

Chapter 6

Age-by-Stage and Leslie Matrix Projection Models

The first MPMs were age-classified, and are also known as Leslie MPMs in honor of their creator (Leslie 1945). However, in many organisms age is seen as less important in determining demography than other variables. Stage-classified, or Lefkovitch, MPMs were developed with this in mind, as they allow the life history of an organism to be stratified by life history stages (Lefkovitch 1965). Life history stages can be defined as necessary by any status variable or combination of status variables (Caswell 2001). So stage-based MPMs provide a great deal of flexibility and power to analyze population dynamics.

For much of the history of the MPM, the dichotomy between age-classified and stage-classified MPMs was driven by the lack of computing power to analyze complex relationships in large matrices. With the advent of powerful home computers, more and more ecologists have begun addressing questions using **age-by-stage MPMs**, which are MPMs that incorporate both age and stage (Caswell & Salguero-Gómez 2013). Here, we provide just a short summary of core theory before building an age-by-stage MPM. We strongly advise readers interested in this style of MPM to read Caswell *et al.* (2018), which is the most comprehensive overview of the theory behind age-by-stage MPMs available.

What is an age-by-stage MPM?

To begin addressing the question of what an age-by-stage MPM is, let us first address the issue of what an age-classified MPM is. Age-classified, or Leslie, MPMs treat the life history of an organism as a series of ages rather than stages. Each age is of equal duration, and the number of ages to include is decided through demographic studies that attempt to determine which groups of ages have unique demographic characteristics.

We will illustrate with an example. Let us suppose that we are studying an organism that can live for potentially many years, such as a long-lived seabird. We conduct some monitoring, and find that the seabird at our monitored population seems to follow a basic pattern in which survival is relatively low in the first year, higher in the second, and from the third year on survival is typically quite high. Although the maximum longevity is unknown, nonetheless birds seem to live not much longer than 20 years. Fecundity occurs from the third year on, with the first two years spent as a juvenile. In this circumstance, we might have a Leslie matrix that looks like this:

$$\begin{bmatrix} 0 & 0 & F_{1,3} \\ S_{2,1} & 0 & 0 \\ 0 & S_{3,2} & S_{3,3} \end{bmatrix} \quad (6.1)$$

This matrix includes only three rows and columns. Survival-transition probabilities are typically just below the diagonal, and represent the probability of surviving from age i to age $i + 1$. There is a notable exception in element $S_{3,3}$, which is the survival-transition probability for an organism to stay alive within the final age group. This approach is standard, because it allows organisms to live on without an explicit maximum longevity, which is generally unknown or perhaps even nonexistent for most organisms. Fecundity occurs in the top row ($F_{1,3}$), since all offspring begin in the first age.

Age-by-stage MPMs differ because they incorporate both age and stage, and so the matrix needs to be expanded to allow both characteristics. The standard approach is to create block matrices in which each age has potentially several stages, and survival-transition probabilities must describe the probability of transitioning from each stage at one age to each stage in the next.

As an example, let's take the three stage life history above, which has a single newborn stage and two adult stages, only one of which is reproductive. Let's further assume that age impacts survival and fecundity only for the first 4 years, beyond which survival and fecundity transitions remain essentially the same. This leads to the following age-by-stage matrix:

$$\begin{bmatrix} 0 & 0 & F_{1A,2C} & 0 & F_{1A,3C} & 0 & F_{1A,4+C} \\ S_{2B,1A} & 0 & 0 & 0 & 0 & 0 & 0 \\ S_{2C,1A} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{3B,2B} & S_{3B,2C} & 0 & 0 & 0 & 0 \\ 0 & S_{3C,2B} & S_{3C,2C} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{4B,3B} & S_{4B,3C} & S_{5+B,4B} & S_{5+B,4C} \\ 0 & 0 & 0 & S_{4C,3B} & S_{4C,3C} & S_{5+C,4B} & S_{5+C,4C} \end{bmatrix} \quad (6.2)$$

Here, we have only one possible initial stage, followed by two possible stages in all later ages. Looking only at the columns, column 1 refers to age 1, which only includes the seedling stage; columns 2 and 3 refer to age 2, which includes non-reproductive and reproductive adult stages; columns 4 and 5 refer to age 3, which also includes non-reproductive and reproductive adult stages; and columns 6 and 7 refer to ages 4 and higher, once again also including non-reproductive and reproductive adult stages. While the columns refer to the *From* ages and stages, the rows refer to the *To* ages and stages, and in the same order as the columns. If we ignore stage and consider only the placement of age-related transitions, then we see that we are still generally following the Leslie MPM pattern of placing survival-transition probabilities below the diagonal for all but the final transitions. We also have more fecundity terms because although only one stage is reproductive, multiple reproductive ages occur, and all of these stay within the first row (other rows are possible only if the life history of the organism can start from multiple different stages).

The above matrix is ahistorical. However, unlike a pure Leslie MPM, the possibility of different stages within each age allows for the estimation of historical age-by-stage MPMs. Package `lefk3` does not currently support historical age-by-stage matrices, but we will eventually add this capability.

Developing age-by-stage MPMs in `lefk3`

For our example, we will use the `lathyrus` dataset that comes with `lefk3` to illustrate the estimation of **age-by-stage function-based MPMs**. First, load the dataset, and then look at a summary as well as its dimensions.

```
data(lathyrus)
summary(lathyrus)
> SUBPLOT          GENET          Volume88          lnVol188
> Min.   :1.000    Min.   : 1.0    Min.   : 3.4    Min.   :1.200
> 1st Qu.:2.000    1st Qu.: 48.0    1st Qu.: 63.0    1st Qu.:4.100
> Median :3.000    Median : 97.0    Median : 732.5    Median :6.600
> Mean   :3.223    Mean   :110.2    Mean   : 749.4    Mean   :5.538
> 3rd Qu.:4.000    3rd Qu.:167.5    3rd Qu.:1025.5    3rd Qu.:6.900
> Max.   :6.000    Max.   :284.0    Max.   :7032.0    Max.   :8.900
> NA's   :404      NA's   :404
> FCODE88          Flow88          Intactseed88  Dead1988          Dormant1988
> Min.   :0.0000    Min.   : 1.00    Min.   : 0      Mode:logical     Mode:logical
> 1st Qu.:0.0000    1st Qu.: 4.00    1st Qu.: 0      NA's:1119         NA's:1119
> Median :0.0000    Median : 8.00    Median : 0
> Mean   :0.3399    Mean   :11.86    Mean   : 3
> 3rd Qu.:1.0000    3rd Qu.:15.00    3rd Qu.: 4
> Max.   :1.0000    Max.   :66.00    Max.   :34
> NA's   :404      NA's   :910     NA's   :875
> Missing1988      Seedling1988      Volume89          lnVol189
> Mode:logical     Min.   :1.000    Min.   : 1.8    Min.   :0.600
> NA's:1119        1st Qu.:2.000    1st Qu.: 15.6    1st Qu.:2.700
> Median :2.000    Median : 118.8    Median :4.800
> Mean   :2.144    Mean   : 573.3    Mean   :4.855
> 3rd Qu.:3.000    3rd Qu.: 968.8    3rd Qu.:6.900
> Max.   :3.000    Max.   :6539.4    Max.   :8.800
```

```

>      NA's :1022  NA's :294  NA's :294
>      FCODE89      Flow89      Intactseed89      Dead1989
> Min. :0.0000  Min. : 1.00  Min. : 0.000  Min. :1
> 1st Qu.:0.0000  1st Qu.: 5.00  1st Qu.: 0.000  1st Qu.:1
> Median :0.0000  Median :11.00  Median : 5.000  Median :1
> Mean :0.2667  Mean :14.88  Mean : 8.273  Mean :1
> 3rd Qu.:1.0000  3rd Qu.:20.00  3rd Qu.:13.000  3rd Qu.:1
> Max. :1.0000  Max. :97.00  Max. :66.000  Max. :1
> NA's :294  NA's :906  NA's :899  NA's :1077
> Dormant1989  Missing1989  Seedling1989  Volume90  lnVol190
> Min. :1  Min. :1  Min. :1.000  Min. : 2.1  Min. :0.700
> 1st Qu.:1  1st Qu.:1  1st Qu.:2.000  1st Qu.: 12.6  1st Qu.:2.500
> Median :1  Median :1  Median :2.000  Median : 61.0  Median :4.100
> Mean :1  Mean :1  Mean :2.136  Mean : 244.1  Mean :4.207
> 3rd Qu.:1  3rd Qu.:1  3rd Qu.:2.000  3rd Qu.: 295.2  3rd Qu.:5.700
> Max. :1  Max. :1  Max. :3.000  Max. :4242.8  Max. :8.400
> NA's :1046  NA's :1112  NA's :1001  NA's :245  NA's :245
> FCODE90      Flow90      Intactseed90      Dead1990
> Min. :0.0000  Min. : 1.000  Min. : 0.000  Min. :1
> 1st Qu.:0.0000  1st Qu.: 3.000  1st Qu.: 0.000  1st Qu.:1
> Median :0.0000  Median : 6.000  Median : 0.000  Median :1
> Mean :0.1581  Mean : 8.104  Mean : 2.514  Mean :1
> 3rd Qu.:0.0000  3rd Qu.:10.750  3rd Qu.: 1.000  3rd Qu.:1
> Max. :1.0000  Max. :54.000  Max. :37.000  Max. :1
> NA's :246  NA's :985  NA's :981  NA's :1007
> Dormant1990  Missing1990  Seedling1990  Volume91  lnVol191
> Min. :1  Min. :1  Min. :1.000  Min. : 4.0  Min. :1.400
> 1st Qu.:1  1st Qu.:1  1st Qu.:2.000  1st Qu.: 12.0  1st Qu.:2.500
> Median :1  Median :1  Median :2.000  Median : 118.5  Median :4.800
> Mean :1  Mean :1  Mean :2.186  Mean : 418.7  Mean :4.642
> 3rd Qu.:1  3rd Qu.:1  3rd Qu.:2.000  3rd Qu.: 689.7  3rd Qu.:6.500
> Max. :1  Max. :1  Max. :3.000  Max. :6645.8  Max. :8.800
> NA's :1054  NA's :1105  NA's :1049  NA's :305  NA's :305
> FCODE91      Flow91      Intactseed91      Dead1991      Dormant1991
> Min. :0.0000  Min. : 1.00  Min. : 0.000  Min. :1  Min. :1
> 1st Qu.:0.0000  1st Qu.: 4.00  1st Qu.: 0.000  1st Qu.:1  1st Qu.:1
> Median :0.0000  Median : 8.00  Median : 3.500  Median :1  Median :1
> Mean :0.2525  Mean :11.12  Mean : 5.805  Mean :1  Mean :1
> 3rd Qu.:1.0000  3rd Qu.:15.00  3rd Qu.:10.000  3rd Qu.:1  3rd Qu.:1
> Max. :1.0000  Max. :48.00  Max. :48.000  Max. :1  Max. :1
> NA's :307  NA's :954  NA's :919  NA's :925  NA's :1034
> Missing1991  Seedling1991
> Min. :1  Min. :1.000
> 1st Qu.:1  1st Qu.:2.000
> Median :1  Median :2.000
> Mean :1  Mean :1.973
> 3rd Qu.:1  3rd Qu.:2.000
> Max. :1  Max. :3.000
> NA's :1095  NA's :1082
dim(lathyrus)
> [1] 1119 38

```

This dataset includes information on 1,119 individuals, so there are 1,119 rows with data (not counting the header). There are 38 columns. The first two columns are variables identifying each individual (SUBPLOT

refers to the patch, and GENET refers to individual identity), with each individual's data entirely restricted to one row. This is followed by four sets of nine columns, each named `VolumeXX`, `lnVolXX`, `FCODEXX`, `FlowXX`, `IntactseedXX`, `Dead19XX`, `DormantXX`, `Missing19XX`, and `SeedlingXX`, where `XX` corresponds to the year of observation and with years organized consecutively. Thus, columns 3-11 refer to year 1988, columns 12-20 refer to year 1989, etc. This strictly repeated pattern allows us to manipulate the original dataset quickly and efficiently via `lefko3`. We should know the total number of years of data in the dataset, which is 4 years here (includes all years from and including 1988 to 1991). Ideally, we should also have arranged the columns in the same order for each year, with years in consecutive order with no extra columns between them. Note that this order is not required, but it makes life easier because following a strictly repeating pattern allows us to skip inputting the names or numbers of each column of data directly later during demographic data formatting (step 2a below).

To begin, we will create a **stageframe** that describes the organism's life cycle for this dataset. In this case, the life history model is a life cycle graph (Fig. 6.1). This model is based on the life history model provided in Ehrlén (2000), but we utilize a different size classification based on the log leaf volume to make the size distribution more closely match a symmetric and somewhat normal distribution.

