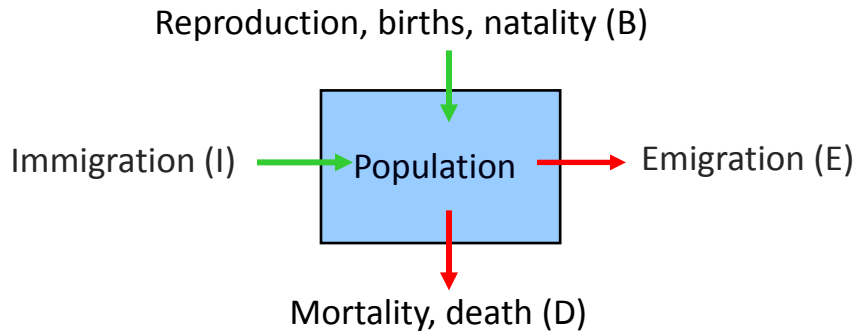


## Demographic based population models



## Demographic based population models

Animals have different vital rates – survival, reproduction during different ages or stages of life.

Understanding these differences and how they account for overall population size and structure can be of great use to wildlife researchers and managers.

Why?



Some terms:

**Fecundity:** average number of offspring born per individual  
(usually broken down to females/female)



**Survival:** proportion of individuals surviving from one time period  
to the next  
(=1 - mortality rate )



Projection matrix structure:

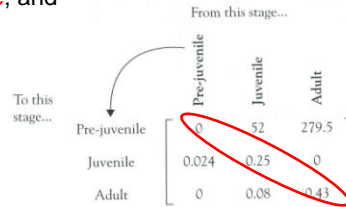
Each Stage (age or other class) has it's own values for **reproduction**, survival, and transitioning to the next stage

		From this stage...		
		Pre-juvenile	Juvenile	Adult
To this stage...	Pre-juvenile	0	52	279.5
	Juvenile	0.024	0.25	0
	Adult	0	0.08	0.43

**Fig. 7.1** Anatomy of a female-based projection matrix, using as an example the common frog (Biek et al. 2002; see also Box 4.8). This species has three stages: pre-juvenile (first year, consisting of the embryo, tadpole, and overwintering metamorph), juvenile (next 2 years), and adult. The projection interval, or time step, for this matrix is 1 year. The first row represents reproduction from each stage to the next year. The diagonal (e.g.  $a_{2,2}=0.25$  and  $a_{3,3}=0.43$ ; see text for an explanation of this notation) represents the proportion of individuals in a stage that will survive and still be in the same stage next year, while the subdiagonal (just below the diagonal; e.g.  $a_{2,1}=0.024$  and  $a_{3,2}=0.08$ ) represents the proportion surviving and advancing to the next stage next year.

Projection matrix structure:

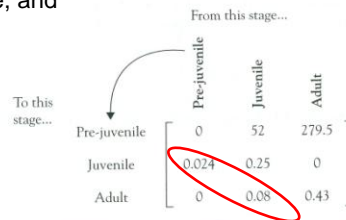
Each Stage (age or other class) has its own values for reproduction, surviving and staying in the current stage, and surviving transitioning to the next stage



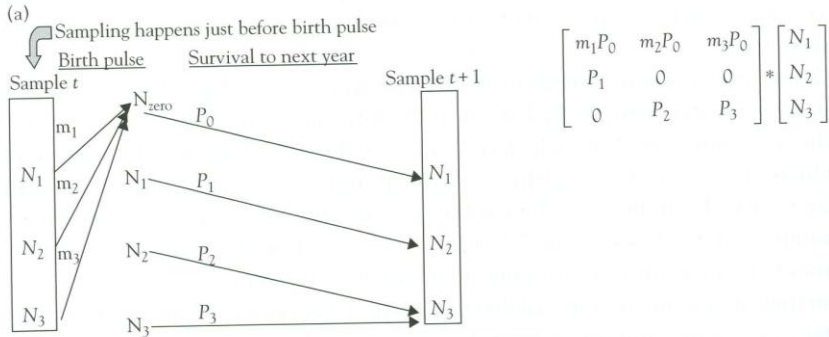
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Each Stage (age or other class) has its own values for reproduction, surviving and staying in the current stage, and surviving transitioning to the next stage

