    0    0     0     0
> [10,]    0    0    0    0    0    0    0    0    0     0     0
> [11,]    0    0    0    0    0    0    0    0    0     0     0
>
>
> $hstages
> [1] NA
>
> $agestages
> [1] NA
>
> $ahstages
>    stage_id stage original_size original_size_b original_size_c min_age max_age
> 1         1    SD           0.0              NA              NA      NA      NA
> 2         2    P1           0.0              NA              NA      NA      NA
> 3         3    P2           0.0              NA              NA      NA      NA
> 4         4    P3           0.0              NA              NA      NA      NA
> 5         5    SL           0.0              NA              NA      NA      NA
> 6         6     D           0.0              NA              NA      NA      NA
> 7         7   XSm           1.0              NA              NA      NA      NA
> 8         8    Sm           3.0              NA              NA      NA      NA
> 9         9    Md           6.0              NA              NA      NA      NA
> 10       10    Lg          11.0              NA              NA      NA      NA
> 11       11   XLg          19.5              NA              NA      NA      NA
```

```
>    repstatus obsstatus propstatus immstatus matstatus entrystage indataset
> 1          0         0          1         0         0          1         0
> 2          0         0          0         1         0          1         0
> 3          0         0          0         1         0          0         0
> 4          0         0          0         1         0          0         0
> 5          0         0          0         1         0          0         0
> 6          0         0          0         0         1          0         1
> 7          1         1          0         0         1          0         1
> 8          1         1          0         0         1          0         1
> 9          1         1          0         0         1          0         1
> 10         1         1          0         0         1          0         1
> 11         1         1          0         0         1          0         1
>    binhalfwidth_raw sizebin_min sizebin_max sizebin_center sizebin_width
> 1               0.0         0.0         0.0            0.0             0
> 2               0.0         0.0         0.0            0.0             0
> 3               0.0         0.0         0.0            0.0             0
> 4               0.0         0.0         0.0            0.0             0
> 5               0.0         0.0         0.0            0.0             0
> 6               0.5        -0.5         0.5            0.0             1
> 7               0.5         0.5         1.5            1.0             1
> 8               1.5         1.5         4.5            3.0             3
> 9               1.5         4.5         7.5            6.0             3
> 10              3.5         7.5        14.5           11.0             7
> 11              5.0        14.5        24.5           19.5            10
>    binhalfwidthb_raw sizebinb_min sizebinb_max sizebinb_center sizebinb_width
> 1                 NA           NA           NA              NA             NA
> 2                 NA           NA           NA              NA             NA
> 3                 NA           NA           NA              NA             NA
> 4                 NA           NA           NA              NA             NA
> 5                 NA           NA           NA              NA             NA
> 6                 NA           NA           NA              NA             NA
> 7                 NA           NA           NA              NA             NA
> 8                 NA           NA           NA              NA             NA
> 9                 NA           NA           NA              NA             NA
> 10                NA           NA           NA              NA             NA
> 11                NA           NA           NA              NA             NA
>    binhalfwidthc_raw sizebinc_min sizebinc_max sizebinc_center sizebinc_width
> 1                 NA           NA           NA              NA             NA
> 2                 NA           NA           NA              NA             NA
> 3                 NA           NA           NA              NA             NA
> 4                 NA           NA           NA              NA             NA
> 5                 NA           NA           NA              NA             NA
> 6                 NA           NA           NA              NA             NA
> 7                 NA           NA           NA              NA             NA
> 8                 NA           NA           NA              NA             NA
> 9                 NA           NA           NA              NA             NA
> 10                NA           NA           NA              NA             NA
> 11                NA           NA           NA              NA             NA
>    group                     comments alive
> 1      0                 Dormant seed     1
> 2      0            1st yr protocorm     1
> 3      0            2nd yr protocorm     1
> 4      0            3rd yr protocorm     1
```

```
> 5      0                    Seedling     1
> 6      0               Dormant adult     1
> 7      0    Extra small adult (1 shoot)     1
> 8      0        Small adult (2-4 shoots)     1
> 9      0       Medium adult (5-7 shoots)     1
> 10     0       Large adult (8-14 shoots)     1
> 11     0 Extra large adult (>14 shoots)     1
>
> $labels
>    pop patch year2
> 1    1     A  2004
> 2    1     A  2005
> 3    1     A  2006
> 4    1     A  2007
> 5    1     A  2008
> 6    1     B  2004
> 7    1     B  2005
> 8    1     B  2006
> 9    1     B  2007
> 10   1     B  2008
> 11   1     C  2004
> 12   1     C  2005
> 13   1     C  2006
> 14   1     C  2007
> 15   1     C  2008
>
> $matrixqc
> [1] 255  70  15
>
> $dataqc
> [1]  74 320
>
> attr(,"class")
> [1] "lefkoMat"
```

The output from this analysis is a `lefkoMat` object, which is a list object with the following elements:

A: a list of full population projection matrices, in order of population, patch, and occasion in time t

U: a list of matrices showing only survival-transition elements, in the same order as A

F: a list of matrices showing only fecundity elements, in the same order as A

hstages: a data frame showing the order of paired stages (given if matrices are historical, otherwise NA)

agestages: this is a data frame showing the order of age-stages (if an age-by-stage MPM has been created, otherwise NA)

ahstages: this is the stageframe used in analysis, with stages reordered and edited as they occur in the matrix

labels: a table showing the order of matrices, according to population, patch, and occasion in time t

matrixqc: a short vector used in `summary` statements to describe the overall quality of each matrix

dataqc: a short vector used in `summary` statements to describe key sampling aspects of the dataset (in raw MPMs)

modelqc: a short vector used in `summary` statements to describe the vital rate models (in function-based MPMs)

Calling particular values and elements within `lefkoMat` objects is not complicated, once you know the structure. The figure below illustrates how to call a particular element from one of the A matrices, for example.

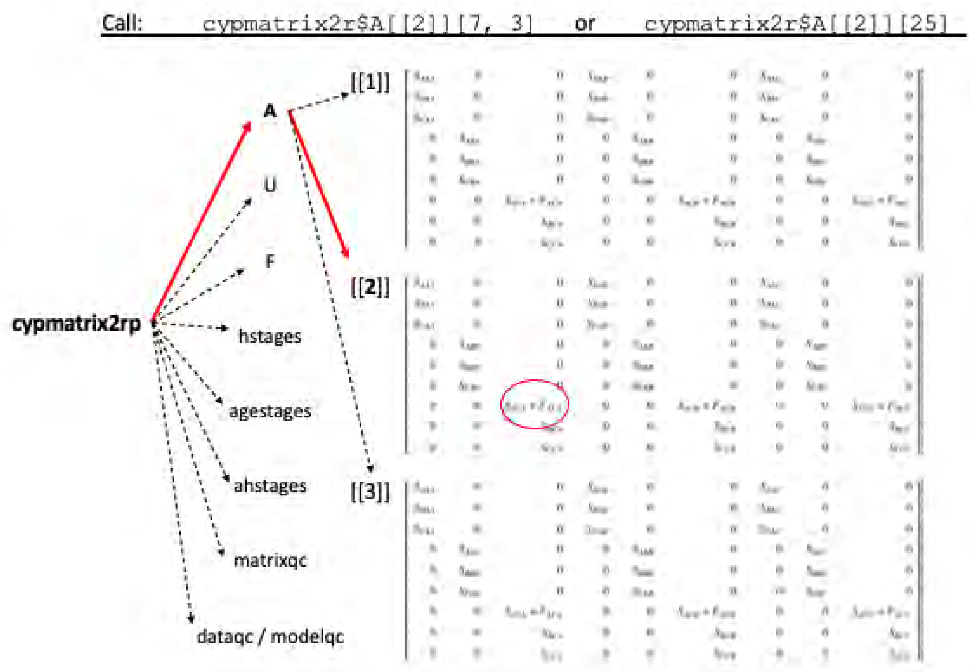


Figure 4.2: Organization of a `lefkoMat` object, and how to call a specific element

Objects of class `lefkoMat` have their own `summary` statements, which we can use to understand more about them.

```
summary(cypmatrix2rp)
>
> This ahistorical lefkoMat object contains 15 matrices.
>
> Each matrix is square with 11 rows and columns, and a total of 121 elements.
> A total of 255 survival transitions were estimated, with 17 per matrix.
> A total of 70 fecundity transitions were estimated, with 4.667 per matrix.
> This lefkoMat object covers 1 populations, 3 patches, and 5 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>          [,1]  [,2]  [,3]  [,4]  [,5]  [,6]  [,7]  [,8]  [,9] [,10] [,11] [,12]
> Min.    0.000 0.000 0.000 0.000 0.000 0.000 0.100 0.100 0.000 0.100 0.000 0.000
> 1st Qu. 0.100 0.050 0.100 0.050 0.100 0.100 0.140 0.140 0.100 0.140 0.100 0.100
> Median  0.180 0.100 0.180 0.100 0.180 0.180 0.909 0.778 0.505 0.857 0.717 0.750
> Mean    0.461 0.389 0.472 0.351 0.406 0.483 0.627 0.604 0.518 0.633 0.563 0.548
> 3rd Qu. 0.955 0.900 1.000 0.692 0.744 1.000 1.000 1.000 0.955 1.000 1.000 1.000
> Max.    1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.000
>         [,13] [,14] [,15]
> Min.    0.000 0.000 0.000
> 1st Qu. 0.100 0.100 0.100
> Median  0.180 0.180 0.300
> Mean    0.435 0.472 0.525
> 3rd Qu. 0.875 1.000 1.000
```

```
> Max.    1.000 1.000 1.000
```

We start off learning that 15 matrices were estimated, and we learn the dimensionality of those matrices. Next we see how many elements were actually estimated, both overall and per matrix, followed by the number of populations, patches or subpopulations, and time steps covered by the MPM. Then we see the number of individuals and transitions the matrices are based on. It is typical for population ecologists to consider the total number of transitions in a dataset as a measure of the statistical power of a matrix, but the number of individuals used is just as important because each transition that an individual experiences is dependent on the other transitions that it also experiences. The final portion of the summary shows us the range of survival probabilities of stages in the matrices, where the survival probabilities are calculated as column sums of each `U` matrix. Since there are 15 matrices, there are 15 summaries. It is important to check to see that no stage survives outside the realm of possibility (i.e. no probability should be greater than 1.0 or lower than 0.0). Unusual stage survival probabilities will result in a warning as a part of the `summary()` output.

The input for the `rlefko2()` function includes `patch = "all"` and `year = "all"`, but can be set to focus on any set of patches/subpopulations or years included within the data. Package `lefko3` includes a great deal of flexibility here, and can estimate many matrices covering all of the populations, patches, and years occurring in a specific dataset. For example, if we had wished to skip the patch divisions within the population and instead estimate only annual matrices at the population level, then we could have eliminated the `patch` option altogether from the input, as below.