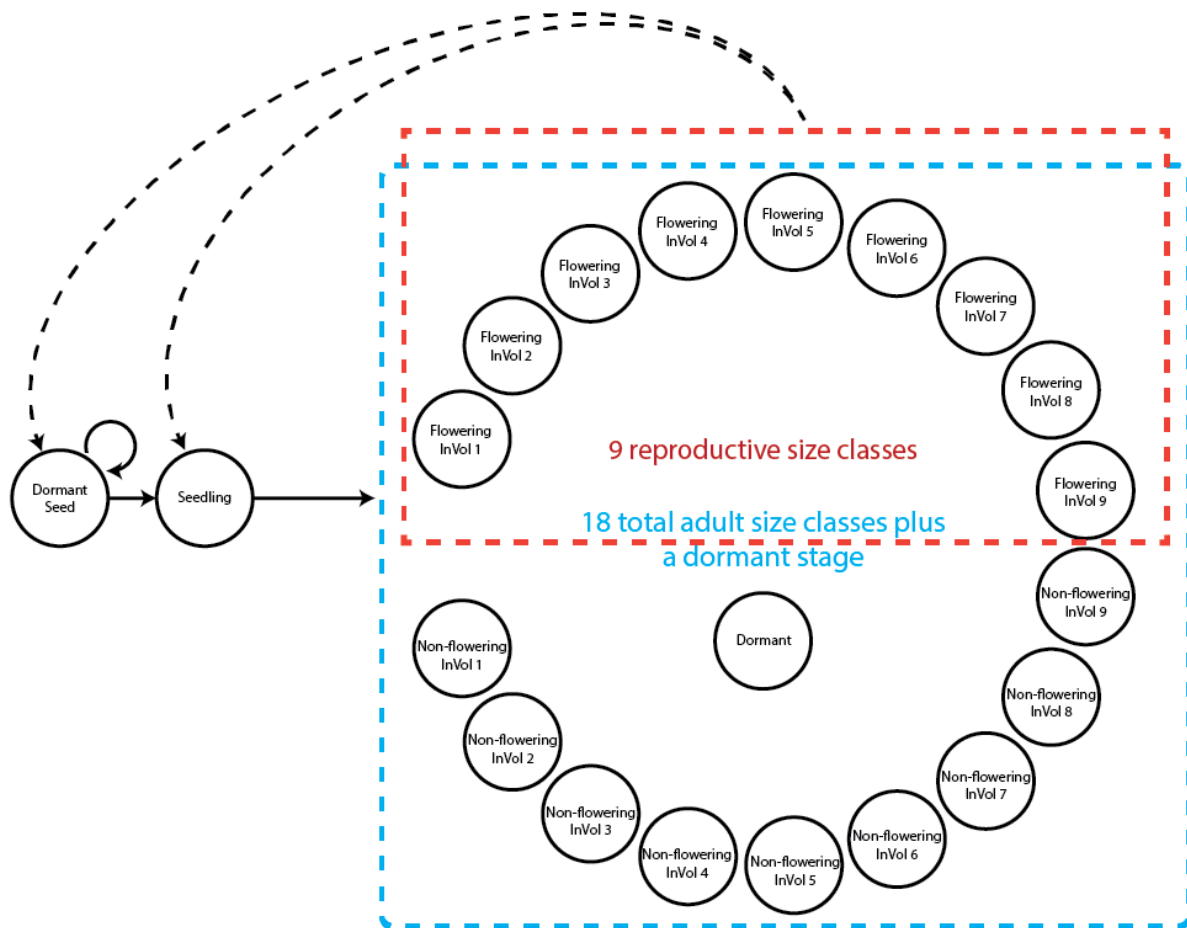


Figure 6.1: Life history model of *Lathyrus vernus* using log leaf volume as the size classification metric

Our stageframe needs to include complete descriptions of all stages that occur in the dataset, with each stage defined uniquely, and also needs to describe for each stage portrayed in our life history model. Since this object can be used for automated classification of individuals, all sizes, reproductive states, and other characteristics defining each proper stage in the dataset need to be accounted for explicitly. This can be difficult if a few data points exist outside the range of sizes specified in the stageframe. Such points can cause

problems, because rare stages can cause an overestimation of survival for existing stages, and can also yield spurious values for survival-transition probabilities and fecundity rates. The final description of each stage occurring in the dataset must also avoid complete overlap with any other stage also found in the dataset, although partial overlap is allowed and expected.

Before creating the stage frame, let's explore the possible size variables. We will particularly look at summaries of the distribution of original and log sizes.

```
summary(c(lathyrus$Volume88, lathyrus$Volume89, lathyrus$Volume90, lathyrus$Volume91))
>   Min. 1st Qu.  Median    Mean 3rd Qu.    Max.   NA's
>   1.8   14.7   123.0   484.2  732.5  7032.0  1248
summary(c(lathyrus$lnVol88, lathyrus$lnVol89, lathyrus$lnVol90, lathyrus$lnVol91))
>   Min. 1st Qu.  Median    Mean 3rd Qu.    Max.   NA's
>   0.600  2.700  4.800  4.777  6.600  8.900  1248
```

The upper summary shows the original size, while the lower line shows the size given in logarithmic terms. We should note the size minima and maxima, because we have been using 0 as the size of vegetatively dormant individuals. The lowest uncorrected size is , with a maximum of . The minimum corrected size is , and the maximum corrected size is . Since the minimum corrected size is above 0 (i.e. all log sizes should be positive), and since the number of NAs has not increased (increased NAs would suggest that some unusable log sizes occur in the dataset), we are still able to use the log size value 0 as an indicator of vegetative dormancy. Note, however, that vegetative dormancy is also currently included in the many NAs that occur in size variables in this dataset.

It can also help to take a look at plots of these distributions. We will plot raw and log volume.

```
par(mfrow=c(1,2))
plot(density(c(lathyrus$Volume88, lathyrus$Volume89, lathyrus$Volume90,
  lathyrus$Volume91), na.rm = TRUE), main = "", xlab = "Volume", bty = "n")
plot(density(c(lathyrus$lnVol88, lathyrus$lnVol89, lathyrus$lnVol90,
  lathyrus$lnVol91), na.rm = TRUE), main = "", xlab = "Log volume", bty = "n")
```

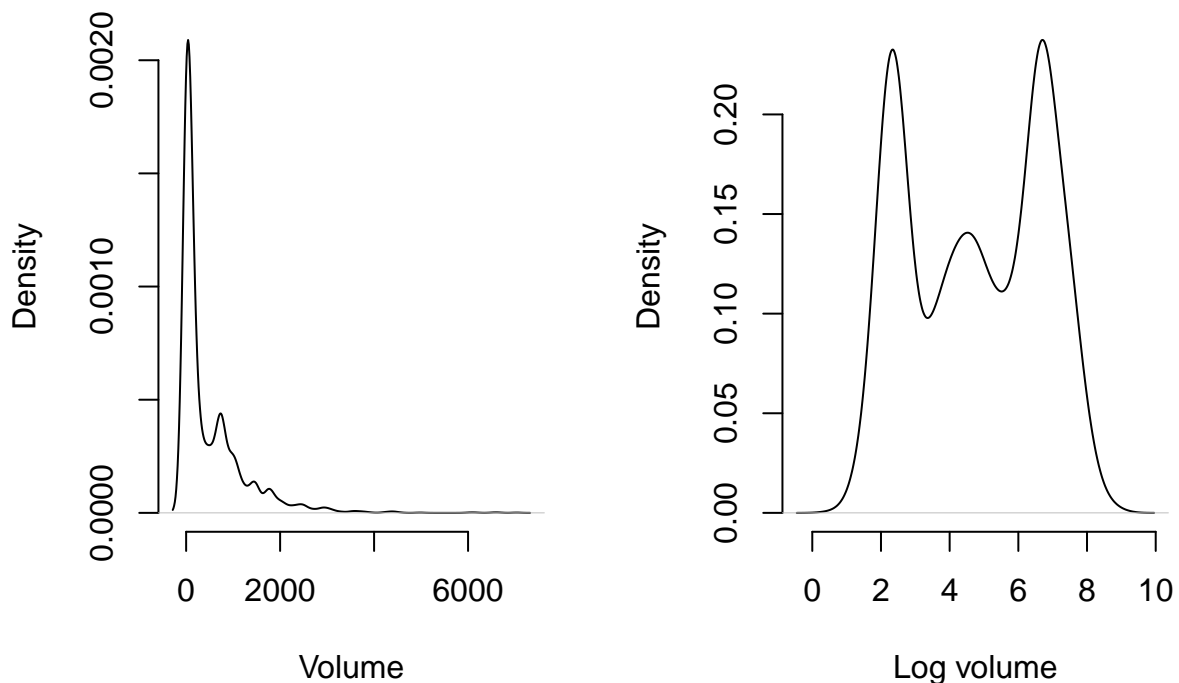


Figure 6.2: Density plot of aboveground plant volume

Note how highly skewed the raw volume distribution is. This might cause some difficulty if we used raw size untransformed and with a Gaussian distribution. Certainly, a Gamma distribution would be perfectly justified, and users are urged to try that approach. We will use the log volume here, which looks ‘better’ than the raw volume distribution in the sense that it is closer to some semblance of a Gaussian distribution, mostly through an increased level of symmetry. We can then assume that log volume is Gaussian-distributed and that the mean bears no relationship to the variance.

We will now develop a stageframe that incorporates the log volume of size. We will build this by creating vectors of the values describing each stage, always in the same order. Because we wish to build an age-by-stage MPM, we will also incorporate age information for each stage. Here, we include minimum and maximum ages for each stage via the vectors `minima` and `maxima` (NA in the maximum age vector is interpreted as meaning that there is no maximum).

```
sizevector <- c(0, 4.6, 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 1, 2, 3, 4, 5, 6, 7, 8, 9)
stagevector <- c("Sd", "Sd1", "Dorm", "Sz1nr", "Sz2nr", "Sz3nr", "Sz4nr",
  "Sz5nr", "Sz6nr", "Sz7nr", "Sz8nr", "Sz9nr", "Sz1r", "Sz2r", "Sz3r", "Sz4r",
  "Sz5r", "Sz6r", "Sz7r", "Sz8r", "Sz9r")
repvector <- c(0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 1, 1, 1, 1, 1, 1, 1)
obsvector <- c(0, 1, 0, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1)
matvector <- c(0, 0, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1)
immvector <- c(1, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0)
propvector <- c(1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0)
indataset <- c(0, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1)
binvec <- c(0, 4.6, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5, 0.5,
  0.5, 0.5, 0.5, 0.5, 0.5, 0.5)
minima <- c(0, 0, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1)
maxima <- c(NA, 1, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA, NA)
comments <- c("Dormant seed", "Seedling", "Dormant", "Size 1 Veg", "Size 2 Veg",
  "Size 3 Veg", "Size 4 Veg", "Size 5 Veg", "Size 6 Veg", "Size 7 Veg",
  "Size 8 Veg", "Size 9 Veg", "Size 1 Flo", "Size 2 Flo", "Size 3 Flo",
  "Size 4 Flo", "Size 5 Flo", "Size 6 Flo", "Size 7 Flo", "Size 8 Flo",
  "Size 9 Flo")
lathframe1n <- sf_create(sizes = sizevector, stagenames = stagevector,
  repstatus = repvector, obsstatus = obsvector, propstatus = propvector,
  immstatus = immvector, matstatus = matvector, indataset = indataset,
  binhalfwidth = binvec, minage = minima, maxage = maxima, comments = comments)

lathframe1n
>   stage size size_b size_c min_age max_age repstatus obsstatus propstatus
> 1    Sd  0.0    NA    NA      0     NA         0         0         1
> 2   Sd1  4.6    NA    NA      0      1         0         1         0
> 3  Dorm  0.0    NA    NA      1     NA         0         0         0
> 4 Sz1nr  1.0    NA    NA      1     NA         0         1         0
> 5 Sz2nr  2.0    NA    NA      1     NA         0         1         0
> 6 Sz3nr  3.0    NA    NA      1     NA         0         1         0
> 7 Sz4nr  4.0    NA    NA      1     NA         0         1         0
> 8 Sz5nr  5.0    NA    NA      1     NA         0         1         0
> 9 Sz6nr  6.0    NA    NA      1     NA         0         1         0
> 10 Sz7nr 7.0    NA    NA      1     NA         0         1         0
> 11 Sz8nr 8.0    NA    NA      1     NA         0         1         0
> 12 Sz9nr 9.0    NA    NA      1     NA         0         1         0
> 13 Sz1r  1.0    NA    NA      1     NA         1         1         0
> 14 Sz2r  2.0    NA    NA      1     NA         1         1         0
> 15 Sz3r  3.0    NA    NA      1     NA         1         1         0
```

```

> 16 Sz4r 4.0 NA NA 1 NA 1 1 0
> 17 Sz5r 5.0 NA NA 1 NA 1 1 0
> 18 Sz6r 6.0 NA NA 1 NA 1 1 0
> 19 Sz7r 7.0 NA NA 1 NA 1 1 0
> 20 Sz8r 8.0 NA NA 1 NA 1 1 0
> 21 Sz9r 9.0 NA NA 1 NA 1 1 0
>   immstatus matstatus indataset binhalfwidth_raw sizebin_min sizebin_max
> 1         1         0         0         0.0         0.0         0.0
> 2         1         0         1         4.6         0.0         9.2
> 3         0         1         1         0.5        -0.5         0.5
> 4         0         1         1         0.5         0.5         1.5
> 5         0         1         1         0.5         1.5         2.5
> 6         0         1         1         0.5         2.5         3.5
> 7         0         1         1         0.5         3.5         4.5
> 8         0         1         1         0.5         4.5         5.5
> 9         0         1         1         0.5         5.5         6.5
> 10        0         1         1         0.5         6.5         7.5
> 11        0         1         1         0.5         7.5         8.5
> 12        0         1         1         0.5         8.5         9.5
> 13        0         1         1         0.5         0.5         1.5
> 14        0         1         1         0.5         1.5         2.5
> 15        0         1         1         0.5         2.5         3.5
> 16        0         1         1         0.5         3.5         4.5
> 17        0         1         1         0.5         4.5         5.5
> 18        0         1         1         0.5         5.5         6.5
> 19        0         1         1         0.5         6.5         7.5
> 20        0         1         1         0.5         7.5         8.5
> 21        0         1         1         0.5         8.5         9.5
>   sizebin_center sizebin_width binhalfwidthb_raw sizebinb_min sizebinb_max
> 1             0.0             0.0             NA             NA             NA
> 2             4.6             9.2             NA             NA             NA
> 3             0.0             1.0             NA             NA             NA
> 4             1.0             1.0             NA             NA             NA
> 5             2.0             1.0             NA             NA             NA
> 6             3.0             1.0             NA             NA             NA
> 7             4.0             1.0             NA             NA             NA
> 8             5.0             1.0             NA             NA             NA
> 9             6.0             1.0             NA             NA             NA
> 10            7.0             1.0             NA             NA             NA
> 11            8.0             1.0             NA             NA             NA
> 12            9.0             1.0             NA             NA             NA
> 13            1.0             1.0             NA             NA             NA
> 14            2.0             1.0             NA             NA             NA
> 15            3.0             1.0             NA             NA             NA
> 16            4.0             1.0             NA             NA             NA
> 17            5.0             1.0             NA             NA             NA
> 18            6.0             1.0             NA             NA             NA
> 19            7.0             1.0             NA             NA             NA
> 20            8.0             1.0             NA             NA             NA
> 21            9.0             1.0             NA             NA             NA
>   sizebinb_center sizebinb_width binhalfwidthc_raw sizebinc_min sizebinc_max
> 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
> 12     NA      NA      NA      NA      NA
> 13     NA      NA      NA      NA      NA
> 14     NA      NA      NA      NA      NA
> 15     NA      NA      NA      NA      NA
> 16     NA      NA      NA      NA      NA
> 17     NA      NA      NA      NA      NA
> 18     NA      NA      NA      NA      NA
> 19     NA      NA      NA      NA      NA
> 20     NA      NA      NA      NA      NA
> 21     NA      NA      NA      NA      NA
>      sizebinc_center sizebinc_width group      comments
> 1      NA      NA      0 Dormant seed
> 2      NA      NA      0      Seedling
> 3      NA      NA      0      Dormant
> 4      NA      NA      0 Size 1 Veg
> 5      NA      NA      0 Size 2 Veg
> 6      NA      NA      0 Size 3 Veg
> 7      NA      NA      0 Size 4 Veg
> 8      NA      NA      0 Size 5 Veg
> 9      NA      NA      0 Size 6 Veg
> 10     NA      NA      0 Size 7 Veg
> 11     NA      NA      0 Size 8 Veg
> 12     NA      NA      0 Size 9 Veg
> 13     NA      NA      0 Size 1 Flo
> 14     NA      NA      0 Size 2 Flo
> 15     NA      NA      0 Size 3 Flo
> 16     NA      NA      0 Size 4 Flo
> 17     NA      NA      0 Size 5 Flo
> 18     NA      NA      0 Size 6 Flo
> 19     NA      NA      0 Size 7 Flo
> 20     NA      NA      0 Size 8 Flo
> 21     NA      NA      0 Size 9 Flo

```

Once the stageframe is created, we can reorganize the dataset into historically-formatted vertical (hfv) format. To handle this, we will use the `verticalize3()` function, which creates historically-formatted vertical datasets, as below. We will also replace NAs in size and fecundity variables with 0s for `modelsearch` to work properly when we build models of vital rates, so we will now set `NAas0 = TRUE`. Some care needs to be taken with this last step, since some authors give missing values extra meaning not present in a value of 0. In our case, a missing value indicates that a plant was dead (both size and fecundity are missing), was alive but not sprouting (size was missing), or was alive but did not produce seed (fecundity was missing). In all cases, these NA values may be replaced by 0, because other variables indicate those conditions.

We also have two choices for use as our reproductive status and fecundity variables. The first choice, `FCODE88` indicates whether a plant flowered. The second choice, `Intactseed88`, indicates the number of seed produced. The choice of which to use depends strongly on the aims of the study. In our case, we would like to treat all plants that flowered as reproductive, but treat fecundity in terms of real seed produced. The

reason is that we believe that flowering plants have a different demography than non-flowering plants, either reflecting reproductive costs, or, conversely, because flowering plants might have more resources and hence higher survival than non-flowering plants, and so we wish to separate transitions among these two groups. So, let's use `FCODE88` to indicate reproductive status, and `Intactseed88` to indicate fecundity. Once complete, we will look at a summary.

Finally, note that in the input to the following function, we utilize a strictly repeating pattern of variable names arranged in the same order for each monitoring occasion. This arrangement allows us to enter only the first variable in each set, as long as `noyears` and `blocksize` are set properly and no gaps or shuffles appear in the dataset. The data management functions that we have created for `lefko3` do not require such repeating patterns, but they do make the required input in the function much shorter and more succinct.

```
lathvertln <- verticalize3(lathyrus, noyears = 4, firstyear = 1988,
  patchidcol = "SUBPLOT", individcol = "GENET", blocksize = 9,
  juvcol = "Seedling1988", sizeacol = "lnVol88", repstracol = "FCODE88",
  fecacol = "Intactseed88", deadacol = "Dead1988",
  nonobsacol = "Dormant1988", stageassign = lathframeln,
  stagesize = "sizea", censorcol = "Missing1988", censorkeep = NA,
  NAas0 = TRUE, censor = TRUE)
dim(lathvertln)
> [1] 2552 42
summary(lathvertln)
>      rowid      popid      patchid      individ      year2
> Min.   : 1.0      :2552      1:674      Length:2552      Min.   :1988
> 1st Qu.: 239.8      :206      2:206      Class :character 1st Qu.:1988
> Median : 523.0      :560      3:560      Mode  :character Median :1989
> Mean   : 538.7      :478      4:478      Mean   :1989
> 3rd Qu.: 823.2      :312      5:312      3rd Qu.:1990
> Max.   :1119.0     :322      6:322      Max.   :1990
>      firstseen      lastseen      obsage      obslifespan      sizea1
> Min.   :1988      Min.   :1988      Min.   :0.0000      Min.   :0.00      Min.   :0.0000
> 1st Qu.:1988      1st Qu.:1991      1st Qu.:0.0000      1st Qu.:2.00      1st Qu.:0.0000
> Median :1988      Median :1991      Median :1.0000      Median :3.00      Median :2.200
> Mean   :1988      Mean   :1991      Mean   :0.8288      Mean   :2.45      Mean   :2.947
> 3rd Qu.:1988      3rd Qu.:1991      3rd Qu.:1.0000      3rd Qu.:3.00      3rd Qu.:6.400
> Max.   :1990      Max.   :1991      Max.   :2.0000      Max.   :3.00      Max.   :8.900
>      repstra1      fecal      juvgiven1      obsstatus1
> Min.   :0.0000      Min.   : 0.0000      Min.   :0.00000      Min.   :0.0000
> 1st Qu.:0.0000      1st Qu.: 0.0000      1st Qu.:0.00000      1st Qu.:0.0000
> Median :0.0000      Median : 0.0000      Median :0.00000      Median :1.0000
> Mean   :0.1795      Mean   : 0.9793      Mean   :0.06309      Mean   :0.5537
> 3rd Qu.:0.0000      3rd Qu.: 0.0000      3rd Qu.:0.00000      3rd Qu.:1.0000
> Max.   :1.0000      Max.   :66.0000      Max.   :1.00000      Max.   :1.0000
>      repstatus1      fecstatus1      matstatus1      alive1
> Min.   :0.0000      Min.   :0.00000      Min.   :0.0000      Min.   :0.0000
> 1st Qu.:0.0000      1st Qu.:0.00000      1st Qu.:0.0000      1st Qu.:0.0000
> Median :0.0000      Median :0.00000      Median :1.0000      Median :1.0000
> Mean   :0.1795      Mean   :0.08895      Mean   :0.5192      Mean   :0.5823
> 3rd Qu.:0.0000      3rd Qu.:0.00000      3rd Qu.:1.0000      3rd Qu.:1.0000
> Max.   :1.0000      Max.   :1.00000      Max.   :1.0000      Max.   :1.0000
>      stage1      stageindex      sizea2      repstra2
> Length:2552      Min.   : 0.000      Min.   :0.000      Min.   :0.0000
> Class :character 1st Qu.: 0.000      1st Qu.:2.500      1st Qu.:0.0000
> Mode  :character Median : 3.000      Median :4.700      Median :0.0000
> Mean   : 6.115      Mean   :4.562      Mean   :0.2355
```

```

>           3rd Qu.:10.000  3rd Qu.:6.600  3rd Qu.:0.0000
>           Max.   :21.000  Max.    :8.900  Max.    :1.0000
>   feca2      juvgiven2      obsstatus2      repstatus2
> Min.   : 0.000  Min.   :0.0000  Min.    :0.0000  Min.    :0.0000
> 1st Qu.: 0.000  1st Qu.:0.0000  1st Qu.:1.0000  1st Qu.:0.0000
> Median : 0.000  Median :0.0000  Median :1.0000  Median :0.0000
> Mean   : 1.136  Mean   :0.1117  Mean    :0.9459  Mean    :0.2355
> 3rd Qu.: 0.000  3rd Qu.:0.0000  3rd Qu.:1.0000  3rd Qu.:0.0000
> Max.   :66.000  Max.   :1.0000  Max.    :1.0000  Max.    :1.0000
>   fecstatus2  matstatus2      alive2      stage2
> Min.   :0.0000  Min.   :0.0000  Min.    :1  Length:2552
> 1st Qu.:0.0000  1st Qu.:1.0000  1st Qu.:1  Class :character
> Median :0.0000  Median :1.0000  Median :1  Mode  :character
> Mean   :0.1046  Mean   :0.8883  Mean    :1
> 3rd Qu.:0.0000  3rd Qu.:1.0000  3rd Qu.:1
> Max.   :1.0000  Max.   :1.0000  Max.    :1
>   stage2index  sizea3      repstra3      feca3      juvgiven3
> Min.   : 2.000  Min.   :0.000  Min.    :0.0000  Min.    : 0.000  Min.    :0
> 1st Qu.: 5.000  1st Qu.:2.300  1st Qu.:0.0000  1st Qu.: 0.000  1st Qu.:0
> Median : 8.000  Median :4.300  Median :0.0000  Median : 0.000  Median :0
> Mean   : 9.305  Mean   :4.003  Mean    :0.2159  Mean    : 1.277  Mean    :0
> 3rd Qu.:10.000  3rd Qu.:6.300  3rd Qu.:0.0000  3rd Qu.: 0.000  3rd Qu.:0
> Max.   :21.000  Max.   :8.800  Max.    :1.0000  Max.    :66.000  Max.    :0
>   obsstatus3  repstatus3  fecstatus3  matstatus3
> Min.   :0.0000  Min.   :0.0000  Min.    :0.0000  Min.    :1
> 1st Qu.:1.0000  1st Qu.:0.0000  1st Qu.:0.0000  1st Qu.:1
> Median :1.0000  Median :0.0000  Median :0.0000  Median :1
> Mean   :0.8264  Mean   :0.2159  Mean    :0.1105  Mean    :1
> 3rd Qu.:1.0000  3rd Qu.:0.0000  3rd Qu.:0.0000  3rd Qu.:1
> Max.   :1.0000  Max.   :1.0000  Max.    :1.0000  Max.    :1
>   alive3      stage3      stage3index
> Min.   :0.0000  Length:2552  Min.    : 0.000
> 1st Qu.:1.0000  Class :character  1st Qu.: 5.000
> Median :1.0000  Mode  :character  Median : 7.000
> Mean   :0.9138  Mean    : 8.632
> 3rd Qu.:1.0000  3rd Qu.:10.000
> Max.   :1.0000  Max.    :21.000

```

This dataset has 2552 rows representing our original dataset of >1100 individuals. Ordinarily, we would now go on to produce either vital rate models to create function-based MPMs. However, the fact that we are incorporating age in our analysis leads to the problem that there are many individuals in our dataset that are of unknown age. The *hfv* dataset that we have created includes an estimated age for each individual in each year, but this is estimated from the time in which the individual is first seen. Many individuals are first seen in the first year of the study, by which time many could have already been alive for years. So, we will proceed by subsetting our data to eliminate individuals first seen in the very first year of the study.

```

lathvertln_small <- subset(lathvertln, firstseen > 1988)
dim(lathvertln_small)
> [1] 542 42
summary(lathvertln_small)
>   rowid      popid  patchid  individ      year2
> Min.   : 30.0    :542    1:131  Length:542  Min.    :1989
> 1st Qu.: 302.5    2: 72  Class :character  1st Qu.:1989
> Median : 583.0    3:101  Mode  :character  Median :1990

```

```

> Mean      : 586.8           4:132           Mean      :1990
> 3rd Qu.: 801.0           5: 70           3rd Qu.:1990
> Max.     :1097.0         6: 36           Max.     :1990
> firstseen      lastseen      obsage      obslifespan      sizea1
> Min.    :1989   Min.    :1989   Min.    :0.0000   Min.    :0.00   Min.    :0.000
> 1st Qu.:1989   1st Qu.:1990   1st Qu.:0.0000   1st Qu.:1.00   1st Qu.:0.000
> Median :1989   Median :1991   Median :0.0000   Median :2.00   Median :0.000
> Mean    :1989   Mean    :1991   Mean    :0.3524   Mean    :1.36   Mean    :1.186
> 3rd Qu.:1989   3rd Qu.:1991   3rd Qu.:1.0000   3rd Qu.:2.00   3rd Qu.:2.200
> Max.    :1990   Max.    :1991   Max.    :1.0000   Max.    :2.00   Max.    :8.400
> repstra1      fecal      juvgiven1      obsstatus1
> Min.    :0.0000   Min.    : 0.0000   Min.    :0.0000   Min.    :0.0000
> 1st Qu.:0.0000   1st Qu.: 0.0000   1st Qu.:0.0000   1st Qu.:0.0000
> Median :0.0000   Median : 0.0000   Median :0.0000   Median :0.0000
> Mean    :0.0203   Mean    : 0.1218   Mean    :0.1624   Mean    :0.3524
> 3rd Qu.:0.0000   3rd Qu.: 0.0000   3rd Qu.:0.0000   3rd Qu.:1.0000
> Max.    :1.0000   Max.    :34.0000   Max.    :1.0000   Max.    :1.0000
> repstatus1    fecstatus1    matstatus1    alive1
> Min.    :0.0000   Min.    :0.00000   Min.    :0.00   Min.    :0.0000
> 1st Qu.:0.0000   1st Qu.:0.00000   1st Qu.:0.00   1st Qu.:0.0000
> Median :0.0000   Median :0.00000   Median :0.00   Median :0.0000
> Mean    :0.0203   Mean    :0.01292   Mean    :0.19   Mean    :0.3524
> 3rd Qu.:0.0000   3rd Qu.:0.00000   3rd Qu.:0.00   3rd Qu.:1.0000
> Max.    :1.0000   Max.    :1.00000   Max.    :1.00   Max.    :1.0000
> stage1      stage1index      sizea2      repstra2
> Length:542   Min.    : 0.000   Min.    :0.000   Min.    :0.00000
> Class :character   1st Qu.: 0.000   1st Qu.:2.200   1st Qu.:0.00000
> Mode  :character   Median : 0.000   Median :2.500   Median :0.00000
> Mean    : 1.893   Mean    :3.059   Mean    :0.03506
> 3rd Qu.: 2.000   3rd Qu.:3.600   3rd Qu.:0.00000
> Max.    :20.000   Max.    :8.400   Max.    :1.00000
> fecal2      juvgiven2      obsstatus2      repstatus2
> Min.    : 0.0000   Min.    :0.0000   Min.    :0.0000   Min.    :0.00000
> 1st Qu.: 0.0000   1st Qu.:0.0000   1st Qu.:1.0000   1st Qu.:0.00000
> Median : 0.0000   Median :0.0000   Median :1.0000   Median :0.00000
> Mean    : 0.1421   Mean    :0.3469   Mean    :0.9815   Mean    :0.03506
> 3rd Qu.: 0.0000   3rd Qu.:1.0000   3rd Qu.:1.0000   3rd Qu.:0.00000
> Max.    :34.0000   Max.    :1.0000   Max.    :1.0000   Max.    :1.00000
> fecstatus2    matstatus2      alive2      stage2
> Min.    :0.00000   Min.    :0.0000   Min.    :1   Length:542
> 1st Qu.:0.00000   1st Qu.:0.0000   1st Qu.:1   Class :character
> Median :0.00000   Median :1.0000   Median :1   Mode  :character
> Mean    :0.01661   Mean    :0.6531   Mean    :1
> 3rd Qu.:0.00000   3rd Qu.:1.0000   3rd Qu.:1
> Max.    :1.00000   Max.    :1.0000   Max.    :1
> stage2index    sizea3      repstra3      fecal3
> Min.    : 2.00   Min.    :0.000   Min.    :0.00000   Min.    : 0.0000
> 1st Qu.: 2.00   1st Qu.:0.000   1st Qu.:0.00000   1st Qu.: 0.0000
> Median : 5.00   Median :2.400   Median :0.00000   Median : 0.0000
> Mean    : 5.19   Mean    :2.303   Mean    :0.04059   Mean    : 0.2454
> 3rd Qu.: 7.00   3rd Qu.:3.200   3rd Qu.:0.00000   3rd Qu.: 0.0000
> Max.    :20.00   Max.    :8.800   Max.    :1.00000   Max.    :48.000
> juvgiven3    obsstatus3      repstatus3      fecstatus3      matstatus3