```
cypmatrix2r <- rlefko2(data = cypraw_v1, stageframe = cypframe_raw,
  year = "all", stages = c("stage3", "stage2"),
  size = c("size3added", "size2added"), supplement = cypsupp2_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ")

summary(cypmatrix2r)
>
> This ahistorical lefkoMat object contains 5 matrices.
>
> Each matrix is square with 11 rows and columns, and a total of 121 elements.
> A total of 115 survival transitions were estimated, with 23 per matrix.
> A total of 40 fecundity transitions were estimated, with 8 per matrix.
> This lefkoMat object covers 1 populations, 1 patches, and 5 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>          [,1]  [,2]  [,3]  [,4]  [,5]
> Min.    0.000 0.100 0.100 0.000 0.100
> 1st Qu. 0.100 0.140 0.140 0.100 0.140
> Median  0.746 0.870 0.864 0.600 0.882
> Mean    0.562 0.642 0.627 0.532 0.615
> 3rd Qu. 1.000 1.000 1.000 0.960 1.000
> Max.    1.000 1.000 1.000 1.000 1.000
```

Notice what happened here. The first call to `rlefko2()` yielded 15 matrices, because there are 3 patches in our dataset, and there are a total of 6 years of data, yielding 5 transitions between years (also refered to as time steps or periods). So, there are $3 \times 5 = 15$ matrices. But in the second call, we no longer recognize patches and so have only estimated one set of 5 matrices covering the whole population. We can also focus in on specific patches and specific sets of years, setting the options appropriately.

Let's try another exercise in this vein. This time, we will estimate matrices at the population level, but only for the years 2006 and 2007. This will result in 6 matrices, since there are 3 patches and 2 monitoring occasions (note that focusing on years 2006 and 2007 means that we will only build matrices in which these are the years in time t).

```
cypmatrix2rp67 <- rlefko2(data = cypraw_v1, stageframe = cypframe_raw,
  year = c(2006, 2007), patch = "all", stages = c("stage3", "stage2"),
  size = c("size3added", "size2added"), supplement = cypsupp2_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ")

summary(cypmatrix2rp67)
>
> This ahistorical lefkoMat object contains 6 matrices.
>
> Each matrix is square with 11 rows and columns, and a total of 121 elements.
> A total of 107 survival transitions were estimated, with 17.833 per matrix.
> A total of 22 fecundity transitions were estimated, with 3.667 per matrix.
> This lefkoMat object covers 1 populations, 3 patches, and 2 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>          [,1]  [,2]  [,3]  [,4]  [,5]  [,6]
> Min.    0.000 0.000 0.100 0.000 0.000 0.000
> 1st Qu. 0.100 0.050 0.140 0.100 0.100 0.100
> Median  0.180 0.100 0.778 0.505 0.180 0.180
> Mean    0.472 0.351 0.604 0.518 0.435 0.472
> 3rd Qu. 1.000 0.692 1.000 0.955 0.875 1.000
> Max.    1.000 1.000 1.000 1.000 1.000 1.000
```

Finally, we will build matrices only for the years 2006 and 2007 in patch A. We expect only 2 matrices.

```
cypmatrix2rA67 <- rlefko2(data = cypraw_v1, stageframe = cypframe_raw,
  year = c(2006, 2007), patch = "A", stages = c("stage3", "stage2"),
  size = c("size3added", "size2added"), supplement = cypsupp2_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ")