```

```

> Min.      :0   Min.      :0.0000   Min.      :0.00000   Min.      :0.00000   Min.      :1
> 1st Qu.   :0   1st Qu.   :0.0000   1st Qu.   :0.00000   1st Qu.   :0.00000   1st Qu.   :1
> Median    :0   Median    :1.0000   Median    :0.00000   Median    :0.00000   Median    :1
> Mean      :0   Mean      :0.7306   Mean      :0.04059   Mean      :0.01292   Mean      :1
> 3rd Qu.   :0   3rd Qu.   :1.0000   3rd Qu.   :0.00000   3rd Qu.   :0.00000   3rd Qu.   :1
> Max.      :0   Max.      :1.0000   Max.      :1.00000   Max.      :1.00000   Max.      :1
>   alive3      stage3      stage3index
> Min.      :0.0000   Length:542      Min.      : 0.000
> 1st Qu.   :1.0000   Class :character 1st Qu.   : 3.000
> Median    :1.0000   Mode  :character Median    : 5.000
> Mean      :0.7989                      Mean      : 4.969
> 3rd Qu.   :1.0000                      3rd Qu.   : 6.000
> Max.      :1.0000                      Max.      :21.000

```

We are now down to only 542 rows, so we have lost close to 80% of the transition data here.

Let's look at fecundity. Fecundity is integer-based, suggesting that it can be treated as a count variable. This package currently allows 8 choices of count distributions: Gaussian, Gamma, Poisson, negative binomial, zero-inflated Poisson, zero-inflated negative binomial, zero-truncated Poisson, and zero-truncated negative binomial. To assess which to use, we should first assess whether the mean and variance of the count are equal using a dispersion test. This test allows us to test whether the variance is greater than that expected under our mean value for fecundity using a chi-squared test. If it is not significantly different, then we may use some variant of the Poisson distribution. If the data are overdispersed, then we should use the negative binomial distribution. We should also test whether the number of zeroes is more than expected under these distributions, and make the distribution zero-inflated if so. Note that, because we have not excluded 0s from fecundity using reproductive status, we should not use a zero-truncated distribution.

Let's start off by looking at a bar plot of the distribution of fecundity.

```
hist(subset(lathvertln_small, repstatus2 == 1)$feca2, main = "Fecundity",
     xlab = "Intact seeds produced in occasion t")
```

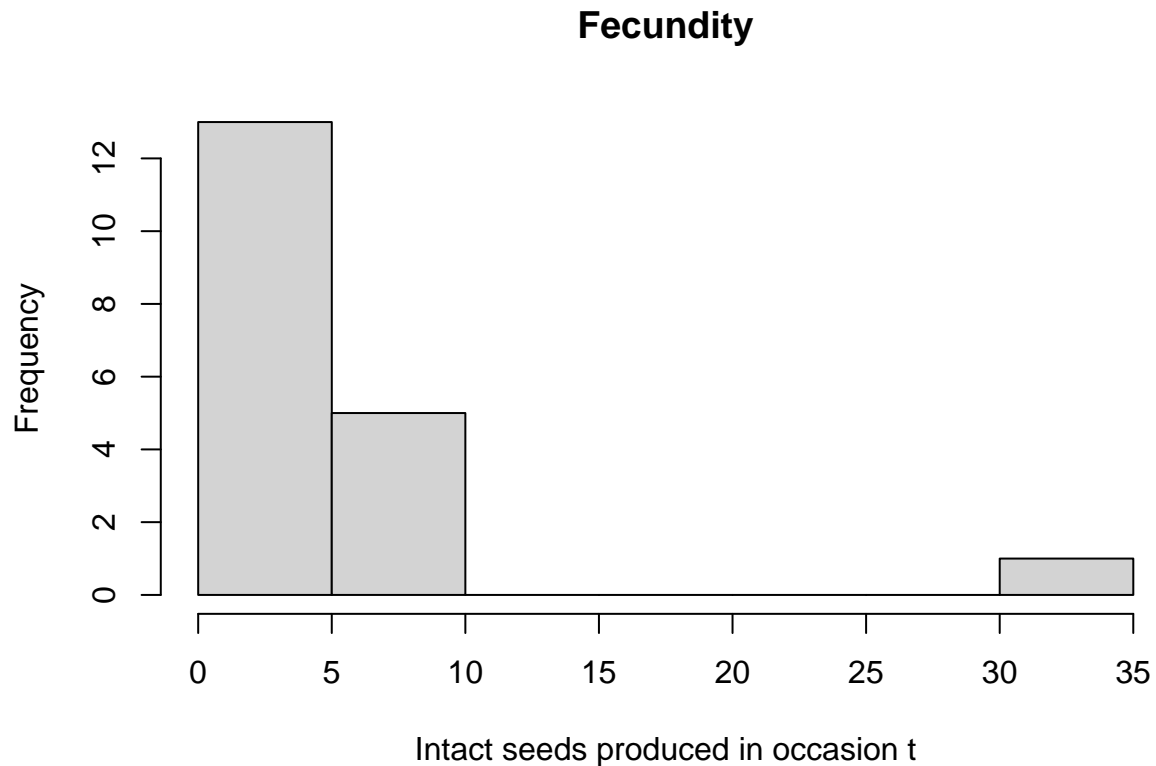


Figure 6.3: Histogram of fecundity in occasion t

We see that the distribution conforms to a classic count variable with a very low mean value. The first bar suggests that there may be too many zeroes, as well. Let's now formally test our assumptions, that the mean equals the variance and that the number of zeroes meets expectation. Both tests use chi-squared distribution-based approaches, with the zero-inflation test in particular based on Broek (1995).

```
sf_distrib(lathvertln_small, sizea = c("sizea3", "sizea2"), fec = c("feca3", "feca2"),
  obs3 = "obsstatus3", repst = c("repstatus3", "repstatus2"))
> Non-integer values detected, so will not test for overdispersion and zero-inflation in sizea
> Mean fec is 4.6
>
> The variance in fec is 73.54
>
> The probability of this dispersion level by chance assuming that
> the true mean fec = variance in fec,
> and an alternative hypothesis of overdispersion, is 3.787e-145
>
> Fecundity is significantly overdispersed.
>
> Mean lambda in fec is 0.01005
> The actual number of 0s in fec is 7
> The expected number of 0s in fec under the null hypothesis is 0.1508
> The probability of this deviation in 0s from expectation by chance is 1.122e-73
>
```

```
> Fecundity is significantly zero-inflated.
```

We see that fecundity is significantly overdispersed, and has a significant excess of zeros. So, we should use a zero-inflated negative binomial distribution here.

Next, let's create an ahistorical supplement table organizing the extra data that we need to incorporate into our matrices. Each row refers to a specific transition. The first two of these transitions are set to specific probabilities, which are the probabilities of germination and seed dormancy, estimated from a separate study. The final two terms are fecundity multipliers, which mark which transitions correspond to fecundity and provide information on what multiple of fecundity estimated via linear modeling applies to each case. Note that we can also include proxy transitions, in which we define a specific transition as being equal to another in the matrix. The latter approach is useful when some transitions cannot be estimated given a particular dataset, and so need to be set to other, proxy values that are estimable.

```
lathsupp2 <- supplemental(stage3 = c("Sd", "Sd1", "Sd", "Sd1"),
  stage2 = c("Sd", "Sd", "rep", "rep"),
  givenrate = c(0.345, 0.054, NA, NA),
  multiplier = c(NA, NA, 0.345, 0.054),
  type = c(1, 1, 3, 3), stageframe = lathframe1n, historical = FALSE)

lathsupp2
>   stage3 stage2 stage1 eststage3 eststage2 eststage1 givenrate multiplier
> 1     Sd     Sd  <NA>      <NA>      <NA>      <NA>      0.345     1.000
> 2     Sd1    Sd  <NA>      <NA>      <NA>      <NA>      0.054     1.000
> 3     Sd     rep  <NA>      <NA>      <NA>      <NA>      NA        0.345
> 4     Sd1    rep  <NA>      <NA>      <NA>      <NA>      NA        0.054
>   convtype convtype_t12
> 1         1           1
> 2         1           1
> 3         3           1
> 4         3           1
```

Next we will run the `modelsearch` function with the new vertical dataset. This function will develop our best-fit vital rate models for us. This function looks simple, but it automates several crucial and complex tasks in MPM analysis. Specifically, it automates 1) the building of global models for each vital rate requested, 2) the exhaustive construction of all reduced models, and 3) the selection of the best-fit models. In relation to our previous uses of this function in chapter 5, the most noteworthy difference is the inclusion of an age term (`age = "obsage"`, which we know from looking at the summary of the vertical dataset). We will only develop the main effects model here, but setting an age term with `suite = full` would also create all two-way interactions between age and other terms, including size and reproductive status. Let's start off by generating a set of vital rate models that covers the entire population.

```
lathmodels1n2 <- modelsearch(lathvert1n_small, historical = FALSE,
  approach = "mixed", suite = "main",
  vitalrates = c("surv", "obs", "size", "repst", "fec"), juvestimate = "Sd1",
  bestfit = "AICc&k", sizedist = "gaussian", fecdist = "negbin",
  indiv = "individ", year = "year2", age = "obsage", year.as.random = TRUE,
  patch.as.random = TRUE, show.model.tables = TRUE, fec.zero = TRUE, quiet = TRUE)
> boundary (singular) fit: see ?isSingular
> boundary (singular) fit: see ?isSingular
> boundary (singular) fit: see ?isSingular
> Warning in checkConv(attr(opt, "derivs"), opt$par, ctrl = control$checkConv, :
> unable to evaluate scaled gradient
> Warning in checkConv(attr(opt, "derivs"), opt$par, ctrl = control$checkConv, :
> Model failed to converge: degenerate Hessian with 1 negative eigenvalues
```

```

> Warning in fitTMB(TMBStruc): Model convergence problem; non-positive-definite
> Hessian matrix. See vignette('troubleshooting')
> Warning in fitTMB(TMBStruc): Model convergence problem; false convergence (8).
> See vignette('troubleshooting')
> boundary (singular) fit: see ?isSingular
> boundary (singular) fit: see ?isSingular
> boundary (singular) fit: see ?isSingular

summary(lathmodelsln2)
> This LefkoMod object includes 8 linear models.
> Best-fit model criterion used: AICc&k
>
>
>
> Survival model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: alive3 ~ repstatus2 + (1 | year2) + (1 | individ)
> Data: subdata
>      AIC      BIC   logLik deviance df.resid
> 315.8615 331.3387 -153.9307 307.8615     350
> Random effects:
> Groups Name      Std.Dev.
> individ (Intercept) 4.412e-07
> year2 (Intercept) 2.739e-01
> Number of obs: 354, groups:  individ, 190; year2, 2
> Fixed Effects:
> (Intercept) repstatus2
>      1.666      23.030
> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Observation model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: obsstatus3 ~ sizea2 + (1 | year2) + (1 | individ)
> Data: subdata
>      AIC      BIC   logLik deviance df.resid
> 179.6353 194.3967 -85.8176 171.6353     292
> Random effects:
> Groups Name      Std.Dev.
> individ (Intercept) 8.6493
> year2 (Intercept) 0.7901
> Number of obs: 296, groups:  individ, 162; year2, 2
> Fixed Effects:
> (Intercept)      sizea2
>      11.0889      -0.4973
>

```

```

>
>
>
> Size model:
> Linear mixed model fit by REML ['lmerMod']
> Formula: sizea3 ~ sizea2 + (1 | year2) + (1 | individ)
> Data: subdata
> REML criterion at convergence: 700.2483
> Random effects:
> Groups Name Std.Dev.
> individ (Intercept) 0.0000
> year2 (Intercept) 0.4826
> Residual 0.8850
> Number of obs: 266, groups: individ, 158; year2, 2
> Fixed Effects:
> (Intercept) sizea2
> 0.7088 0.7777
> optimizer (nloptwrap) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Secondary size model:
> [1] 1
>
>
>
> Tertiary size model:
> [1] 1
>
>
>
> Reproductive status model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: repstatus3 ~ obsage + repstatus2 + sizea2 + (1 | individ)
> Data: subdata
> AIC BIC logLik deviance df.resid
> 72.4486 90.3661 -31.2243 62.4486 261
> Random effects:
> Groups Name Std.Dev.
> individ (Intercept) 96.43
> Number of obs: 266, groups: individ, 158
> Fixed Effects:
> (Intercept) obsage repstatus2 sizea2
> -162.867 59.552 -7.476 19.076
> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 2 lme4 warnings
>
>
>