summary(cypmatrix2rA67)
>
> This ahistorical lefkoMat object contains 2 matrices.
>
> Each matrix is square with 11 rows and columns, and a total of 121 elements.
> A total of 29 survival transitions were estimated, with 14.5 per matrix.
> A total of 0 fecundity transitions were estimated, with 0 per matrix.
> This lefkoMat object covers 1 populations, 1 patches, and 2 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>          [,1]  [,2]
> Min.    0.000 0.000
> 1st Qu. 0.100 0.050
> Median  0.180 0.100
> Mean    0.472 0.351
> 3rd Qu. 1.000 0.692
> Max.    1.000 1.000
```

This output is also interesting because it showcases one of the strengths and weaknesses of the raw MPM approach. We see that no individuals produced any offspring in patch A over these two time steps, so no fecundity terms were estimated. While this is a very accurate result, it can lead to problems if we think of the MPM as reflecting the underlying biology of the species. In this case, fecundity is missing most likely because there were too few individuals in this patch at these times, and so the luck of the draw left us with some biologically estimable elements not being estimated.

Ahistorical vs. historical matrix models

The matrices that we have built so far are all examples of **ahistorical MPMs** (ahMPMs). These are projection models in which the future stage of an individual is dependent only on its current stage, and not on previous stages. In other words, individual history is not incorporated into ahMPMs. It may seem odd that individual history is not incorporated into the matrices given that demographic datasets are composed of records of individual histories spanning several or even many monitoring occasions. However, construction of an ahMPM breaks up these individual histories into pairs of consecutive stages across time, with each stage-pair treated as independent of every other pair of consecutive stages. For example, if an individual is in stage A in occasion 1, stage B in occasion 2, stage E in occasion 3, and dead in occasion 4, then its individual history is broken up into A-B, B-E, and E-Dead, with each pair assumed to be independent. The resulting projection matrix would be the same if these transitions originated from different individuals or the same one - their order and relationships do not have any impacts in ahMPM construction.

The independence of consecutive stage-pairs reflects a central assumption in ahMPM analysis: the stage of an individual in the next occasion is influenced only by its current stage. Conceptually, if an organism's stage in the next occasion is entirely determined by its current stage, then its previous states do not influence these transitions. Thus, standard ahMPMs are two dimensional and reflect only the current and next immediate stage of individuals, given by the columns and rows, respectively. This is ultimately an extension of the ***iid* assumption** in statistics - that the states of individuals are ***i*ndependent** and originate from ***i*dentically-*d*istributed** random variables. This assumption helped make matrix projection models relatively easy to estimate even before the advent of personal computers.

MPMs have been estimated since the 1940s, beginning with Leslie's introduction of the age-structured model (Leslie 1945; Caswell 2001). We have never done a meta-analysis of all of these studies, but nonetheless it is safe to say that studies considering individual history are rare. The typical MPM study involves only ahMPMs, and so assumes independence of stage transitions across time even from the same individual. In fact, at the time of writing, we are aware of only 5 examples of studies breaking these assumptions and using a **historical** approach, in which some degree of individual history is incorporated into matrix estimation and analysis (Ehrlén 2000; Shefferson *et al.* 2014, 2017, 2018; Vries & Caswell 2018).

The **historical MPM** (hMPM) is an extension of the matrix projection model that incorporates information on one previous occasion into the determination of vital rates. Thus, the expected survival-transition probability of an individual in stage j at occasion t to stage k at occasion t+1 depends not only on its stage in occasion t but also on its stage in occasion t-1. Population ecologists considering this problem analytically might be inclined to add an extra dimension to the matrix to deal with this, thus creating a 3d array or cube. However, this is mathematically intractable, with many analyses becoming impossible (Vries & Caswell 2018). Instead, we utilize the approach developed by Ehrlén (2000), in which rows and columns represent life history stages paired in consecutive occasions. Thus, columns now represent the **From** pair of stages (stages in occasions t and t-1), and rows now represent the **To** pair of stages (stages in occasions t and t+1), as in Figure 4.3. This model is equivalent to the second-order model proposed by Vries & Caswell (2018), although the latter incorporates more history into transitions involving individuals just born (we explain the difference further in this vignette).

	S_{t-1} S_t	S_{t-1} J_t	J_{t-1} J_t	J_{t-1} V_t	J_{t-1} D_t	J_{t-1} F_t	V_{t-1} V_t	V_{t-1} D_t	V_{t-1} F_t	D_{t-1} V_t	D_{t-1} D_t	D_{t-1} F_t	F_{t-1} V_t	F_{t-1} D_t	F_{t-1} F_t	F_{t-1} S_t	F_{t-1} J_t
S_{t+1} S_t	S_{SSS}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S_{SSF}	0
J_{t+1} S_t	S_{JSS}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S_{JSF}	0
J_{t+1} J_t	0	S_{JJS}	S_{JJJ}	0	0	0	0	0	0	0	0	0	0	0	0	0	S_{JJF}
V_{t+1} J_t	0	S_{VJS}	S_{VJJ}	0	0	0	0	0	0	0	0	0	0	0	0	0	S_{VJF}
D_{t+1} J_t	0	S_{DJS}	S_{DJJ}	0	0	0	0	0	0	0	0	0	0	0	0	0	S_{DJF}
F_{t+1} J_t	0	S_{FJS}	S_{FJJ}	0	0	0	0	0	0	0	0	0	0	0	0	0	S_{FJF}
V_{t+1} V_t	0	0	0	S_{VVJ}	0	0	S_{VVV}	0	0	S_{VVD}	0	0	S_{VVF}	0	0	0	0
D_{t+1} V_t	0	0	0	S_{DVJ}	0	0	S_{DVV}	0	0	S_{DVD}	0	0	S_{DVF}	0	0	0	0
F_{t+1} V_t	0	0	0	S_{FVJ}	0	0	S_{FVV}	0	0	S_{FVD}	0	0	S_{FVF}	0	0	0	0
V_{t+1} D_t	0	0	0	0	S_{VDJ}	0	0	S_{VDV}	0	0	S_{VDD}	0	0	S_{VDF}	0	0	0
D_{t+1} D_t	0	0	0	0	S_{DDJ}	0	0	S_{DDV}	0	0	S_{DDD}	0	0	S_{DDF}	0	0	0
F_{t+1} D_t	0	0	0	0	S_{FDJ}	0	0	S_{FDV}	0	0	S_{FDD}	0	0	S_{FDF}	0	0	0
V_{t+1} F_t	0	0	0	0	0	0	0	0	S_{VFV}	0	0	S_{VFD}	0	0	S_{VFF}	0	0
D_{t+1} F_t	0	0	0	0	0	0	0	0	S_{DFV}	0	0	S_{DFD}	0	0	S_{DFF}	0	0
F_{t+1} F_t	0	0	0	0	0	0	0	0	S_{FFV}	0	0	S_{FFD}	0	0	S_{FFF}	0	0
S_{t+1} F_t	0	0	0	0	0	F_{SFJ}	0	0	F_{SFV}	0	0	F_{SFD}	0	0	F_{SFF}	0	0
J_{t+1} F_t	0	0	0	0	0	F_{JFJ}	0	0	F_{JFV}	0	0	F_{JFD}	0	0	F_{JFF}	0	0

Figure 4.3: Historical MPM for *Cypripedium candidum*, a North American herbaceous plant

Historical MPMs can be projected forward in the same way that ahMPMs can. In equation 4.4 we see an example of a projection going forward one time step using the hMPM shown in figure 4.3.

$$
\begin{bmatrix} n_{2,SS} \\ n_{2,JS} \\ n_{2,JJ} \\ n_{2,VJ} \\ n_{2,DJ} \\ n_{2,FJ} \\ n_{2,VV} \\ n_{2,DV} \\ n_{2,FV} \\ n_{2,VD} \\ n_{2,DD} \\ n_{2,FD} \\ n_{2,VF} \\ n_{2,DF} \\ n_{2,FF} \\ n_{2,SF} \\ n_{2,JF} \end{bmatrix}
=
\begin{bmatrix}
S_{SSS} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & F_{SSF} & 0 \\
S_{JSS} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & F_{JSF} & 0 \\
0 & S_{JJS} & S_{JJJ} & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & F_{JJF} \\
0 & S_{VJS} & S_{VJJ} & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & F_{VJF} \\
0 & S_{DJS} & S_{DJJ} & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & F_{DJF} \\
0 & S_{FJS} & S_{FJJ} & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & F_{FJF} \\
0 & 0 & 0 & S_{VVJ} & 0 & 0 & S_{VVV} & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & S_{DVJ} & 0 & 0 & S_{DVV} & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & S_{FVJ} & 0 & 0 & S_{FVV} & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & 0 & S_{VDJ} & 0 & 0 & S_{VDV} & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & 0 & S_{DDJ} & 0 & 0 & S_{DDV} & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & 0 & S_{FDJ} & 0 & 0 & S_{FDV} & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{VFV} & \cdots & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{DFV} & \cdots & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{FFV} & \cdots & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & F_{SFJ} & 0 & 0 & F_{SFV} & \cdots & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & F_{JFJ} & 0 & 0 & F_{JFV} & \cdots & 0 & 0
\end{bmatrix}
\begin{bmatrix} n_{1,SS} \\ n_{1,JS} \\ n_{1,JJ} \\ n_{1,VJ} \\ n_{1,DJ} \\ n_{1,FJ} \\ n_{1,VV} \\ n_{1,DV} \\ n_{1,FV} \\ n_{1,VD} \\ n_{1,DD} \\ n_{1,FD} \\ n_{1,VF} \\ n_{1,DF} \\ n_{1,FF} \\ n_{1,SF} \\ n_{1,JF} \end{bmatrix}
\tag{4.4}
$$

Here, $n_{1,SS}$ is the number of individuals that were in stage S in both occasions 0 and 1, and $n_{2,DF}$ is the number of individuals that were in stage D in occasion 2 and stage F in occasion 1.

Ahistorical matrices and historical martices can be derived from the same datasets provided that individual fates are noted for three consecutive times each. We can refer to matrix elements as a_{kjl}, where the element represents the rate at which individuals transition to stage k in occasion t+1 after having been in stage j in occasion t and in stage l in occasion t-1. If n_{kjl} is the number of individuals making this transition, $n_{.jl}$

is the total number of individuals in stage j in occasion t and stage l in occasion t-1 regardless of stage or even status as alive or dead in occasion t+1, m is the number of stages in the life history model, and d is the number of stages plus death in the life history model (so that $d = m + 1$), then we have:

$$a_{kjl} = \frac{n_{kjl}}{n_{.jl}} = \frac{n_{kjl}}{\sum_{i=1}^{d} n_{ijl}} \tag{4.5}$$

Note that although one can use the actual numbers of individuals making historical transitions to estimate ahistorical MPMs, one cannot use the matrix elements in a historical MPM to calculate the associated ahistorical MPM elements, nor can one use the elements in an ahistorical MPM to calculate the elements in a historical MPM. This is due to the fact that historical transitions must be weighted by the *numbers of individuals* in each previous stage in occasions t and t-1 ($n_{.jl}$) to produce the proper ahistorical transition rates. Historical matrix elements contain no information about these weights. Thus, we have the following relationships between ahistorical survival-transition terms and the historical datasets:

$$a_{kj} = \frac{\sum_{l=1}^{m} n_{kjl}}{\sum_{l=1}^{m} \sum_{i=1}^{d} n_{ijl}} \tag{4.6}$$

Historical MPMs normally require a much larger number of elements to be parameterized than ahMPMs do. Figure 4.3 illustrates this issue. Typically, a historical matrix has dimensions equal to the number of stages squared (although this may sometimes be reduced, if certain conditions are met). However, most of the increase in matrix elements is in structural zeros. In an ahistorical matrix, the only true zeros will be those elements corresponding to biologically impossible transitions, or those elements without any individuals taking the respective transition in a given time step. However, most elements in a historical MPM are structural zeros, because transition elements in hMPMs are only estimable if stage at occasion t is equal in the column and row stage pairs. For example, the transition probability between stage A in occasion t-1 and stage B in occasion t (column stage-pair), to stage C in occasion t and stage D in occasion t+1 (row stage-pair) equals 0, because an organism cannot be in both stages B and C in occasion t. Increasing the number of stages in the life history model causes these structural zeros to increase at a faster rate than the rate at which the number of truly estimable elements increases. In fact, if there are m stages in a life history, yielding m^2 elements in an ahistorical matrix, then although there will be m^4 elements in the historical matrix, only m^3 will be *potentially* estimable while $(m-1)m^3$ will be structural zeros (we say *potentially* because some of the logically possible transitions may still be biologically impossible, or may have no data to yield values other than 0).

Let's build our first historical MPM with the *Cypripedium candidum* data. As before, we will build our MPM to cover all years and all patches.

```
cypmatrix3rp <- rlefko3(data = cypraw_v1, stageframe = cypframe_raw,
  year = "all", patch = "all", stages = c("stage3", "stage2", "stage1"),
  size = c("size3added", "size2added", "size1added"), supplement = cypsupp3_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ")

summary(cypmatrix3rp)
>
> This historical lefkoMat object contains 12 matrices.
>
> Each matrix is square with 121 rows and columns, and a total of 14641 elements.
> A total of 386 survival transitions were estimated, with 32.167 per matrix.
> A total of 68 fecundity transitions were estimated, with 5.667 per matrix.
> This lefkoMat object covers 1 populations, 3 patches, and 4 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>           [,1]   [,2]   [,3]   [,4]   [,5]  [,6]   [,7]   [,8]   [,9]  [,10]  [,11]
```

```
> Min.    0.0000 0.0000 0.0000 0.0000 0.000 0.00 0.000 0.000 0.0000 0.000 0.0000
> 1st Qu. 0.0000 0.0000 0.0000 0.0000 0.000 0.00 0.000 0.000 0.0000 0.000 0.0000
> Median  0.0000 0.0000 0.0000 0.0000 0.000 0.00 0.000 0.000 0.0000 0.000 0.0000
> Mean    0.0862 0.0706 0.0665 0.0754 0.124 0.13 0.123 0.135 0.0968 0.072 0.0968
> 3rd Qu. 0.0000 0.0000 0.0000 0.0000 0.000 0.00 0.000 0.000 0.0000 0.000 0.0000
> Max.    1.0000 1.0000 1.0000 1.0000 1.000 1.00 1.000 1.000 1.0500 1.000 1.0000
>         [,12]
> Min.    0.000
> 1st Qu. 0.000
> Median  0.000
> Mean    0.113
> 3rd Qu. 0.000
> Max.    1.000
> Warning: Some matrices include stages with survival probability greater than
> 1.0.
```

Quickly scanning this output shows a number of differences relative to the ahMPM. First, there are 3 fewer matrices here than in the ahistorical case. There are 3 patches that we are estimating matrices for, and 6 years of data for each patch, leading to 5 possible ahistorical time steps and 15 possible ahistorical matrices. Since historical matrices require 3 years of transition data, only 4 historical transitions are possible per patch, leading to 12 total historical matrices. Second, the dimensionality of the matrices is the square of the dimensions of the ahistorical matrices. This leads to vastly more matrix elements within each matrix, although it turns out that most of these matrix elements are structural zeros because they reflect impossible transitions. Indeed, in this case, although there are 14,641 elements in each matrix, on average only 37.83 are actually estimated greater than 0. Finally, we see that one of our matrices has a survival probability greater than 1.0. This is a problem for us, and normally we would need to correct the situation via the supplement table. However, for the time being we will proceed without correction (no other MPMs here will have this problem).

Let's look at the first matrix, corresponding to the transition from 2004 and 2005 to 2006 in the first patch (patch A, according to the `labels` element). Because this is a huge matrix, we will only look at the top corner, followed by a middle section. Particularly note the sparseness - most elements are zeros, because most transitions are actually impossible. These matrices may also be exported to Excel or another spreadsheet program to look over in greater detail.