```



```

>
> Fecundity model:
> Formula:
> feca2 ~ obsage + repstatus2 + sizea2 + (1 | year2) + (1 | individ)
> Zero inflation:      ~obsage + sizea2 + (1 | year2) + (1 | individ)
> Data: subdata
>      AIC      BIC    logLik  df.resid
> -1992.864 -1981.530  1008.432      7
> Random-effects (co)variances:
>
> Conditional model:
> Groups  Name      Std.Dev.
> year2   (Intercept) 1.701e-08
> individ (Intercept) 4.453e-05
>
> Zero-inflation model:
> Groups  Name      Std.Dev.
> year2   (Intercept) 9.635e-05
> individ (Intercept) 2.220e+01
>
> Number of obs: 19 / Conditional model: year2, 2; individ, 16 / Zero-inflation model: year2, 2; individ, 16
>
> Dispersion parameter for nbinom2 family (): 2.74e+16
>
> Fixed Effects:
>
> Conditional model:
> (Intercept)      obsage  repstatus2      sizea2
>   -3.2697        0.6173    -3.2697        1.1855
>
> Zero-inflation model:
> (Intercept)      obsage      sizea2
>   -0.6848        18.8872    -1.0040
>
>
>
> Juvenile survival model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: alive3 ~ (1 | year2) + (1 | individ)
> Data: subdata
>      AIC      BIC    logLik  deviance  df.resid
>  225.7193  235.4286 -109.8596  219.7193    185
> Random effects:
> Groups  Name      Std.Dev.
> individ (Intercept) 0.3755
> year2   (Intercept) 0.0000
> Number of obs: 188, groups:  individ, 155; year2, 2
> Fixed Effects:
> (Intercept)
>      1.024

```

```

> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Juvenile observation model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: obsstatus3 ~ (1 | year2) + (1 | individ)
> Data: subdata
>      AIC      BIC  logLik deviance df.resid
> 28.1909 36.9509 -11.0955  22.1909     134
> Random effects:
> Groups Name      Std.Dev.
> individ (Intercept) 5.638e+01
> year2   (Intercept) 1.312e-05
> Number of obs: 137, groups:  individ, 122; year2, 2
> Fixed Effects:
> (Intercept)
>      13.8
> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Juvenile size model:
> Linear mixed model fit by REML ['lmerMod']
> Formula: sizea3 ~ (1 | year2) + (1 | individ)
> Data: subdata
> REML criterion at convergence: 145.4426
> Random effects:
> Groups Name      Std.Dev.
> individ (Intercept) 4.504e-06
> year2   (Intercept) 1.430e-01
> Residual                4.139e-01
> Number of obs: 130, groups:  individ, 115; year2, 2
> Fixed Effects:
> (Intercept)
>      2.288
> optimizer (nloptwrap) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Juvenile secondary size model:
> [1] 1
>
>
>
> Juvenile tertiary size model:
> [1] 1

```

```

>
>
>
>
> Juvenile reproduction model:
> [1] 0
>
>
>
>
> Number of models in survival table: 8
>
> Number of models in observation table: 8
>
> Number of models in size table: 8
>
> Number of models in secondary size table: 1
>
> Number of models in tertiary size table: 1
>
> Number of models in reproduction status table: 7
>
> Number of models in fecundity table: 58
>
> Number of models in juvenile survival table: 1
>
> Number of models in juvenile observation table: 1
>
> Number of models in juvenile size table: 1
>
> Number of models in juvenile secondary size table: 1
>
> Number of models in juvenile tertiary size table: 1
>
> Number of models in juvenile reproduction table: 1
>
>
>
>
> General model parameter names (column 1), and
> specific names used in these models (column 2):
>
>      parameter_names mainparams
> 1      time t      year2
> 2      individual  individ
> 3      patch      patch
> 4      alive in time t+1  surv3
> 5      observed in time t+1  obs3
> 6      sizea in time t+1  size3
> 7      sizeb in time t+1  sizeb3
> 8      sizec in time t+1  sizec3
> 9      reproductive status in time t+1  repst3

```

```

> 10          fecundity in time t+1      fec3
> 11          fecundity in time t       fec2
> 12          sizea in time t          size2
> 13          sizea in time t-1        size1
> 14          sizeb in time t          sizeb2
> 15          sizeb in time t-1        sizeb1
> 16          sizec in time t          sizec2
> 17          sizec in time t-1        sizec1
> 18    reproductive status in time t   repst2
> 19    reproductive status in time t-1 repst1
> 20          age in time t            age
> 21          density in time t        density
> 22    individual covariate a in time t indcova2
> 23    individual covariate a in time t-1 indcova1
> 24    individual covariate b in time t indcovb2
> 25    individual covariate b in time t-1 indcovb1
> 26    individual covariate c in time t indcovc2
> 27    individual covariate c in time t-1 indcovc1
> 28          stage group in time t    group2
> 29          stage group in time t-1  group1
>
>
>
>
> Quality control:
>
> Survival estimated with 190 individuals and 354 individual transitions.
> Survival accuracy is 0.836.
> Observation estimated with 162 individuals and 296 individual transitions.
> Observation accuracy is 0.953.
> Size estimated with 158 individuals and 266 individual transitions.
> Secondary size transition not estimated.
> Tertiary size transition not estimated.
> Reproductive status estimated with 158 individuals and 266 individual transitions.
> Reproductive status accuracy is 1.
> Fecundity estimated with 16 individuals and 19 individual transitions.
> Juvenile survival estimated with 155 individuals and 188 individual transitions.
> Juvenile survival accuracy is 0.729.
> Juvenile observation estimated with 122 individuals and 137 individual transitions.
> Juvenile observation accuracy is 1.
> Juvenile size estimated with 115 individuals and 130 individual transitions.
> Juvenile secondary size transition not estimated.
> Juvenile tertiary size transition not estimated.
> Juvenile reproduction probability not estimated.

```

We see that age is influential in reproductive status and fecundity, though not in other vital rates. Accuracy in our binomial models is quite high, for the most part.

Next, we will create a second set that includes patch as a random factor. This model set will allow us to explore patch dynamics in addition to the population dynamics of the previous set.

```

lathmodelsln2p <- modelsearch(lathvertln_small, historical = FALSE,
  approach = "mixed", suite = "main",
  vitalrates = c("surv", "obs", "size", "repst", "fec"), juvestimate = "Sd1",

```

```

bestfit = "AICc&k", sizedist = "gaussian", fecdist = "negbin",
indiv = "individ", patch = "patchid", year = "year2", age = "obsage",
year.as.random = TRUE, patch.as.random = TRUE, show.model.tables = TRUE,
fec.zero = TRUE, quiet = TRUE)
> boundary (singular) fit: see ?isSingular
> boundary (singular) fit: see ?isSingular
> boundary (singular) fit: see ?isSingular
> Warning in checkConv(attr(opt, "derivs"), opt$par, ctrl = control$checkConv, :
> unable to evaluate scaled gradient
> Warning in checkConv(attr(opt, "derivs"), opt$par, ctrl = control$checkConv, :
> Model failed to converge: degenerate Hessian with 1 negative eigenvalues
> Warning in (function (start, objective, gradient = NULL, hessian = NULL, : NA/
> NaN function evaluation

> Warning in (function (start, objective, gradient = NULL, hessian = NULL, : NA/
> NaN function evaluation

> Warning in (function (start, objective, gradient = NULL, hessian = NULL, : NA/
> NaN function evaluation

> Warning in (function (start, objective, gradient = NULL, hessian = NULL, : NA/
> NaN function evaluation

> Warning in (function (start, objective, gradient = NULL, hessian = NULL, : NA/
> NaN function evaluation

> Warning in fitTMB(TMBStruc): Model convergence problem; non-positive-definite
> Hessian matrix. See vignette('troubleshooting')
> Warning in fitTMB(TMBStruc): Model convergence problem; false convergence (8).
> See vignette('troubleshooting')
> boundary (singular) fit: see ?isSingular
> boundary (singular) fit: see ?isSingular
> boundary (singular) fit: see ?isSingular

summary(lathmodelsln2p)
> This LefkoMod object includes 8 linear models.
> Best-fit model criterion used: AICc&k
>
>
>
>
> Survival model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: alive3 ~ repstatus2 + (1 | year2) + (1 | patchid) + (1 | individ)
> Data: subdata
>      AIC      BIC    logLik deviance df.resid
> 308.0613 327.4078 -149.0307 298.0613      349
> Random effects:
> Groups Name          Std.Dev.

```

```

> individ (Intercept) 1.758e-07
> patchid (Intercept) 6.077e-01
> year2 (Intercept) 3.527e-01
> Number of obs: 354, groups: individ, 190; patchid, 6; year2, 2
> Fixed Effects:
> (Intercept) repstatus2
> 1.833 21.352
> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Observation model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: obsstatus3 ~ sizea2 + (1 | year2) + (1 | patchid) + (1 | individ)
> Data: subdata
> AIC BIC logLik deviance df.resid
> 181.6354 200.0872 -85.8177 171.6354 291
> Random effects:
> Groups Name Std.Dev.
> individ (Intercept) 8.6487
> patchid (Intercept) 0.0000
> year2 (Intercept) 0.7901
> Number of obs: 296, groups: individ, 162; patchid, 6; year2, 2
> Fixed Effects:
> (Intercept) sizea2
> 11.0883 -0.4973
> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Size model:
> Linear mixed model fit by REML ['lmerMod']
> Formula: sizea3 ~ sizea2 + (1 | year2) + (1 | patchid) + (1 | individ)
> Data: subdata
> REML criterion at convergence: 700.2483
> Random effects:
> Groups Name Std.Dev.
> individ (Intercept) 0.0000
> patchid (Intercept) 0.0000
> year2 (Intercept) 0.4826
> Residual 0.8850
> Number of obs: 266, groups: individ, 158; patchid, 6; year2, 2
> Fixed Effects:
> (Intercept) sizea2
> 0.7088 0.7777
> optimizer (nloptwrap) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>

```

```

>
> Secondary size model:
> [1] 1
>
>
>
> Tertiary size model:
> [1] 1
>
>
>
> Reproductive status model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: repstatus3 ~ obsage + repstatus2 + sizea2 + (1 | individ)
> Data: subdata
>      AIC      BIC  logLik deviance df.resid
> 72.4486  90.3661 -31.2243  62.4486     261
> Random effects:
> Groups Name      Std.Dev.
> individ (Intercept) 96.43
> Number of obs: 266, groups:  individ, 158
> Fixed Effects:
> (Intercept)      obsage  repstatus2      sizea2
>   -162.867      59.552      -7.476      19.076
> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 2 lme4 warnings
>
>
>
> Fecundity model:
> Formula:
> feca2 ~ obsage + repstatus2 + sizea2 + (1 | year2) + (1 | individ)
> Zero inflation:      -obsage + sizea2 + (1 | year2) + (1 | individ)
> Data: subdata
>      AIC      BIC  logLik  df.resid
> -1992.864 -1981.530 1008.432      7
> Random-effects (co)variances:
>
> Conditional model:
> Groups Name      Std.Dev.
> year2 (Intercept) 1.701e-08
> individ (Intercept) 4.453e-05
>
> Zero-inflation model:
> Groups Name      Std.Dev.
> year2 (Intercept) 9.635e-05
> individ (Intercept) 2.220e+01
>
> Number of obs: 19 / Conditional model: year2, 2; individ, 16 / Zero-inflation model: year2, 2; individ, 16

```

```

>
> Dispersion parameter for nbinom2 family (): 2.74e+16
>
> Fixed Effects:
>
> Conditional model:
> (Intercept)      obsage  repstatus2      sizea2
>    -3.2697      0.6173    -3.2697      1.1855
>
> Zero-inflation model:
> (Intercept)      obsage      sizea2
>    -0.6848      18.8872     -1.0040
>
>
>
> Juvenile survival model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: alive3 ~ (1 | year2) + (1 | patchid) + (1 | individ)
> Data: subdata
>      AIC      BIC   logLik deviance df.resid
> 227.5465 240.4922 -109.7732 219.5465    184
> Random effects:
> Groups Name      Std.Dev.
> individ (Intercept) 0.3386
> patchid (Intercept) 0.2282
> year2 (Intercept) 0.0000
> Number of obs: 188, groups:  individ, 155; patchid, 6; year2, 2
> Fixed Effects:
> (Intercept)
>      1.015
> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Juvenile observation model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: obsstatus3 ~ (1 | year2) + (1 | patchid) + (1 | individ)
> Data: subdata
>      AIC      BIC   logLik deviance df.resid
> 30.1909 41.8709 -11.0955 22.1909    133
> Random effects:
> Groups Name      Std.Dev.
> individ (Intercept) 5.638e+01
> patchid (Intercept) 0.000e+00
> year2 (Intercept) 1.494e-04
> Number of obs: 137, groups:  individ, 122; patchid, 6; year2, 2
> Fixed Effects:

```



```

> (Intercept)
>      13.8
> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Juvenile size model:
> Linear mixed model fit by REML ['lmerMod']
> Formula: sizea3 ~ (1 | year2) + (1 | patchid) + (1 | individ)
> Data: subdata
> REML criterion at convergence: 145.4426
> Random effects:
> Groups   Name          Std.Dev.
> individ  (Intercept)  0.0000
> patchid  (Intercept)  0.0000
> year2    (Intercept)  0.1430
> Residual                    0.4139
> Number of obs: 130, groups:  individ, 115; patchid, 6; year2, 2
> Fixed Effects:
> (Intercept)
>      2.288
> optimizer (nloptwrap) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Juvenile secondary size model:
> [1] 1
>
>
>
> Juvenile tertiary size model:
> [1] 1
>
>
>
> Juvenile reproduction model:
> [1] 0
>
>
>
>
> Number of models in survival table: 8
>
> Number of models in observation table: 8
>
> Number of models in size table: 8
>
> Number of models in secondary size table: 1

```

```

>
> Number of models in tertiary size table: 1
>
> Number of models in reproduction status table: 7
>
> Number of models in fecundity table: 58
>
> Number of models in juvenile survival table: 1
>
> Number of models in juvenile observation table: 1
>
> Number of models in juvenile size table: 1
>
> Number of models in juvenile secondary size table: 1
>
> Number of models in juvenile tertiary size table: 1
>
> Number of models in juvenile reproduction table: 1
>
>
>
>
> General model parameter names (column 1), and
> specific names used in these models (column 2):
>
>           parameter_names mainparams
> 1           time t          year2
> 2           individual      individ
> 3           patch          patch
> 4           alive in time t+1  surv3
> 5           observed in time t+1  obs3
> 6           sizea in time t+1    size3
> 7           sizeb in time t+1    sizeb3
> 8           sizec in time t+1    sizec3
> 9           reproductive status in time t+1  repst3
> 10          fecundity in time t+1    fec3
> 11          fecundity in time t      fec2
> 12          sizea in time t          size2
> 13          sizea in time t-1        size1
> 14          sizeb in time t          sizeb2
> 15          sizeb in time t-1        sizeb1
> 16          sizec in time t          sizec2
> 17          sizec in time t-1        sizec1
> 18          reproductive status in time t  repst2
> 19          reproductive status in time t-1  repst1
> 20          age in time t           age
> 21          density in time t       density
> 22          individual covariate a in time t  indcova2
> 23          individual covariate a in time t-1  indcoval
> 24          individual covariate b in time t  indcovb2
> 25          individual covariate b in time t-1  indcovb1
> 26          individual covariate c in time t  indcovc2
> 27          individual covariate c in time t-1  indcovc1

```

```

> 28          stage group in time t      group2
> 29          stage group in time t-1    group1
>
>
>
>
> Quality control:
>
> Survival estimated with 190 individuals and 354 individual transitions.
> Survival accuracy is 0.836.
> Observation estimated with 162 individuals and 296 individual transitions.
> Observation accuracy is 0.953.
> Size estimated with 158 individuals and 266 individual transitions.
> Secondary size transition not estimated.
> Tertiary size transition not estimated.
> Reproductive status estimated with 158 individuals and 266 individual transitions.
> Reproductive status accuracy is 1.
> Fecundity estimated with 16 individuals and 19 individual transitions.
> Juvenile survival estimated with 155 individuals and 188 individual transitions.
> Juvenile survival accuracy is 0.729.
> Juvenile observation estimated with 122 individuals and 137 individual transitions.
> Juvenile observation accuracy is 1.
> Juvenile size estimated with 115 individuals and 130 individual transitions.
> Juvenile secondary size transition not estimated.
> Juvenile tertiary size transition not estimated.
> Juvenile reproduction probability not estimated.

```

Next, we will estimate the ahistorical sets of matrices. We will match the ahistorical age-by-stage matrix estimation function, `aflefk2()`, with the appropriate ahistorical input, including the ahistorical `lefkMod` objects `lathmodelsln2` and `lathmodelsln2p`. Model sets that include historical terms should not be used to create ahistorical matrices, since the coefficients in the best-fit models are estimated assuming a specific model structure that either relies on historical terms or does not. Historical vital rate models may yield biased results if used to construct ahistorical matrices. Also note that `lefk3` does not currently allow the construction of historical age-by-stage MPMs. Let's start off by developing the population-only MPM.

```

lathmat2age <- aflefk2(year = "all", stageframe = lathframeIn,
  modelsuite = lathmodelsln2, data = lathvertln_small, supplement = lathsupp2,
  patchcol = "patchid", yearcol = "year2", year.as.random = FALSE,
  patch.as.random = FALSE, final_age = 2, continue = TRUE, reduce = FALSE)

summary(lathmat2age)
>
> This ahistorical lefkoMat object contains 2 matrices.
>
> Each matrix is square with 63 rows and columns, and a total of 3969 elements.
> A total of 1200 survival transitions were estimated, with 600 per matrix.
> A total of 72 fecundity transitions were estimated, with 36 per matrix.
> This lefkoMat object covers 1 populations, 1 patches, and 2 time steps.
>
> Vital rate modeling quality control:
>
> Survival estimated with 190 individuals and 354 individual transitions.
> Observation estimated with 162 individuals and 296 individual transitions.

```

```

> Size estimated with 158 individuals and 266 individual transitions.
> Reproduction probability not estimated.
> Fecundity not estimated.
> Juvenile survival estimated with 158 individuals and 266 individual transitions.
> Juvenile observation estimated with 16 individuals and 19 individual transitions.
> Juvenile size estimated with 155 individuals and 188 individual transitions.
> Juvenile reproduction estimated with 122 individuals and 137 individual transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>      [,1] [,2]
> Min.  0.000 0.000
> 1st Qu. 0.000 0.000
> Median 0.827 0.827
> Mean  0.550 0.550
> 3rd Qu. 0.932 0.932
> Max.  1.000 1.000

```

This first model set led to the development of two matrices, because although there are four years of data, we have limited our use of the data to individuals first seen from the second year on. In the input for `aflefk2()`, we included a maximum age of 2yrs (`final_age = 2`) but informed the function that this age was not terminal and that the demography of that age should continue onward (`continue = TRUE`). This resulted in a block matrix with 3 ages and 21 stages, and so 63 age-stage combinations and 63 rows and columns. Of course, this particular plant species is actually long-lived, and so setting `final_age = 2` may seem artificial; however, as our dataset only includes four years of study and we do not have absolute ages for any plant, we can only incur about four years of relative age at best. Thus, our settings are actually the most parsimonious possible under the circumstances.

The quality control section gives us a sense of the amount of data used to model each vital rate, and also shows us that the survival-transition (U) matrices are composed entirely of proper probabilities yielding stage survival probability falling between 0.0 and 1.0. Matrix estimation can sometimes create spurious values, such as stage survival greater than 1.0. Such values can occur for a variety of reasons, but the most common is the inclusion through a supplemental table or overwrite table of externally-determined survival probabilities that are too high. Make sure to check your matrix column sums each time you estimate MPMs to prevent this problem. Survival greater than 1.0 can lead to strange effects on metrics of population dynamics.

Let's now develop the patch-level MPMs.

```

lathmat2agep <- aflefk2(year = "all", patch = "all", stageframe = lathframeIn,
  modelsuite = lathmodelsIn2p, data = lathvertIn_small, supplement = lathsupp2,
  patchcol = "patchid", yearcol = "year2", year.as.random = FALSE,
  patch.as.random = FALSE, final_age = 2, continue = TRUE, reduce = FALSE)

summary(lathmat2agep)
>
> This ahistorical lefkoMat object contains 12 matrices.
>
> Each matrix is square with 63 rows and columns, and a total of 3969 elements.
> A total of 7200 survival transitions were estimated, with 600 per matrix.
> A total of 432 fecundity transitions were estimated, with 36 per matrix.
> This lefkoMat object covers 1 populations, 6 patches, and 2 time steps.
>
> Vital rate modeling quality control:
>
> Survival estimated with 190 individuals and 354 individual transitions.
> Observation estimated with 162 individuals and 296 individual transitions.
> Size estimated with 158 individuals and 266 individual transitions.

```

```

> Reproduction probability not estimated.
> Fecundity not estimated.
> Juvenile survival estimated with 158 individuals and 266 individual transitions.
> Juvenile observation estimated with 16 individuals and 19 individual transitions.
> Juvenile size estimated with 155 individuals and 188 individual transitions.
> Juvenile reproduction estimated with 122 individuals and 137 individual 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 0.848 0.848 0.848 0.848 0.848 0.848 0.848 0.848 0.848 0.848 0.848 0.848
> Mean   0.557 0.557 0.557 0.557 0.557 0.557 0.557 0.557 0.557 0.557 0.557 0.557
> 3rd Qu. 0.932 0.932 0.932 0.932 0.932 0.932 0.932 0.932 0.932 0.932 0.932 0.932
> 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

```

This second model set led to the development of 12 matrices, reflecting our subset number of three years and six patches. The rest of the output looks quite similar and even the survival-transition matrix column sum summaries look extremely similar, suggesting little impact of patch.

We can get a sense of what these matrices look like by visualizing them. Let's use the `image3()` function to look at just one.

```
image3(lathmat2age, used = 1)
```

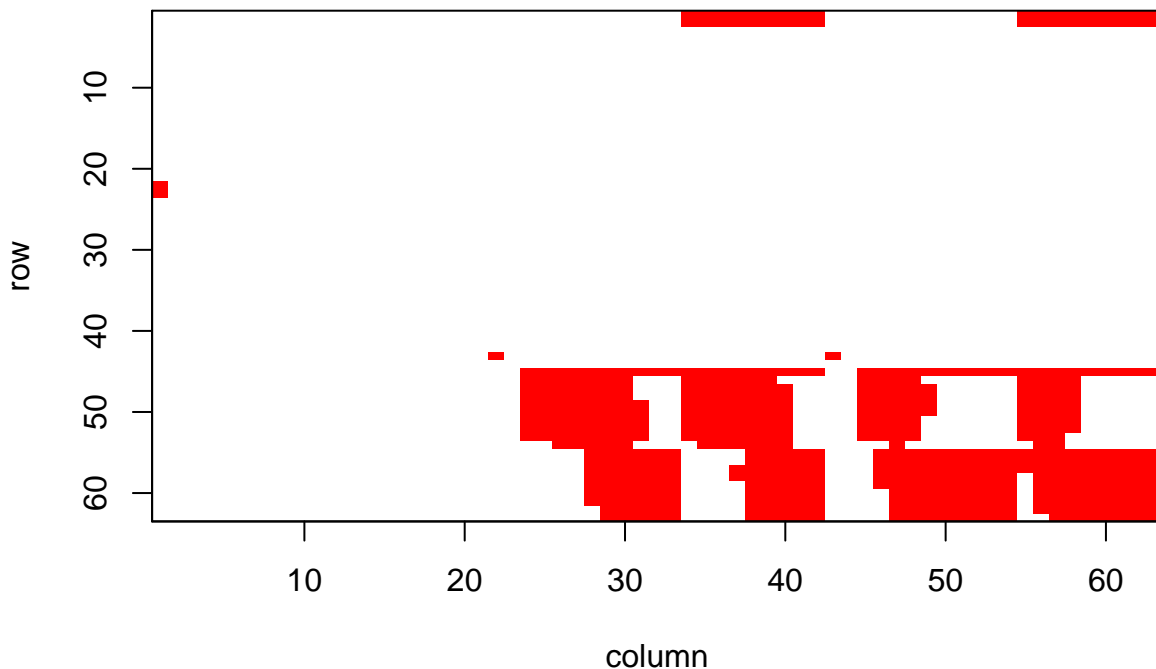


Figure 6.4: Visualization of 1st A Matrix

```

> $`1`
> NULL

```

The clear squares refer to zero elements, and the red elements refer to non-zero values corresponding to survival transitions and fecundity. The vast number of 0s may be surprising, but this matrix is a supermatrix

organized by age first, with stage organizing within-age blocks. The first age is age 0, which cannot be adult, and age 1 corresponds to seedlings, leading to most non-zero elements in the adult portion. The adult block occurs from age 2, and this block can perpetuate indefinitely. The number of elements estimated is greater now than in the typical ahistorical MPM, because now we have added age as a major factor for analysis. This matrix is overwhelmingly composed of elements that must be 0, and so it is a rather sparse matrix $((600 + 36) / 3969 = 16.0\%$ of elements).

Given the amount of white space, we might prefer to rid ourselves of impossible age-stage combinations. We can do this by recreating our matrices with `reduce = TRUE`. Let's try that with the main population set.

```
lathmat2age_red <- aflefk2(year = "all", stageframe = lathframeln,
  modelsuite = lathmodelsln2, data = lathvertln_small, supplement = lathsupp2,
  patchcol = "patchid", yearcol = "year2", year.as.random = FALSE,
  patch.as.random = FALSE, final_age = 2, continue = TRUE, reduce = TRUE)

summary(lathmat2age_red)
>
> This ahistorical lefkoMat object contains 2 matrices.
>
> Each matrix is square with 43 rows and columns, and a total of 1849 elements.
> A total of 1200 survival transitions were estimated, with 600 per matrix.
> A total of 72 fecundity transitions were estimated, with 36 per matrix.
> This lefkoMat object covers 1 populations, 1 patches, and 2 time steps.
>
> Vital rate modeling quality control:
>
> Survival estimated with 190 individuals and 354 individual transitions.
> Observation estimated with 162 individuals and 296 individual transitions.
> Size estimated with 158 individuals and 266 individual transitions.
> Reproduction probability not estimated.
> Fecundity not estimated.
> Juvenile survival estimated with 158 individuals and 266 individual transitions.
> Juvenile observation estimated with 16 individuals and 19 individual transitions.
> Juvenile size estimated with 155 individuals and 188 individual transitions.
> Juvenile reproduction estimated with 122 individuals and 137 individual transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>      [,1] [,2]
> Min.  0.000 0.000
> 1st Qu. 0.827 0.827
> Median 0.841 0.841
> Mean   0.806 0.806
> 3rd Qu. 0.999 0.999
> Max.   1.000 1.000
```

This exercise has eliminated 20 rows and columns, yielding a matrix with 43 rows and 43 columns. The total number of estimated elements has not changed, meaning that our matrices are now less sparse $((600 + 36) / 1849 = 34.4\%)$. Let's take a look at an image of the first matrix.

```
image3(lathmat2age_red, used = 1)
```

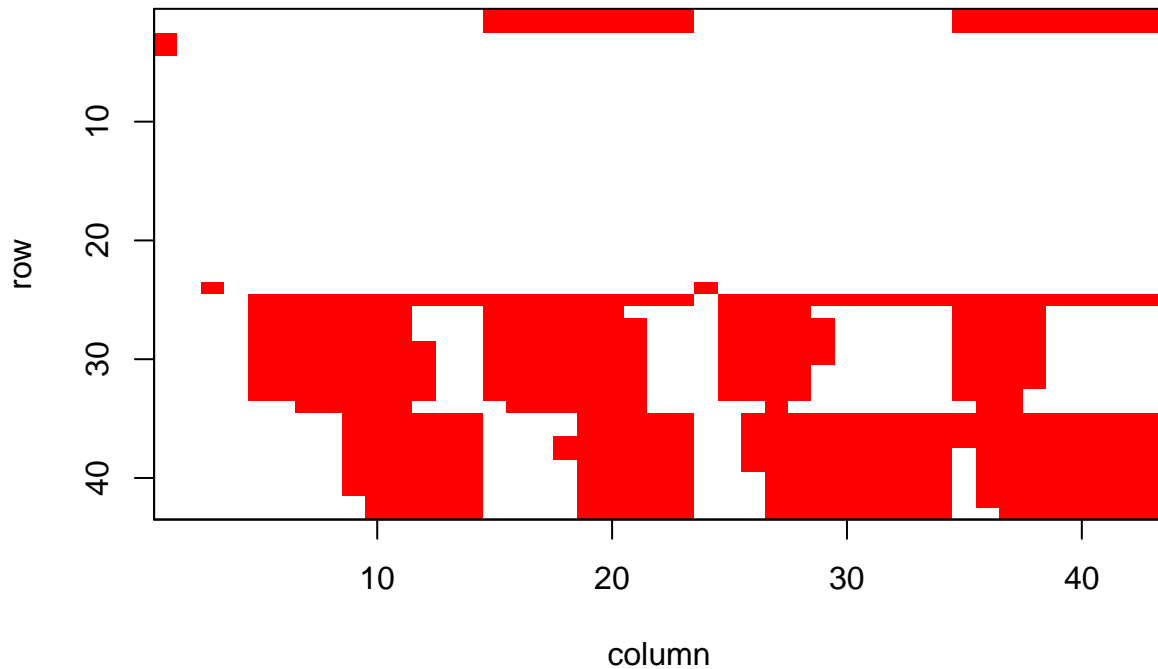


Figure 6.5: Visualization of 1st A Matrix

```
> $`1`  
> NULL
```

Some of the white space has been reduced, and we see greater coverage of the matrix by non-zero elements.