```
cypmatrix3rp$A[[1]][1:20,1:10]
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10]
>  [1,] 0.01  0.0    0    0    0    0    0    0    0     0
>  [2,] 0.10  0.0    0    0    0    0    0    0    0     0
>  [3,] 0.00  0.0    0    0    0    0    0    0    0     0
>  [4,] 0.00  0.0    0    0    0    0    0    0    0     0
>  [5,] 0.00  0.0    0    0    0    0    0    0    0     0
>  [6,] 0.00  0.0    0    0    0    0    0    0    0     0
>  [7,] 0.00  0.0    0    0    0    0    0    0    0     0
>  [8,] 0.00  0.0    0    0    0    0    0    0    0     0
>  [9,] 0.00  0.0    0    0    0    0    0    0    0     0
> [10,] 0.00  0.0    0    0    0    0    0    0    0     0
> [11,] 0.00  0.0    0    0    0    0    0    0    0     0
> [12,] 0.00  0.0    0    0    0    0    0    0    0     0
> [13,] 0.00  0.0    0    0    0    0    0    0    0     0
> [14,] 0.00  0.1    0    0    0    0    0    0    0     0
> [15,] 0.00  0.0    0    0    0    0    0    0    0     0
> [16,] 0.00  0.0    0    0    0    0    0    0    0     0
> [17,] 0.00  0.0    0    0    0    0    0    0    0     0
> [18,] 0.00  0.0    0    0    0    0    0    0    0     0
```

```
> [19,] 0.00  0.0    0    0    0    0    0    0    0     0
> [20,] 0.00  0.0    0    0    0    0    0    0    0     0
print(cypmatrix3rp$A[[1]][66:85,73:81], digits = 3)
>          [,1]     [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9]
>  [1,]   0.000    0.000    0    0    0    0    0    0    0
>  [2,] 357.143    0.000    0    0    0    0    0    0    0
>  [3,] 357.143    0.000    0    0    0    0    0    0    0
>  [4,]   0.000    0.000    0    0    0    0    0    0    0
>  [5,]   0.000    0.000    0    0    0    0    0    0    0
>  [6,]   0.000    0.000    0    0    0    0    0    0    0
>  [7,]   0.143    0.000    0    0    0    0    0    0    0
>  [8,]   0.714    0.000    0    0    0    0    0    0    0
>  [9,]   0.000    0.000    0    0    0    0    0    0    0
> [10,]   0.000    0.000    0    0    0    0    0    0    0
> [11,]   0.000    0.000    0    0    0    0    0    0    0
> [12,]   0.000    0.000    0    0    0    0    0    0    0
> [13,]   0.000 1666.667    0    0    0    0    0    0    0
> [14,]   0.000 1666.667    0    0    0    0    0    0    0
> [15,]   0.000    0.000    0    0    0    0    0    0    0
> [16,]   0.000    0.000    0    0    0    0    0    0    0
> [17,]   0.000    0.000    0    0    0    0    0    0    0
> [18,]   0.000    0.000    0    0    0    0    0    0    0
> [19,]   0.000    0.667    0    0    0    0    0    0    0
> [20,]   0.000    0.333    0    0    0    0    0    0    0
```

As before, we can create matrices at the full population level by not specifying any patches to focus on, as below.

```
cypmatrix3r <- rlefko3(data = cypraw_v1, stageframe = cypframe_raw,
  year = "all", stages = c("stage3", "stage2", "stage1"),
  size = c("size3added", "size2added", "size1added"), supplement = cypsupp3_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ")

summary(cypmatrix3r)
>
> This historical lefkoMat object contains 4 matrices.
>
> Each matrix is square with 121 rows and columns, and a total of 14641 elements.
> A total of 188 survival transitions were estimated, with 47 per matrix.
> A total of 52 fecundity transitions were estimated, with 13 per matrix.
> This lefkoMat object covers 1 populations, 1 patches, and 4 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>          [,1]  [,2]  [,3]  [,4]
> Min.    0.000 0.000 0.000 0.000
> 1st Qu. 0.000 0.000 0.000 0.000
> Median  0.000 0.000 0.000 0.000
> Mean    0.142 0.149 0.148 0.164
> 3rd Qu. 0.000 0.000 0.000 0.000
> Max.    1.000 1.000 1.000 1.000
```

We now have only four matrices, corresponding to the full population in each year at time t. Next, let's focus only on years 2006 and 2007 in all patches, as before.

```
cypmatrix3rp67 <- rlefko3(data = cypraw_v1, stageframe = cypframe_raw,
  year = c(2006, 2007), patch = "all", stages = c("stage3", "stage2", "stage1"),
  size = c("size3added", "size2added", "size1added"), supplement = cypsupp3_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ")

summary(cypmatrix3rp67)
>
> This historical lefkoMat object contains 6 matrices.
>
> Each matrix is square with 121 rows and columns, and a total of 14641 elements.
> A total of 196 survival transitions were estimated, with 32.667 per matrix.
> A total of 30 fecundity transitions were estimated, with 5 per matrix.
> This lefkoMat object covers 1 populations, 3 patches, and 2 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>           [,1]   [,2] [,3]  [,4]  [,5]   [,6]
> Min.    0.0000 0.0000 0.00 0.000 0.000 0.0000
> 1st Qu. 0.0000 0.0000 0.00 0.000 0.000 0.0000
> Median  0.0000 0.0000 0.00 0.000 0.000 0.0000
> Mean    0.0706 0.0665 0.13 0.123 0.072 0.0968
> 3rd Qu. 0.0000 0.0000 0.00 0.000 0.000 0.0000
> Max.    1.0000 1.0000 1.00 1.000 1.000 1.0000
```

We find six matrices, corresponding to the years 2006 and 2007 for each of the three patches. And now let's focus in on years 2006 and 2007 in the first patch, patch A.

```
cypmatrix3rA67 <- rlefko3(data = cypraw_v1, stageframe = cypframe_raw,
  year = c(2006, 2007), patch = "A", stages = c("stage3", "stage2", "stage1"),
  size = c("size3added", "size2added", "size1added"), supplement = cypsupp3_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ")

summary(cypmatrix3rA67)
>
> This historical lefkoMat object contains 2 matrices.
>
> Each matrix is square with 121 rows and columns, and a total of 14641 elements.
> A total of 57 survival transitions were estimated, with 28.5 per matrix.
> A total of 0 fecundity transitions were estimated, with 0 per matrix.
> This lefkoMat object covers 1 populations, 1 patches, and 2 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>           [,1]   [,2]
> Min.    0.0000 0.0000
> 1st Qu. 0.0000 0.0000
> Median  0.0000 0.0000
> Mean    0.0706 0.0665
> 3rd Qu. 0.0000 0.0000
> Max.    1.0000 1.0000
```

Arithmetic mean matrices

Now that we have created our MPMs, we might wish to create element-wise arithmetic mean matrices to aid inference and further analysis. For example, we might be interested in developing patch-level means and an overall population mean, but one in which the element means weight each patch and each year equally. For this purpose, we can use the `lmean()` function. Let's take a look at the element-wise mean raw ahMPM first.

```
cyp2rp_mean <- lmean(cypmatrix2rp)

cyp2rp_mean
> $A
> $A[[1]]
>       [,1] [,2] [,3] [,4]       [,5]       [,6]        [,7]         [,8]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000 0.00000000 62.50000000 422.22222222
>  [2,] 0.15  0.0  0.0  0.0 0.00000000 0.00000000 62.50000000 422.22222222
>  [3,] 0.00  0.1  0.0  0.0 0.00000000 0.00000000  0.00000000   0.00000000
>  [4,] 0.00  0.0  0.1  0.0 0.00000000 0.00000000  0.00000000   0.00000000
>  [5,] 0.00  0.0  0.0  0.1 0.05000000 0.00000000  0.00000000   0.00000000
>  [6,] 0.00  0.0  0.0  0.0 0.05833333 0.00000000  0.05833333   0.04444444
>  [7,] 0.00  0.0  0.0  0.0 0.59949495 0.06666667  0.59949495   0.19555556
>  [8,] 0.00  0.0  0.0  0.0 0.00000000 0.33333333  0.21010101   0.59555556
>  [9,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000  0.00000000   0.08444444
> [10,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000  0.00000000   0.00000000
> [11,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000  0.00000000   0.00000000
>               [,9] [,10] [,11]
>  [1,] 1.583333e+03   0.0     0
>  [2,] 1.583333e+03   0.0     0
>  [3,] 0.000000e+00   0.0     0
>  [4,] 0.000000e+00   0.0     0
>  [5,] 0.000000e+00   0.0     0
>  [6,] 0.000000e+00   0.0     0
>  [7,] 6.666667e-02   0.0     0
>  [8,] 2.500000e-01   0.2     0
>  [9,] 4.833333e-01   0.0     0
> [10,] 2.000000e-01   0.0     0
> [11,] 0.000000e+00   0.0     0
>
> $A[[2]]
>       [,1] [,2] [,3] [,4]       [,5]       [,6]        [,7]         [,8]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000 0.00000000 55.55555556 572.91666667
>  [2,] 0.15  0.0  0.0  0.0 0.00000000 0.00000000 55.55555556 572.91666667
>  [3,] 0.00  0.1  0.0  0.0 0.00000000 0.00000000  0.00000000   0.00000000
>  [4,] 0.00  0.0  0.1  0.0 0.00000000 0.00000000  0.00000000   0.00000000
>  [5,] 0.00  0.0  0.0  0.1 0.05000000 0.00000000  0.00000000   0.00000000
>  [6,] 0.00  0.0  0.0  0.0 0.07676768 0.06666667  0.07676768   0.05416667
>  [7,] 0.00  0.0  0.0  0.0 0.45974026 0.46666667  0.45974026   0.23083333
>  [8,] 0.00  0.0  0.0  0.0 0.00000000 0.20000000  0.30966811   0.50166667
>  [9,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000  0.02222222   0.14416667
> [10,] 0.00  0.0  0.0  0.0 0.00000000 0.06666667  0.02222222   0.01250000
> [11,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000  0.00000000   0.00000000
>               [,9]  [,10] [,11]
>  [1,] 2392.8571429 2875.0 6e+03
>  [2,] 2392.8571429 2875.0 6e+03
>  [3,]    0.0000000    0.0 0e+00
```

```
>  [4,]     0.0000000    0.0 0e+00
>  [5,]     0.0000000    0.0 0e+00
>  [6,]     0.0000000    0.0 0e+00
>  [7,]     0.0500000    0.0 0e+00
>  [8,]     0.4000000    0.1 0e+00
>  [9,]     0.3428571    0.2 0e+00
> [10,]     0.2071429    0.6 2e-01
> [11,]     0.0000000    0.1 4e-01
>
> $A[[3]]
>       [,1] [,2] [,3] [,4]       [,5] [,6]       [,7]         [,8]         [,9]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000  0.0 0.00000000 422.61904762 1625.0000000
>  [2,] 0.15  0.0  0.0  0.0 0.00000000  0.0 0.00000000 422.61904762 1625.0000000
>  [3,] 0.00  0.1  0.0  0.0 0.00000000  0.0 0.00000000   0.00000000    0.0000000
>  [4,] 0.00  0.0  0.1  0.0 0.00000000  0.0 0.00000000   0.00000000    0.0000000
>  [5,] 0.00  0.0  0.0  0.1 0.05000000  0.0 0.00000000   0.00000000    0.0000000
>  [6,] 0.00  0.0  0.0  0.0 0.06666667  0.0 0.06666667   0.03333333    0.0000000
>  [7,] 0.00  0.0  0.0  0.0 0.50000000  0.1 0.50000000   0.11666667    0.1333333
>  [8,] 0.00  0.0  0.0  0.0 0.00000000  0.1 0.26666667   0.54761905    0.3333333
>  [9,] 0.00  0.0  0.0  0.0 0.00000000  0.0 0.06666667   0.22380952    0.5333333
> [10,] 0.00  0.0  0.0  0.0 0.00000000  0.0 0.00000000   0.07857143    0.0000000
> [11,] 0.00  0.0  0.0  0.0 0.00000000  0.0 0.00000000   0.00000000    0.0000000
>       [,10]  [,11]
>  [1,] 750.0 2500.0
>  [2,] 750.0 2500.0
>  [3,]   0.0    0.0
>  [4,]   0.0    0.0
>  [5,]   0.0    0.0
>  [6,]   0.0    0.0
>  [7,]   0.0    0.0
>  [8,]   0.1    0.0
>  [9,]   0.2    0.0
> [10,]   0.4    0.2
> [11,]   0.1    0.4
>
> $A[[4]]
>       [,1] [,2] [,3] [,4]       [,5]       [,6]         [,7]         [,8]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000 0.00000000 39.351851852 472.58597884
>  [2,] 0.15  0.0  0.0  0.0 0.00000000 0.00000000 39.351851852 472.58597884
>  [3,] 0.00  0.1  0.0  0.0 0.00000000 0.00000000  0.000000000   0.00000000
>  [4,] 0.00  0.0  0.1  0.0 0.00000000 0.00000000  0.000000000   0.00000000
>  [5,] 0.00  0.0  0.0  0.1 0.05000000 0.00000000  0.000000000   0.00000000
>  [6,] 0.00  0.0  0.0  0.0 0.06725589 0.02222222  0.067255892   0.04398148
>  [7,] 0.00  0.0  0.0  0.0 0.51974507 0.21111111  0.519745070   0.18101852
>  [8,] 0.00  0.0  0.0  0.0 0.00000000 0.21111111  0.262145262   0.54828042
>  [9,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000  0.029629630   0.15080688
> [10,] 0.00  0.0  0.0  0.0 0.00000000 0.02222222  0.007407407   0.03035714
> [11,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000  0.000000000   0.00000000
>               [,9]        [,10]        [,11]
>  [1,] 1.867063e+03 1.208333e+03 2833.3333333
>  [2,] 1.867063e+03 1.208333e+03 2833.3333333
>  [3,] 0.000000e+00 0.000000e+00    0.0000000
>  [4,] 0.000000e+00 0.000000e+00    0.0000000
```

```
>  [5,] 0.000000e+00 0.000000e+00    0.0000000
>  [6,] 0.000000e+00 0.000000e+00    0.0000000
>  [7,] 8.333333e-02 0.000000e+00    0.0000000
>  [8,] 3.277778e-01 1.333333e-01    0.0000000
>  [9,] 4.531746e-01 1.333333e-01    0.0000000
> [10,] 1.357143e-01 3.333333e-01    0.1333333
> [11,] 0.000000e+00 6.666667e-02    0.2666667
>
>
> $U
> $U[[1]]
>       [,1] [,2] [,3] [,4]       [,5]       [,6]       [,7]       [,8]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000 0.00000000 0.00000000 0.00000000
>  [2,] 0.15  0.0  0.0  0.0 0.00000000 0.00000000 0.00000000 0.00000000
>  [3,] 0.00  0.1  0.0  0.0 0.00000000 0.00000000 0.00000000 0.00000000
>  [4,] 0.00  0.0  0.1  0.0 0.00000000 0.00000000 0.00000000 0.00000000
>  [5,] 0.00  0.0  0.0  0.1 0.05000000 0.00000000 0.00000000 0.00000000
>  [6,] 0.00  0.0  0.0  0.0 0.05833333 0.00000000 0.05833333 0.04444444
>  [7,] 0.00  0.0  0.0  0.0 0.59949495 0.06666667 0.59949495 0.19555556
>  [8,] 0.00  0.0  0.0  0.0 0.00000000 0.33333333 0.21010101 0.59555556
>  [9,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000 0.00000000 0.08444444
> [10,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000 0.00000000 0.00000000
> [11,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000 0.00000000 0.00000000
>             [,9] [,10] [,11]
>  [1,] 0.00000000   0.0     0
>  [2,] 0.00000000   0.0     0
>  [3,] 0.00000000   0.0     0
>  [4,] 0.00000000   0.0     0
>  [5,] 0.00000000   0.0     0
>  [6,] 0.00000000   0.0     0
>  [7,] 0.06666667   0.0     0
>  [8,] 0.25000000   0.2     0
>  [9,] 0.48333333   0.0     0
> [10,] 0.20000000   0.0     0
> [11,] 0.00000000   0.0     0
>
> $U[[2]]
>       [,1] [,2] [,3] [,4]       [,5]       [,6]       [,7]       [,8]      [,9]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000 0.00000000 0.00000000 0.00000000 0.0000000
>  [2,] 0.15  0.0  0.0  0.0 0.00000000 0.00000000 0.00000000 0.00000000 0.0000000
>  [3,] 0.00  0.1  0.0  0.0 0.00000000 0.00000000 0.00000000 0.00000000 0.0000000
>  [4,] 0.00  0.0  0.1  0.0 0.00000000 0.00000000 0.00000000 0.00000000 0.0000000
>  [5,] 0.00  0.0  0.0  0.1 0.05000000 0.00000000 0.00000000 0.00000000 0.0000000
>  [6,] 0.00  0.0  0.0  0.0 0.07676768 0.06666667 0.07676768 0.05416667 0.0000000
>  [7,] 0.00  0.0  0.0  0.0 0.45974026 0.46666667 0.45974026 0.23083333 0.0500000
>  [8,] 0.00  0.0  0.0  0.0 0.00000000 0.20000000 0.30966811 0.50166667 0.4000000
>  [9,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000 0.02222222 0.14416667 0.3428571
> [10,] 0.00  0.0  0.0  0.0 0.00000000 0.06666667 0.02222222 0.01250000 0.2071429
> [11,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000 0.00000000 0.00000000 0.0000000
>       [,10] [,11]
>  [1,]   0.0   0.0
>  [2,]   0.0   0.0
>  [3,]   0.0   0.0
```