We can see the order of ages and stages using the `agestages` element of the `lefkMat` object we produced, as below. Note that our matrix is 43 rows by 43 columns, and this object gives us the exact order used.

```
lathmat2age_red$agestages  
>   stage_id stage age  
> 1         1   Sd   0  
> 2         2   Sd1  0  
> 1.1       1   Sd   1  
> 2.1       2   Sd1  1  
> 3.1       3   Dorm 1  
> 4.1       4   Sz1nr 1  
> 5.1       5   Sz2nr 1  
> 6.1       6   Sz3nr 1  
> 7.1       7   Sz4nr 1  
> 8.1       8   Sz5nr 1  
> 9.1       9   Sz6nr 1  
> 10.1      10  Sz7nr 1  
> 11.1      11  Sz8nr 1  
> 12.1      12  Sz9nr 1  
> 13.1      13  Sz1r  1  
> 14.1      14  Sz2r  1  
> 15.1      15  Sz3r  1
```

```

> 16.1      16  Sz4r   1
> 17.1      17  Sz5r   1
> 18.1      18  Sz6r   1
> 19.1      19  Sz7r   1
> 20.1      20  Sz8r   1
> 21.1      21  Sz9r   1
> 1.2        1   Sd    2
> 3.2        3   Dorm  2
> 4.2        4  Sz1nr  2
> 5.2        5  Sz2nr  2
> 6.2        6  Sz3nr  2
> 7.2        7  Sz4nr  2
> 8.2        8  Sz5nr  2
> 9.2        9  Sz6nr  2
> 10.2       10  Sz7nr  2
> 11.2       11  Sz8nr  2
> 12.2       12  Sz9nr  2
> 13.2       13  Sz1r   2
> 14.2       14  Sz2r   2
> 15.2       15  Sz3r   2
> 16.2       16  Sz4r   2
> 17.2       17  Sz5r   2
> 18.2       18  Sz6r   2
> 19.2       19  Sz7r   2
> 20.2       20  Sz8r   2
> 21.2       21  Sz9r   2

```

Now let's estimate the element-wise arithmetic mean matrices. The first `lefkoMat` object created will include a single mean matrix, while the second will include 6 mean matrices for the patches, followed by a grand mean matrix, yielding a total of 7 matrices.

```

lathmat2mean <- lmean(lathmat2age)
summary(lathmat2mean)
>
> This ahistorical lefkoMat object contains 1 matrix.
>
> Each matrix is square with 63 rows and columns, and a total of 3969 elements.
> A total of 600 survival transitions were estimated, with 600 per matrix.
> A total of 36 fecundity transitions were estimated, with 36 per matrix.
> This lefkoMat object covers 1 populations, 1 patches, and 0 time steps.
>
> Survival probability sum check (each matrix represented by column in order):
>      [,1]
> Min.   0.000
> 1st Qu. 0.000
> Median 0.827
> Mean   0.550
> 3rd Qu. 0.932
> Max.   1.000

lathmat2pmean <- lmean(lathmat2agep)
summary(lathmat2pmean)
>
> This ahistorical lefkoMat object contains 7 matrices.

```



```

>
> Each matrix is square with 63 rows and columns, and a total of 3969 elements.
> A total of 4200 survival transitions were estimated, with 600 per matrix.
> A total of 252 fecundity transitions were estimated, with 36 per matrix.
> This lefkoMat object covers 1 populations, 7 patches, and 0 time steps.
>
> Survival probability sum check (each matrix represented by column in order):
>      [,1] [,2] [,3] [,4] [,5] [,6] [,7]
> Min.   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
> Median 0.848 0.848 0.848 0.848 0.848 0.848 0.848
> Mean   0.557 0.557 0.557 0.557 0.557 0.557 0.557
> 3rd Qu. 0.932 0.932 0.932 0.932 0.932 0.932 0.932
> Max.   1.000 1.000 1.000 1.000 1.000 1.000 1.000

```

We see one overall population mean in the first case, and a set of 6 patch-level means and one population mean in the second case. Note that the population mean in each case should be a little different, because the population mean in the second set weights each patch equally, while the overall population mean in the first case does not weight data by patch.

Age-classified (Leslie) MPM

Package `lefko3` can also be used to estimate Leslie MPMs, which are purely age-based and so include no individual history. Here, we will illustrate how to create both raw and function-based Leslie MPMs using the `rleslie()` and `fleslie()` functions, respectively. We will ignore the dormant seed stage, as including dormant seeds would require using an age-by-stage approach. Our final matrices will take the following form.

$$\begin{bmatrix} F_{0,0} & F_{0,1} & F_{0,2} & F_{0,3} \\ S_{1,0} & 0 & 0 & 0 \\ 0 & S_{2,1} & 0 & 0 \\ 0 & 0 & S_{3,2} & S_{3,3} \end{bmatrix} \quad (6.3)$$

Normally, we would need to develop a stageframe. However, in this case, a stageframe is unnecessary and instead all we need is the standardized *hfv* dataset. So, let's start with creating that. Most of the setting will be as before. However, we need to include both `NRasRep = TRUE` and `NOasObs = TRUE` to make sure that stage classification ignores whether the individual was actually reproductive and actually observed at each time (the latter has to do with the fact that individuals can be alive with a size of 0 if they are vegetatively dormant). We will also subset our data to only those individuals whose age we are reasonably sure of, by eliminating those individuals first observed in the first monitoring session.

```

lathvert_base <- verticalize3(lathyrus, noyears = 4, firstyear = 1988,
  patchidcol = "SUBPLOT", individcol = "GENET", blocksize = 9,
  sizeacol = "Volume88", repstracol = "FCODE88", fecacol = "Intactseed88",
  deadacol = "Dead1988", censorcol = "Missing1988", censorkeep = NA,
  censor = TRUE, NRasRep = TRUE, NOasObs = TRUE)

```

```

lathvert_age <- subset(lathvert_base, firstseen > 1988)

```

```

summary(lathvert_age)
>      rowid      popid patchid  individ      year2
> Min.   : 30.0    :542    1:131  Length:542  Min.   :1989
> 1st Qu.: 302.5      2: 72   Class :character 1st Qu.:1989
> Median : 583.0      3:101  Mode  :character Median :1990
> Mean   : 586.8      4:132                Mean   :1990
> 3rd Qu.: 801.0      5: 70                3rd Qu.:1990

```

```

> Max. :1097.0          6: 36          Max. :1990
>
> firstseen      lastseen      obsage      obslifespan
> Min. :1989      Min. :1989      Min. :0.0000  Min. :0.00
> 1st Qu.:1989    1st Qu.:1990    1st Qu.:0.0000  1st Qu.:1.00
> Median :1989    Median :1991    Median :0.0000  Median :2.00
> Mean  :1989    Mean  :1991    Mean  :0.3524   Mean  :1.36
> 3rd Qu.:1989    3rd Qu.:1991    3rd Qu.:1.0000  3rd Qu.:2.00
> Max.  :1990    Max.  :1991    Max.  :1.0000   Max.  :2.00
>
> sizea1         repstra1         feca1         fecladded         juvgiven1
> Min. : 0.00      Min. :0.00000      Min. : 0       Min. : 0.00000     Min. :0
> 1st Qu.: 0.00    1st Qu.:0.00000    1st Qu.: 0     1st Qu.: 0.00000   1st Qu.:0
> Median : 0.00    Median :0.00000    Median : 4     Median : 0.00000   Median :0
> Mean  : 59.41    Mean  :0.0576      Mean  : 6     Mean  : 0.1218     Mean  :0
> 3rd Qu.: 9.00    3rd Qu.:0.00000    3rd Qu.: 6     3rd Qu.: 0.00000   3rd Qu.:0
> Max.  :4394.20   Max.  :1.0000      Max. :34      Max. :34.0000     Max. :0
>
>                NA's :351      NA's :531
> obsstatus1     repstatus1     fecstatus1     matstatus1
> Min. :0.00000   Min. :0.00000     Min. :0.00000   Min. :1
> 1st Qu.:0.00000 1st Qu.:0.00000   1st Qu.:0.00000 1st Qu.:1
> Median :0.00000  Median :0.00000   Median :0.00000 Median :1
> Mean  :0.3524   Mean  :0.0203     Mean  :0.01292  Mean  :1
> 3rd Qu.:1.00000 3rd Qu.:0.00000   3rd Qu.:0.00000 3rd Qu.:1
> Max.  :1.00000  Max.  :1.00000     Max. :1.00000   Max. :1
>
> alive1         stage1         stage1index     sizea2
> Min. :0.00000   Length:542        Min. :0         Min. : 0.00
> 1st Qu.:0.00000 Class :character   1st Qu.:0       1st Qu.: 9.00
> Median :0.00000 Mode  :character   Median :0        Median : 12.60
> Mean  :0.3524   Mean  :0           Mean  :0         Mean  : 97.24
> 3rd Qu.:1.00000 3rd Qu.:0         3rd Qu.:0       3rd Qu.: 37.40
> Max.  :1.00000  Max.  :0           Max. :0         Max. :4394.20
>
> repstra2         feca2         fec2added         juvgiven2
> Min. :0.00000    Min. : 0.000     Min. : 0.00000    Min. :0
> 1st Qu.:0.00000  1st Qu.: 0.000   1st Qu.: 0.00000  1st Qu.:0
> Median :0.00000  Median : 0.000   Median : 0.00000  Median :0
> Mean  :0.03571   Mean  : 4.053    Mean  : 0.1421    Mean  :0
> 3rd Qu.:0.00000  3rd Qu.: 6.000   3rd Qu.: 0.00000  3rd Qu.:0
> Max.  :1.00000   Max. :34.000    Max. :34.00000   Max. :0
>
> NA's :10      NA's :523
> obsstatus2     repstatus2     fecstatus2     matstatus2     alive2
> Min. :0.00000   Min. :0.00000     Min. :0.00000   Min. :1         Min. :1
> 1st Qu.:1.00000 1st Qu.:0.00000   1st Qu.:0.00000 1st Qu.:1       1st Qu.:1
> Median :1.00000  Median :0.00000   Median :0.00000 Median :1         Median :1
> Mean  :0.9815   Mean  :0.03506    Mean  :0.01661   Mean  :1         Mean  :1
> 3rd Qu.:1.00000 3rd Qu.:0.00000   3rd Qu.:0.00000 3rd Qu.:1       3rd Qu.:1
> Max.  :1.00000  Max.  :1.00000     Max. :1.00000   Max. :1         Max. :1
>
> stage2         stage2index     sizea3         repstra3
> Length:542     Min. :0         Min. : 0.00     Min. :0.00000
> Class :character 1st Qu.:0     1st Qu.: 0.00   1st Qu.:0.00000

```

```

> Mode :character Median :0 Median : 10.50 Median :0.00000
> Mean :0 Mean : 76.21 Mean :0.05556
> 3rd Qu.:0 3rd Qu.: 24.50 3rd Qu.:0.00000
> Max. :0 Max. :6645.80 Max. :1.00000
> NA's :146
> feca3 fec3added juvgiven3 obsstatus3
> Min. : 0.000 Min. : 0.0000 Min. :0 Min. :0.0000
> 1st Qu.: 0.000 1st Qu.: 0.0000 1st Qu.:0 1st Qu.:0.0000
> Median : 0.000 Median : 0.0000 Median :0 Median :1.0000
> Mean : 6.045 Mean : 0.2454 Mean :0 Mean :0.7306
> 3rd Qu.: 7.500 3rd Qu.: 0.0000 3rd Qu.:0 3rd Qu.:1.0000
> Max. :48.000 Max. :48.0000 Max. :0 Max. :1.0000
> NA's :520
> repstatus3 fecstatus3 matstatus3 alive3
> Min. :0.00000 Min. :0.00000 Min. :1 Min. :0.0000
> 1st Qu.:0.00000 1st Qu.:0.00000 1st Qu.:1 1st Qu.:1.0000
> Median :0.00000 Median :0.00000 Median :1 Median :1.0000
> Mean :0.04059 Mean :0.01292 Mean :1 Mean :0.7528
> 3rd Qu.:0.00000 3rd Qu.:0.00000 3rd Qu.:1 3rd Qu.:1.0000
> Max. :1.00000 Max. :1.00000 Max. :1 Max. :1.0000
>
> stage3 stage3index
> Length:542 Min. :0
> Class :character 1st Qu.:0
> Mode :character Median :0
> Mean :0
> 3rd Qu.:0
> Max. :0
>

```

So far so good! Now let's create the vital rate models. This will go much more quickly than last time, because we no longer care about size and reproductive status as factors determining vital rates. So, we will set `suite = "cons"` to prevent these factors from being tested, and set `age = "obsage"` to incorporate our age at time t variable into all models.

```

lathmodels2_age <- modelsearch(lathvert_age, historical = FALSE,
  approach = "mixed", suite = "cons", bestfit = "AICc&k", age = "obsage",
  vitalrates = c("surv", "fec"), fecdist = "negbin", indiv = "individ",
  year = "year2", year.as.random = TRUE, patch.as.random = TRUE,
  show.model.tables = TRUE, fec.zero = TRUE, quiet = TRUE)
> boundary (singular) fit: see ?isSingular
> Warning in (function (start, objective, gradient = NULL, hessian = NULL, : NA/
> NaN function evaluation
> Warning in fitTMB(TMBStruc): Model convergence problem; non-positive-definite
> Hessian matrix. See vignette('troubleshooting')
> Warning in fitTMB(TMBStruc): Model convergence problem; false convergence (8).
> See vignette('troubleshooting')

summary(lathmodels2_age)
> This LefkoMod object includes 2 linear models.
> Best-fit model criterion used: AICc&k
>
>
>