```
>  [4,]   0.0   0.0
>  [5,]   0.0   0.0
>  [6,]   0.0   0.0
>  [7,]   0.0   0.0
>  [8,]   0.1   0.0
>  [9,]   0.2   0.0
> [10,]   0.6   0.2
> [11,]   0.1   0.4
>
> $U[[3]]
>       [,1] [,2] [,3] [,4]       [,5] [,6]       [,7]       [,8]      [,9] [,10]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000  0.0 0.00000000 0.00000000 0.0000000   0.0
>  [2,] 0.15  0.0  0.0  0.0 0.00000000  0.0 0.00000000 0.00000000 0.0000000   0.0
>  [3,] 0.00  0.1  0.0  0.0 0.00000000  0.0 0.00000000 0.00000000 0.0000000   0.0
>  [4,] 0.00  0.0  0.1  0.0 0.00000000  0.0 0.00000000 0.00000000 0.0000000   0.0
>  [5,] 0.00  0.0  0.0  0.1 0.05000000  0.0 0.00000000 0.00000000 0.0000000   0.0
>  [6,] 0.00  0.0  0.0  0.0 0.06666667  0.0 0.06666667 0.03333333 0.0000000   0.0
>  [7,] 0.00  0.0  0.0  0.0 0.50000000  0.1 0.50000000 0.11666667 0.1333333   0.0
>  [8,] 0.00  0.0  0.0  0.0 0.00000000  0.1 0.26666667 0.54761905 0.3333333   0.1
>  [9,] 0.00  0.0  0.0  0.0 0.00000000  0.0 0.06666667 0.22380952 0.5333333   0.2
> [10,] 0.00  0.0  0.0  0.0 0.00000000  0.0 0.00000000 0.07857143 0.0000000   0.4
> [11,] 0.00  0.0  0.0  0.0 0.00000000  0.0 0.00000000 0.00000000 0.0000000   0.1
>       [,11]
>  [1,]   0.0
>  [2,]   0.0
>  [3,]   0.0
>  [4,]   0.0
>  [5,]   0.0
>  [6,]   0.0
>  [7,]   0.0
>  [8,]   0.0
>  [9,]   0.0
> [10,]   0.2
> [11,]   0.4
>
> $U[[4]]
>       [,1] [,2] [,3] [,4]       [,5]       [,6]        [,7]       [,8]
>  [1,] 0.03  0.0  0.0  0.0 0.00000000 0.00000000 0.000000000 0.00000000
>  [2,] 0.15  0.0  0.0  0.0 0.00000000 0.00000000 0.000000000 0.00000000
>  [3,] 0.00  0.1  0.0  0.0 0.00000000 0.00000000 0.000000000 0.00000000
>  [4,] 0.00  0.0  0.1  0.0 0.00000000 0.00000000 0.000000000 0.00000000
>  [5,] 0.00  0.0  0.0  0.1 0.05000000 0.00000000 0.000000000 0.00000000
>  [6,] 0.00  0.0  0.0  0.0 0.06725589 0.02222222 0.067255892 0.04398148
>  [7,] 0.00  0.0  0.0  0.0 0.51974507 0.21111111 0.519745070 0.18101852
>  [8,] 0.00  0.0  0.0  0.0 0.00000000 0.21111111 0.262145262 0.54828042
>  [9,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000 0.029629630 0.15080688
> [10,] 0.00  0.0  0.0  0.0 0.00000000 0.02222222 0.007407407 0.03035714
> [11,] 0.00  0.0  0.0  0.0 0.00000000 0.00000000 0.000000000 0.00000000
>             [,9]      [,10]     [,11]
>  [1,] 0.00000000 0.00000000 0.0000000
>  [2,] 0.00000000 0.00000000 0.0000000
>  [3,] 0.00000000 0.00000000 0.0000000
>  [4,] 0.00000000 0.00000000 0.0000000
```

```
>  [5,] 0.00000000 0.00000000 0.0000000
>  [6,] 0.00000000 0.00000000 0.0000000
>  [7,] 0.08333333 0.00000000 0.0000000
>  [8,] 0.32777778 0.13333333 0.0000000
>  [9,] 0.45317460 0.13333333 0.0000000
> [10,] 0.13571429 0.33333333 0.1333333
> [11,] 0.00000000 0.06666667 0.2666667
>
>
> $F
> $F[[1]]
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]     [,8]     [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0 62.5 422.2222 1583.333     0     0
>  [2,]    0    0    0    0    0    0 62.5 422.2222 1583.333     0     0
>  [3,]    0    0    0    0    0    0  0.0   0.0000    0.000     0     0
>  [4,]    0    0    0    0    0    0  0.0   0.0000    0.000     0     0
>  [5,]    0    0    0    0    0    0  0.0   0.0000    0.000     0     0
>  [6,]    0    0    0    0    0    0  0.0   0.0000    0.000     0     0
>  [7,]    0    0    0    0    0    0  0.0   0.0000    0.000     0     0
>  [8,]    0    0    0    0    0    0  0.0   0.0000    0.000     0     0
>  [9,]    0    0    0    0    0    0  0.0   0.0000    0.000     0     0
> [10,]    0    0    0    0    0    0  0.0   0.0000    0.000     0     0
> [11,]    0    0    0    0    0    0  0.0   0.0000    0.000     0     0
>
> $F[[2]]
>       [,1] [,2] [,3] [,4] [,5] [,6]     [,7]     [,8]     [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0 55.55556 572.9167 2392.857  2875  6000
>  [2,]    0    0    0    0    0    0 55.55556 572.9167 2392.857  2875  6000
>  [3,]    0    0    0    0    0    0  0.00000   0.0000    0.000     0     0
>  [4,]    0    0    0    0    0    0  0.00000   0.0000    0.000     0     0
>  [5,]    0    0    0    0    0    0  0.00000   0.0000    0.000     0     0
>  [6,]    0    0    0    0    0    0  0.00000   0.0000    0.000     0     0
>  [7,]    0    0    0    0    0    0  0.00000   0.0000    0.000     0     0
>  [8,]    0    0    0    0    0    0  0.00000   0.0000    0.000     0     0
>  [9,]    0    0    0    0    0    0  0.00000   0.0000    0.000     0     0
> [10,]    0    0    0    0    0    0  0.00000   0.0000    0.000     0     0
> [11,]    0    0    0    0    0    0  0.00000   0.0000    0.000     0     0
>
> $F[[3]]
>       [,1] [,2] [,3] [,4] [,5] [,6] [,7]    [,8] [,9] [,10] [,11]
>  [1,]    0    0    0    0    0    0    0 422.619 1625   750  2500
>  [2,]    0    0    0    0    0    0    0 422.619 1625   750  2500
>  [3,]    0    0    0    0    0    0    0   0.000    0     0     0
>  [4,]    0    0    0    0    0    0    0   0.000    0     0     0
>  [5,]    0    0    0    0    0    0    0   0.000    0     0     0
>  [6,]    0    0    0    0    0    0    0   0.000    0     0     0
>  [7,]    0    0    0    0    0    0    0   0.000    0     0     0
>  [8,]    0    0    0    0    0    0    0   0.000    0     0     0
>  [9,]    0    0    0    0    0    0    0   0.000    0     0     0
> [10,]    0    0    0    0    0    0    0   0.000    0     0     0
> [11,]    0    0    0    0    0    0    0   0.000    0     0     0
>
> $F[[4]]
```

```
>       [,1] [,2] [,3] [,4] [,5] [,6]     [,7]    [,8]     [,9]    [,10]    [,11]
>  [1,]    0    0    0    0    0    0 39.35185 472.586 1867.063 1208.333 2833.333
>  [2,]    0    0    0    0    0    0 39.35185 472.586 1867.063 1208.333 2833.333
>  [3,]    0    0    0    0    0    0  0.00000   0.000    0.000    0.000    0.000
>  [4,]    0    0    0    0    0    0  0.00000   0.000    0.000    0.000    0.000
>  [5,]    0    0    0    0    0    0  0.00000   0.000    0.000    0.000    0.000
>  [6,]    0    0    0    0    0    0  0.00000   0.000    0.000    0.000    0.000
>  [7,]    0    0    0    0    0    0  0.00000   0.000    0.000    0.000    0.000
>  [8,]    0    0    0    0    0    0  0.00000   0.000    0.000    0.000    0.000
>  [9,]    0    0    0    0    0    0  0.00000   0.000    0.000    0.000    0.000
> [10,]    0    0    0    0    0    0  0.00000   0.000    0.000    0.000    0.000
> [11,]    0    0    0    0    0    0  0.00000   0.000    0.000    0.000    0.000
>
>
> $hstages
> [1] NA
>
> $agestages
>   NA
> 1 NA
>
> $ahstages
>    stage_id stage original_size original_size_b original_size_c min_age max_age
> 1         1    SD           0.0              NA              NA      NA      NA
> 2         2    P1           0.0              NA              NA      NA      NA
> 3         3    P2           0.0              NA              NA      NA      NA
> 4         4    P3           0.0              NA              NA      NA      NA
> 5         5    SL           0.0              NA              NA      NA      NA
> 6         6     D           0.0              NA              NA      NA      NA
> 7         7   XSm           1.0              NA              NA      NA      NA
> 8         8    Sm           3.0              NA              NA      NA      NA
> 9         9    Md           6.0              NA              NA      NA      NA
> 10       10    Lg          11.0              NA              NA      NA      NA
> 11       11   XLg          19.5              NA              NA      NA      NA
>    repstatus obsstatus propstatus immstatus matstatus entrystage indataset
> 1          0         0          1         0         0          1         0
> 2          0         0          0         1         0          1         0
> 3          0         0          0         1         0          0         0
> 4          0         0          0         1         0          0         0
> 5          0         0          0         1         0          0         0
> 6          0         0          0         0         1          0         1
> 7          1         1          0         0         1          0         1
> 8          1         1          0         0         1          0         1
> 9          1         1          0         0         1          0         1
> 10         1         1          0         0         1          0         1
> 11         1         1          0         0         1          0         1
>    binhalfwidth_raw sizebin_min sizebin_max sizebin_center sizebin_width
> 1               0.0         0.0         0.0            0.0             0
> 2               0.0         0.0         0.0            0.0             0
> 3               0.0         0.0         0.0            0.0             0
> 4               0.0         0.0         0.0            0.0             0
> 5               0.0         0.0         0.0            0.0             0
> 6               0.5        -0.5         0.5            0.0             1
```

```
> 7              0.5        0.5        1.5          1.0           1
> 8              1.5        1.5        4.5          3.0           3
> 9              1.5        4.5        7.5          6.0           3
> 10             3.5        7.5       14.5         11.0           7
> 11             5.0       14.5       24.5         19.5          10
>    binhalfwidthb_raw sizebinb_min sizebinb_max sizebinb_center sizebinb_width
> 1                 NA           NA           NA              NA             NA
> 2                 NA           NA           NA              NA             NA
> 3                 NA           NA           NA              NA             NA
> 4                 NA           NA           NA              NA             NA
> 5                 NA           NA           NA              NA             NA
> 6                 NA           NA           NA              NA             NA
> 7                 NA           NA           NA              NA             NA
> 8                 NA           NA           NA              NA             NA
> 9                 NA           NA           NA              NA             NA
> 10                NA           NA           NA              NA             NA
> 11                NA           NA           NA              NA             NA
>    binhalfwidthc_raw sizebinc_min sizebinc_max sizebinc_center sizebinc_width
> 1                 NA           NA           NA              NA             NA
> 2                 NA           NA           NA              NA             NA
> 3                 NA           NA           NA              NA             NA
> 4                 NA           NA           NA              NA             NA
> 5                 NA           NA           NA              NA             NA
> 6                 NA           NA           NA              NA             NA
> 7                 NA           NA           NA              NA             NA
> 8                 NA           NA           NA              NA             NA
> 9                 NA           NA           NA              NA             NA
> 10                NA           NA           NA              NA             NA
> 11                NA           NA           NA              NA             NA
>    group                       comments alive
> 1      0                   Dormant seed     1
> 2      0               1st yr protocorm     1
> 3      0               2nd yr protocorm     1
> 4      0               3rd yr protocorm     1
> 5      0                       Seedling     1
> 6      0                  Dormant adult     1
> 7      0    Extra small adult (1 shoot)     1
> 8      0       Small adult (2-4 shoots)     1
> 9      0      Medium adult (5-7 shoots)     1
> 10     0      Large adult (8-14 shoots)     1
> 11     0 Extra large adult (>14 shoots)     1
>
> $labels
>   pop patch
> 1   1     A
> 2   1     B
> 3   1     C
> 4   1     0
>
> $matrixqc
>       [,1]
> [1,]   114
> [2,]    34
```

```
> [3,]    4
>
> attr(,"class")
> [1] "lefkoMat"
```

A quick scan through our output shows that we have 4 matrices. The `labels` element shows us the order of these. There is no time term in the `labels` element, because all matrices are temporal means. Instead, we see that the first 3 matrices are the patch-level means for patches `A`, `B`, and `C`. This is followed by the overall population mean matrix, listed as patch `0`. It also pays to look at the summary.

```
summary(cyp2rp_mean)
>
> This ahistorical lefkoMat object contains 4 matrices.
>
> Each matrix is square with 11 rows and columns, and a total of 121 elements.
> A total of 114 survival transitions were estimated, with 28.5 per matrix.
> A total of 34 fecundity transitions were estimated, with 8.5 per matrix.
> This lefkoMat object covers 1 populations, 4 patches, and 0 time steps.
>
> Survival probability sum check (each matrix represented by column in order):
>          [,1]  [,2]  [,3]  [,4]
> Min.    0.000 0.100 0.100 0.100
> 1st Qu. 0.100 0.140 0.140 0.140
> Median  0.200 0.600 0.600 0.467
> Mean    0.416 0.573 0.509 0.499
> 3rd Qu. 0.788 0.917 0.850 0.776
> Max.    1.000 1.000 1.000 1.000
```

We now have 4 matrices, and we see that these matrices have slightly more elements estimated, on average, than in the raw ahistorical MPM. This happened because some of the zeros in the original raw MPM were zeros only because of a sampling issue - no individuals actually transitioned through a particular transition in a particular year, but may have transitioned in other years, yielding higher numbers of non-zero elements in the arithmetic mean matrices than in the original raw matrices. Unfortunately these zeros will nonetheless drag these mean element values down artificially, potentially impacting our analyses.

Now let's create the final sets of arithmetic mean matrices for the hMPMs.

```
cyp3rp_mean <- lmean(cypmatrix3rp)

summary(cyp3rp_mean)
>
> This historical lefkoMat object contains 4 matrices.
>
> Each matrix is square with 121 rows and columns, and a total of 14641 elements.
> A total of 242 survival transitions were estimated, with 60.5 per matrix.
> A total of 74 fecundity transitions were estimated, with 18.5 per matrix.
> This lefkoMat object covers 1 populations, 4 patches, and 0 time steps.
>
> Survival probability sum check (each matrix represented by column in order):
>            [,1]  [,2]   [,3]   [,4]
> Min.    0.0000 0.000 0.0000 0.0000
> 1st Qu. 0.0000 0.000 0.0000 0.0000
> Median  0.0000 0.000 0.0000 0.0000
> Mean    0.0747 0.128 0.0947 0.0991
```

```
> 3rd Qu. 0.0000 0.250 0.0000 0.1000
> Max.    1.0000 1.000 1.0000 0.9907
```

Different parameterizations of the historical MPM

Vries & Caswell (2018) detail different approaches to the development of hMPMs, differing in how state or stage in occasion *t*-1 is incorporated into the matrix. **Full prior stage dependence models** deal with history by incorporating prior condition as the exact stage of an organism in occasion *t*-1, yielding a 2d matrix showing stage pairs in occasion *t*-1 and *t* along the columns of the matrix, and stage pairs in occasion *t* and *t*+1 along the rows of the matrix. **Prior condition models** deal with history by making the transition from stage *t* to stage *t*+1 a function of stage at occasion *t* and condition in occasion *t*-1. Prior condition can be determined in the same way that current stage is determined (e.g. size classification), or a different measure of condition can be used, such as growth (i.e. the change in size between occasions *t*-1 and *t*).

One key feature proposed by Vries & Caswell (2018) is the addition of a stage to account for the prior status of newborn individuals. This reflects a different interpretation from Ehrlén Ehrlén (2000) of the historical transition. In Ehrlén (2000), all matrix elements simply reflect the order of the events in a single transition, including both fecundity and survival-transition events. However, in Vries & Caswell (2018), these matrix elements must also reflect the history of specific individuals. In the latter case, the fact that a newborn in occasion *t* did not exist in occasion *t*-1 requires that a new prior stage is constructed and used in the matrix. This new stage only exists in the prior occasion, and is only used for newborns in the first survival transition from birth. So, for example, in a historical MPM where the 1st stage is the newborn stage and only the 3rd stage is reproductive, we add a 4th stage to the prior portion of the row and column. Thus, we may start with the following hMPM in Ehrlén (2000) format:

$$\begin{bmatrix} n_{2,AA} \\ n_{2,BA} \\ n_{2,CA} \\ n_{2,AB} \\ n_{2,BB} \\ n_{2,CB} \\ n_{2,AC} \\ n_{2,BC} \\ n_{2,CC} \end{bmatrix} = \begin{bmatrix} s_{AAA} & 0 & 0 & s_{AAB} & 0 & 0 & s_{AAC} & 0 & 0 \\ s_{BAA} & 0 & 0 & s_{BAB} & 0 & 0 & s_{BAC} & 0 & 0 \\ s_{CAA} & 0 & 0 & s_{CAB} & 0 & 0 & s_{CAC} & 0 & 0 \\ 0 & s_{ABA} & 0 & 0 & s_{ABB} & 0 & 0 & s_{ABC} & 0 \\ 0 & s_{BBA} & 0 & 0 & s_{BBB} & 0 & 0 & s_{BBC} & 0 \\ 0 & s_{CBA} & 0 & 0 & s_{CBB} & 0 & 0 & s_{CBC} & 0 \\ 0 & 0 & s_{ACA}+F_{ACA} & 0 & 0 & s_{ACB}+F_{ACB} & 0 & 0 & s_{ACC}+F_{ACC} \\ 0 & 0 & s_{BCA} & 0 & 0 & s_{BCB} & 0 & 0 & s_{BCC} \\ 0 & 0 & s_{CCA} & 0 & 0 & s_{CCB} & 0 & 0 & s_{CCC} \end{bmatrix} \begin{bmatrix} n_{1,AA} \\ n_{1,BA} \\ n_{1,CA} \\ n_{1,AB} \\ n_{1,BB} \\ n_{1,CB} \\ n_{1,AC} \\ n_{1,BC} \\ n_{1,CC} \end{bmatrix} \tag{4.7}$$

This hMPM becomes as follows in Vries & Caswell (2018) format, where the prior "pre-born" stage is shown as *P*.

$$\begin{bmatrix} n_{2,AA} \\ n_{2,BA} \\ n_{2,CA} \\ n_{2,AB} \\ n_{2,BB} \\ n_{2,CB} \\ n_{2,AC} \\ n_{2,BC} \\ n_{2,CC} \\ n_{2,AP} \\ n_{2,BP} \\ n_{2,CP} \end{bmatrix} = \begin{bmatrix} s_{AAA} & 0 & 0 & s_{AAB} & 0 & 0 & s_{AAC} & 0 & 0 & s_{AA,AP} & 0 & 0 \\ s_{BAA} & 0 & 0 & s_{BAB} & 0 & 0 & s_{BAC} & 0 & 0 & s_{BA,AP} & 0 & 0 \\ s_{CAA} & 0 & 0 & s_{CAB} & 0 & 0 & s_{CAC} & 0 & 0 & s_{CA,AP} & 0 & 0 \\ 0 & s_{ABA} & 0 & 0 & s_{ABB} & 0 & 0 & s_{ABC} & 0 & 0 & 0 & 0 \\ 0 & s_{BBA} & 0 & 0 & s_{BBB} & 0 & 0 & s_{BBC} & 0 & 0 & 0 & 0 \\ 0 & s_{CBA} & 0 & 0 & s_{CBB} & 0 & 0 & s_{CBC} & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{ACA} & 0 & 0 & s_{ACB} & 0 & 0 & s_{ACC} & 0 & 0 & 0 \\ 0 & 0 & s_{BCA} & 0 & 0 & s_{BCB} & 0 & 0 & s_{BCC} & 0 & 0 & 0 \\ 0 & 0 & s_{CCA} & 0 & 0 & s_{CCB} & 0 & 0 & s_{CCC} & 0 & 0 & 0 \\ 0 & 0 & F_{AP,CA} & 0 & 0 & F_{AP,CB} & 0 & 0 & F_{AP,CC} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} n_{1,AA} \\ n_{1,BA} \\ n_{1,CA} \\ n_{1,AB} \\ n_{1,BB} \\ n_{1,CB} \\ n_{1,AC} \\ n_{1,BC} \\ n_{1,CC} \\ n_{1,AP} \\ n_{1,BP} \\ n_{1,CP} \end{bmatrix} \tag{4.8}$$

Package `lefko3` generally implements the full prior stage dependence model approach, particularly in the development of raw matrices. However, in principle, function-based matrices developed with `lefko3` can be seen as falling within the prior condition model approach where prior condition is determined in the same way as current stage. We also implement both the Ehrlén (2000) format and the Vries & Caswell (2018) format, and use the former as the default. We leave it to the user to decide which approach to use, and point out only that the literature suggests that maternal condition can have long-term effects on offspring survival, for example through maternal care and epigenetic influences (Descamps *et al.* 2008; Beamonte-Barrientos *et al.* 2010; Dogra & Dani 2019). Thus, retaining maternal state as the prior condition of a newborn makes some logical sense and has a basis in the literature.

Vries & Caswell (2018) also suggest that hMPMs can be organized differently to yield more intuitive models. In particular, matrices may be as organized as block matrices where the component blocks are essentially matrices showing the transitions from all stages in occasion *t* to stages in occasion *t*+1 conditioned on individuals having been in the same stage in occasion *t*-1. These block component matrices can be extracted and compared against purely ahistorical matrices, thus providing an easier format to assess the influence of history even by eye. We refer to these extracted matrices as **conditional matrices**, since they show transitions from occasion *t* to occasion *t*+1 conditional on the same previous stage in occasion *t*-1. We have developed function `cond_hmpm()` to take full hMPMs and decompose them into their associated conditional matrices.

Let's build a de Vries format hMPM for the *Cypripedium candidum* dataset.