```

```

>
> Survival model:
> Generalized linear mixed model fit by maximum likelihood (Laplace
> Approximation) [glmerMod]
> Family: binomial ( logit )
> Formula: alive3 ~ obsage + (1 | year2) + (1 | individ)
> Data: subdata
>      AIC      BIC    logLik  deviance  df.resid
> 608.1500 625.3311 -300.0750  600.1500     538
> Random effects:
> Groups Name      Std.Dev.
> individ (Intercept) 0.0000315
> year2 (Intercept) 0.3738203
> Number of obs: 542, groups:  individ, 232; year2, 2
> Fixed Effects:
> (Intercept)      obsage
>      1.1262      0.1817
> optimizer (Nelder_Mead) convergence code: 0 (OK) ; 0 optimizer warnings; 1 lme4 warnings
>
>
>
> Observation model:
> [1] 1
>
>
>
>
> Size model:
> [1] 1
>
>
>
>
> Secondary size model:
> [1] 1
>
>
>
>
> Tertiary size model:
> [1] 1
>
>
>
>
> Reproductive status model:
> [1] 1
>
>
>
>
> Fecundity model:

```

```

> Formula:          fecal2 ~ obsage + (1 | year2) + (1 | individ)
> Zero inflation:   ~.
> Data: subdata
>      AIC      BIC  logLik df.resid
>      NA      NA      NA      10
> Random-effects (co)variances:
>
> Conditional model:
> Groups Name      Std.Dev.
> year2  (Intercept) 2.179e-12
> individ (Intercept) 7.809e-01
>
> Zero-inflation model:
> Groups Name      Std.Dev.
> year2  (Intercept) 5.929e-09
> individ (Intercept) 2.780e+01
>
> Number of obs: 19 / Conditional model: year2, 2; individ, 16 / Zero-inflation model: year2, 2; individ, 16
>
> Dispersion parameter for nbinom2 family (): 4.52e+15
>
> Fixed Effects:
>
> Conditional model:
> (Intercept)      obsage
>      1.8944      0.2526
>
> Zero-inflation model:
> (Intercept)      obsage
>      -10.68      26.05
>
>
>
> Juvenile survival model:
> [1] 1
>
>
>
> Juvenile observation model:
> [1] 1
>
>
>
> Juvenile size model:
> [1] 1
>
>
>
> Juvenile secondary size model:

```

```

> [1] 1
>
>
>
>
> Juvenile tertiary size model:
> [1] 1
>
>
>
> Juvenile reproduction model:
> [1] 1
>
>
>
>
> Number of models in survival table: 1
>
> Number of models in observation table: 1
>
> Number of models in size table: 1
>
> Number of models in secondary size table: 1
>
> Number of models in tertiary size table: 1
>
> Number of models in reproduction status table: 1
>
> Number of models in fecundity table: 1
>
> Number of models in juvenile survival table: 1
>
> Number of models in juvenile observation table: 1
>
> Number of models in juvenile size table: 1
>
> Number of models in juvenile secondary size table: 1
>
> Number of models in juvenile tertiary size table: 1
>
> Number of models in juvenile reproduction table: 1
>
>
>
>
> General model parameter names (column 1), and
> specific names used in these models (column 2):
>
>           parameter_names mainparams
> 1           time t       year2
> 2           individual   individ

```

```

> 3          patch          patch
> 4      alive in time t+1    surv3
> 5      observed in time t+1  obs3
> 6      sizea in time t+1    size3
> 7      sizeb in time t+1    sizeb3
> 8      sizec in time t+1    sizec3
> 9      reproductive status in time t+1  repst3
> 10     fecundity in time t+1    fec3
> 11     fecundity in time t      fec2
> 12     sizea in time t          size2
> 13     sizea in time t-1        size1
> 14     sizeb in time t          sizeb2
> 15     sizeb in time t-1        sizeb1
> 16     sizec in time t          sizec2
> 17     sizec in time t-1        sizec1
> 18     reproductive status in time t    repst2
> 19     reproductive status in time t-1  repst1
> 20     age in time t           age
> 21     density in time t       density
> 22     individual covariate a in time t  indcova2
> 23     individual covariate a in time t-1  indcova1
> 24     individual covariate b in time t    indcovb2
> 25     individual covariate b in time t-1  indcovb1
> 26     individual covariate c in time t    indcovc2
> 27     individual covariate c in time t-1  indcovc1
> 28     stage group in time t             group2
> 29     stage group in time t-1           group1
>
>
>
>
> Quality control:
>
> Survival estimated with 232 individuals and 542 individual transitions.
> Survival accuracy is 0.753.
> Observation probability not estimated.
> Size transition not estimated.
> Secondary size transition not estimated.
> Tertiary size transition not estimated.
> Reproduction probability not estimated.
> Fecundity estimated with 16 individuals and 19 individual transitions.
> Juvenile survival not estimated.
> Juvenile observation probability not estimated.
> Juvenile size transition not estimated.
> Juvenile secondary size transition not estimated.
> Juvenile tertiary size transition not estimated.
> Juvenile reproduction probability not estimated.

```

The two models all include observed age, as well as our random terms. Now we will create the raw matrices.

```

lathmat2ageonly_raw <- rleslie(data = lathvert_age, year = "all",
  yearcol = "year2", indivcol = "individ")

lathmat2ageonly_raw
> $A
> $A$`1`
>           [,1]      [,2] [,3]
> [1,] 0.02521008 0.04188482  0
> [2,] 0.66386555 0.00000000  0
> [3,] 0.00000000 0.72251309  0
>
>
> $U
> $U$`1`
>           [,1]      [,2] [,3]
> [1,] 0.00000000 0.00000000  0
> [2,] 0.6638655  0.00000000  0
> [3,] 0.00000000 0.7225131  0
>
>
> $F
> $F$`1`
>           [,1]      [,2] [,3]
> [1,] 0.02521008 0.04188482  0
> [2,] 0.00000000 0.00000000  0
> [3,] 0.00000000 0.00000000  0
>
>
> $hstages
> [1] NA
>
> $agestages
> [1] NA
>
> $ahstages
>   stage size size_b size_c min_age max_age repstatus obsstatus propstatus
> 1 Age0   NA    NA    NA     0     0         1         1         0
> 2 Age1   NA    NA    NA     1     1         1         1         0
> 3 Age2   NA    NA    NA     2     NA        1         1         0
>   immstatus matstatus indataset binhalfwidth_raw sizebin_min sizebin_max
> 1         0         1         1                NA         NA         NA
> 2         0         1         1                NA         NA         NA
> 3         0         1         1                NA         NA         NA
>   sizebin_center sizebin_width binhalfwidthb_raw sizebinb_min sizebinb_max
> 1             NA             NA                NA         NA         NA
> 2             NA             NA                NA         NA         NA
> 3             NA             NA                NA         NA         NA
>   sizebinb_center sizebinb_width binhalfwidthc_raw sizebinc_min sizebinc_max
> 1             NA             NA                NA         NA         NA
> 2             NA             NA                NA         NA         NA
> 3             NA             NA                NA         NA         NA
>   sizebinc_center sizebinc_width group      comments
> 1             NA             NA     0 No description

```



```

> 2          NA          NA      0 No description
> 3          NA          NA      0 No description
>
> $labels
>   pop patch year2
> 1   1     1   1990
>
> $matrixqc
> [1] 2 2 1
>
> $dataqc
> [1] 232 542
>
> attr("class")
> [1] "lefkMat"
summary(lathmat2ageonly_raw)
>
> This ahistorical lefkoMat object contains 1 matrix.
>
> Each matrix is square with 3 rows and columns, and a total of 9 elements.
> A total of 2 survival transitions were estimated, with 2 per matrix.
> A total of 2 fecundity transitions were estimated, with 2 per matrix.
> This lefkoMat object covers 1 populations, 1 patches, and 1 time steps.
>
> The dataset contains a total of 232 unique individuals and 542 unique transitions.
>
> Survival probability sum check (each matrix represented by column in order):
>      [,1]
> Min.  0.000
> 1st Qu. 0.332
> Median 0.664
> Mean   0.462
> 3rd Qu. 0.693
> Max.   0.723

```

We have just created the basic raw MPMs. We have a single matrix, because we needed to eliminate the first year of data to estimate age properly, leaving only three observation periods. The quality control looks reasonable in terms of the survival-transition probabilities falling within the range of 0.0 to 1.0.

Let's now build the function-based versions and see what happens.

```

lathmat2ageonly_func <- fleslie(year = "all", data = lathvert_age,
  modelsuite = lathmodels2_age, yearcol = "year2")

lathmat2ageonly_func
> $A
> $A$`1`
>      [,1]      [,2]      [,3]
> [1,] 2.306431e-05 0.9999998 1.0000000
> [2,] 7.551400e-01 0.0000000 0.0000000
> [3,] 0.000000e+00 0.7871592 0.8160115
>
> $A$`2`
>      [,1]      [,2]      [,3]
> [1,] 2.306431e-05 0.9999998 1.0000000

```

```

> [2,] 7.551400e-01 0.0000000 0.0000000
> [3,] 0.000000e+00 0.7871592 0.8160115
>
>
> $U
> $U$`1`
>           [,1]      [,2]      [,3]
> [1,] 0.000000 0.0000000 0.0000000
> [2,] 0.75514  0.0000000 0.0000000
> [3,] 0.000000 0.7871592 0.8160115
>
> $U$`2`
>           [,1]      [,2]      [,3]
> [1,] 0.000000 0.0000000 0.0000000
> [2,] 0.75514  0.0000000 0.0000000
> [3,] 0.000000 0.7871592 0.8160115
>
>
> $F
> $F$`1`
>           [,1]      [,2] [,3]
> [1,] 2.306431e-05 0.9999998  1
> [2,] 0.000000e+00 0.0000000  0
> [3,] 0.000000e+00 0.0000000  0
>
> $F$`2`
>           [,1]      [,2] [,3]
> [1,] 2.306431e-05 0.9999998  1
> [2,] 0.000000e+00 0.0000000  0
> [3,] 0.000000e+00 0.0000000  0
>
>
> $hstages
> [1] NA
>
> $agestages
> [1] NA
>
> $ahstages
>   stage size size_b size_c min_age max_age repstatus obsstatus propstatus
> 1 Age0  NA    NA    NA      0      0          1          1          0
> 2 Age1  NA    NA    NA      1      1          1          1          0
> 3 Age2  NA    NA    NA      2     NA          1          1          0
>   immstatus matstatus indataset binhalfwidth_raw sizebin_min sizebin_max
> 1          0          1          1                NA          NA          NA
> 2          0          1          1                NA          NA          NA
> 3          0          1          1                NA          NA          NA
>   sizebin_center sizebin_width binhalfwidthb_raw sizebinb_min sizebinb_max
> 1              NA              NA                NA          NA          NA
> 2              NA              NA                NA          NA          NA
> 3              NA              NA                NA          NA          NA
>   sizebinb_center sizebinb_width binhalfwidthc_raw sizebinc_min sizebinc_max
> 1                NA                NA                NA          NA          NA

```

```

> 2          NA          NA          NA          NA          NA
> 3          NA          NA          NA          NA          NA
> sizebinc_center sizebinc_width group      comments
> 1          NA          NA          0 No description
> 2          NA          NA          0 No description
> 3          NA          NA          0 No description
>
> $labels
> pop patch year2
> 1  1    1 1989
> 2  1    1 1990
>
> $matrixqc
> [1] 6 6 2
>
> $modelqc
>          vital_rate individuals transitions accuracy
> 1          survival          232          542 0.7527675
> 2          observation           0           0          NA
> 3              size           0           0          NA
> 4              sizeb           0           0          NA
> 5              sizec           0           0          NA
> 6          reproduction           0           0          NA
> 7              fecundity          16          19          NA
> 8          juvenile_survival           0           0          NA
> 9          juvnil_observation           0           0          NA
> 10         juvenile_size           0           0          NA
> 11         juvenile_sizeb           0           0          NA
> 12         juvenile_sizec           0           0          NA
> 13 juvenile_reproduction           0           0          NA
>
> attr(,"class")
> [1] "lefkMat"
summary(lathmat2ageonly_func)
>
> This ahistorical lefkoMat object contains 2 matrices.
>
> Each matrix is square with 3 rows and columns, and a total of 9 elements.
> A total of 6 survival transitions were estimated, with 3 per matrix.
> A total of 6 fecundity transitions were estimated, with 3 per matrix.
> This lefkoMat object covers 1 populations, 1 patches, and 2 time steps.
>
> Vital rate modeling quality control:
>
> Survival estimated with 232 individuals and 542 individual transitions.
> Observation probability not estimated.
> Size transition not estimated.
> Reproduction probability not estimated.
> Fecundity not estimated.
> Juvenile survival not estimated.
> Juvenile observation estimated with 16 individuals and 19 individual transitions.
> Juvenile size transition not estimated.
> Juvenile reproduction probability not estimated.

```

```
>  
> Survival probability sum check (each matrix represented by column in order):  
>      [,1] [,2]  
> Min.  0.755 0.755  
> 1st Qu. 0.771 0.771  
> Median 0.787 0.787  
> Mean   0.786 0.786  
> 3rd Qu. 0.802 0.802  
> Max.   0.816 0.816
```

Everything looks quite good! Congratulations on creating your Leslie MPMs!

Literature cited

- Broek, J. van den. (1995). A score test for zero inflation in a Poisson distribution. *Biometrics*, 51, 738–743.
- Caswell, H. (2001). *Matrix population models: Construction, analysis, and interpretation*. Second edition. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- Caswell, H. & Salguero-Gómez, R. (2013). Age, stage and senescence in plants. *Journal of Ecology*, 101, 585–595.
- Caswell, H., Vries, C. de, Hartemink, N., Roth, G. & Daalen, S.F. van. (2018). Age \times stage-classified demographic analysis: A comprehensive approach. *Ecological Monographs*, 88, 560–584.
- Ehrlén, J. (2000). The dynamics of plant populations: Does the history of individuals matter? *Ecology*, 81, 1675–1684.
- Lefkovich, L.P. (1965). The study of population growth in organisms grouped by stages. *Biometrics*, 21, 1–18.
- Leslie, P.H. (1945). On the use of matrices in certain population mathematics. *Biometrika*, 33, 183–212.