```
cypmatrix3rp_dev <- rlefko3(data = cypraw_v1, stageframe = cypframe_raw,
  year = "all", patch = "all", stages = c("stage3", "stage2", "stage1"),
  size = c("size3added", "size2added", "size1added"), supplement = cypsupp3_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ",
  format = "deVries")

summary(cypmatrix3rp_dev)
>
> This historical lefkoMat object contains 12 matrices.
>
> Each matrix is square with 132 rows and columns, and a total of 17424 elements.
> A total of 290 survival transitions were estimated, with 24.167 per matrix.
> A total of 70 fecundity transitions were estimated, with 5.833 per matrix.
> This lefkoMat object covers 1 populations, 3 patches, and 4 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>           [,1]   [,2]   [,3]   [,4]  [,5]  [,6]  [,7]  [,8]   [,9]  [,10]
> Min.    0.0000 0.0000 0.0000 0.0000 0.000 0.000 0.000 0.000 0.0000 0.0000
> 1st Qu. 0.0000 0.0000 0.0000 0.0000 0.000 0.000 0.000 0.000 0.0000 0.0000
> Median  0.0000 0.0000 0.0000 0.0000 0.000 0.000 0.000 0.000 0.0000 0.0000
> Mean    0.0714 0.0571 0.0534 0.0616 0.106 0.111 0.105 0.116 0.0811 0.0584
> 3rd Qu. 0.0000 0.0000 0.0000 0.0000 0.000 0.000 0.000 0.000 0.0000 0.0000
> Max.    1.0000 1.0000 1.0000 1.0000 1.000 1.000 1.000 1.000 1.0500 1.0000
>          [,11]  [,12]
> Min.    0.0000 0.0000
> 1st Qu. 0.0000 0.0000
> Median  0.0000 0.0000
> Mean    0.0811 0.0963
> 3rd Qu. 0.0000 0.0000
> Max.    1.0000 1.0000
> Warning: Some matrices include stages with survival probability greater than
> 1.0.
```

Our new matrices have 11 more rows and columns, and 2,783 more elements. To see what is different, compare the `hstages` element in each on your own, and you will see the inclusion of some new stage pairs with the `AlmostBorn` stage. It is also possible for some transitions to be split, occasionally yielding more transitions that were estimated, though only by about 3000 elements or so.

Matrix reduction

A final issue to discuss is matrix dimensionality reduction. Occasionally, historical matrices end up being produced in which stage-pairs exist that are not associated with any transitions. This is particularly the case with raw MPMs. The result is that sometimes all of the rows and columns associated with such a stage pair are completely full of zeros. In these situations, matrices can be reduced by eliminating the stage-pair altogether. The result is a set of smaller matrices, which is useful considering that historical MPMs are generally large and can take up a great deal of memory. We can tell R to develop reduced MPMs by using the `reduce = TRUE` option in the matrix generating function that we are using. Note that this option is available in ALL matrix generating functions, even for those creating ahistorical MPMs, and that rows and columns will be reduced only if ALL matrices within the `lefkoMat` object being produced have empty rows and columns associated with a particular stage or stage-pair.

```
cypmatrix3rp_red <- rlefko3(data = cypraw_v1, stageframe = cypframe_raw,
  year = "all", patch = "all", stages = c("stage3", "stage2", "stage1"),
  size = c("size3added", "size2added", "size1added"), supplement = cypsupp3_raw,
  yearcol = "year2", patchcol = "patchid", indivcol = "individ",
  reduce = TRUE)

summary(cypmatrix3rp_red)
>
> This historical lefkoMat object contains 12 matrices.
>
> Each matrix is square with 41 rows and columns, and a total of 1681 elements.
> A total of 386 survival transitions were estimated, with 32.167 per matrix.
> A total of 68 fecundity transitions were estimated, with 5.667 per matrix.
> This lefkoMat object covers 1 populations, 3 patches, and 4 time steps.
>
> The dataset contains a total of 74 unique individuals and 320 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>          [,1]  [,2]  [,3]  [,4]  [,5]  [,6]  [,7]  [,8]  [,9] [,10] [,11] [,12]
> Min.    0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000
> 1st Qu. 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000
> Median  0.000 0.000 0.000 0.000 0.110 0.110 0.110 0.110 0.000 0.000 0.000 0.050
> Mean    0.254 0.208 0.196 0.223 0.366 0.383 0.362 0.399 0.286 0.212 0.286 0.334
> 3rd Qu. 0.250 0.250 0.250 0.250 1.000 1.000 1.000 1.000 0.250 0.250 0.550 1.000
> Max.    1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.050 1.000 1.000 1.000
> Warning: Some matrices include stages with survival probability greater than
> 1.0.
```

Our new hMPM has matrices with 41 rows and columns, while the original unreduced hMPM has matrices with 121 rows and columns. This is a reduction of 80 rows and columns, with an overall reduction in the size of the matrix by $14641 - 1681 = 12960$ elements. This should speed up later calculations greatly.

Decomposed conditional matrices

Users wishing to check the output MPMs for errors or simply understand more about them may utilize functions `summary()` and `cond_hmpm()`. Function `summary()` summarizes each `lefkoMat` object used as input, and also checks the survival of stages, stage-pairs, or age-stages by assessing the column sums for each `U` matrix and providing warnings if any survival probabilities fall below 0 or are greater than 1. Function `cond_hmpm()` decomposes hMPMs into MPMs showing transitions from occasion t to occasion t+1, but conditioned on the same stage at occasion t-1. Thus, a single hMPM with 5 stages and 25 stage pairs would be broken down into 5 conditional MPMs, one for each stage at occasion t-1, with 5 columns and 5 rows denoting stage at occasions t and t+1, respectively. These can be examined individually, and the survival of stages from occasion t to occasion t+1 can be assessed as a function of stage in occasion t-1 by taking the associated column sums of these conditional matrices.

Literature cited

Beamonte-Barrientos, R., Velando, A., Drummond, H. & Torres, R. (2010). Senescence of maternal effects: Aging influences egg quality and rearing capacities of a long-lived bird. *The American Naturalist*, 175, 469–480.

Caswell, H. (2001). *Matrix population models: Construction, analysis, and interpretation.* Second edition. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Descamps, S., Boutin, S., Berteaux, D. & Gaillard, J.-M. (2008). Age-specific variation in survival, reproductive success and offspring quality in red squirrels: Evidence of senescence. *Oikos*, 117, 1406–1416.

Dogra, H. & Dani, K.G.S. (2019). Defining features of age-specific fertility and seed quality in senescing indeterminate annuals. *American Journal of Botany*, 106, 604–610.

Ehrlén, J. (2000). The dynamics of plant populations: Does the history of individuals matter? *Ecology*, 81, 1675–1684.

Leslie, P.H. (1945). On the use of matrices in certain population mathematics. *Biometrika*, 33, 183–212.

Shefferson, R.P., Kull, T., Hutchings, M.J., Selosse, M.-A., Jacquemyn, H., Kellett, K.M., *et al.* (2018). Drivers of vegetative dormancy across herbaceous perennial plant species. *Ecology Letters*, 21, 724–733.

Shefferson, R.P., Mizuta, R. & Hutchings, M.J. (2017). Predicting evolution in response to climate change: The example of sprouting probability in three dormancy-prone orchid species. *Royal Society Open Science*, 4, 160647.

Shefferson, R.P., Warren II, R.J. & Pulliam, H.R. (2014). Life history costs make perfect sprouting maladaptive in two herbaceous perennials. *Journal of Ecology*, 102, 1318–1328.

Vries, C. de & Caswell, H. (2018). Demography when history matters: Construction and analysis of second-order matrix population models. *Theoretical Ecology*, 11, 129–140.