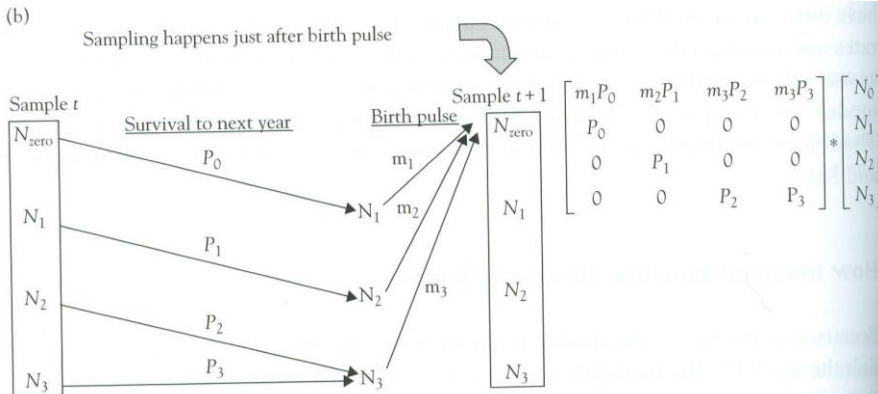


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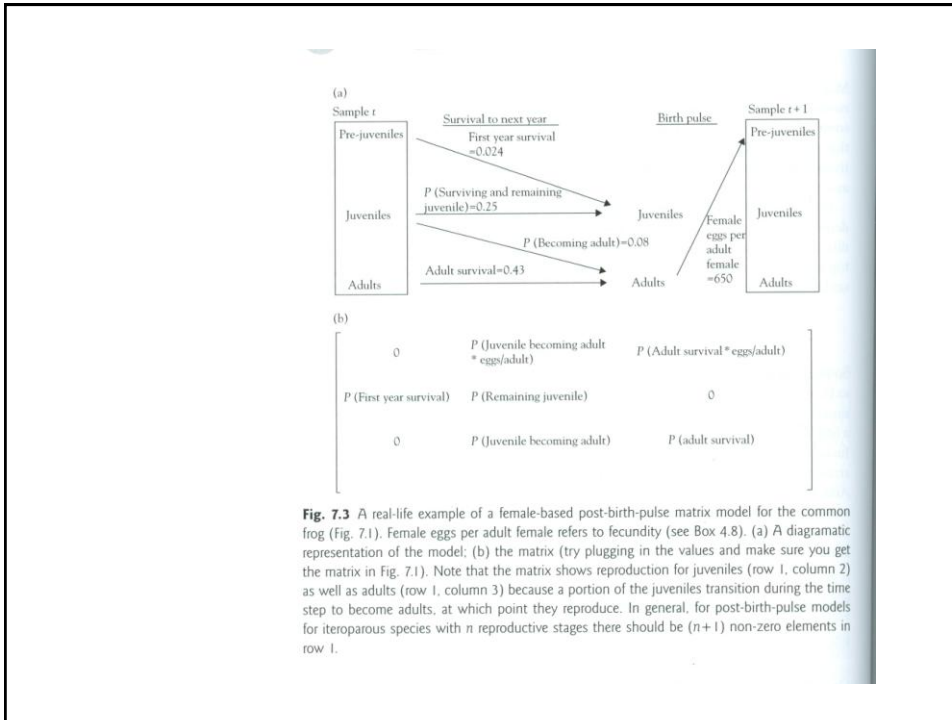
We use this matrix and information on numbers of individuals in each stage (**population vector**) at a particular time to predict numbers into future time steps

**Fig. 7.2** General schematics of the birth and death processes captured when the sampling is either (a) before the birth pulse or (b) after the birth pulse. The animals sampled at times  $t$  and  $t+1$  are boxed, with  $N_j$  representing number of individuals in each stage class  $j$ . This example assumes that animals stay in each stage for only one time step, except that those in the last stage can survive and remain in that stage for multiple time steps. Fecundity for each age class ( $m_i$ ) represents the average number of offspring born to each individual of  $N_i$ . The probability of survival through one time step is represented by  $P_i$ . To the right of each schematic is the resulting projection matrix and population-size vector. In (a), note that newborns ( $N_0$ ) are not seen until they have survived through their first year ( $P_0$ ) to be counted as  $N_1$  at the next sample interval; likewise, individuals in age class 1 ( $N_1$ ) are just about to become 2 years old, and so on. The next batch of  $N_0$  individuals are born just after sampling. In (b), note that there is an extra column and row in the post-birth-pulse matrix (compared to the case of the pre-birth pulse) because post-birth sampling occurs just after reproduction, making  $N_0$  recognizable as its own class.

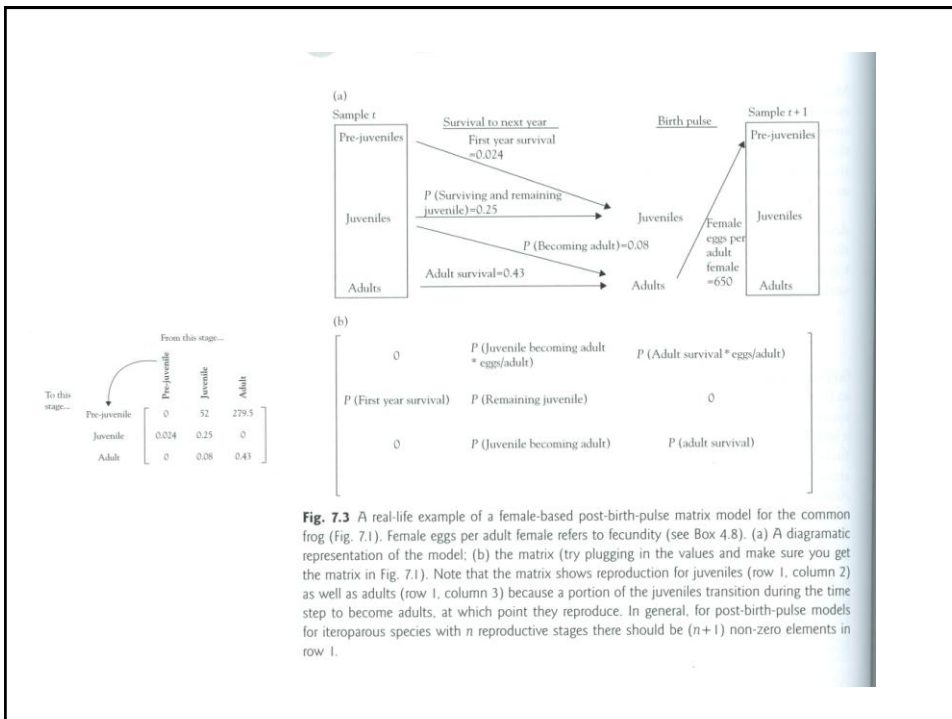


When sampling occurs will influence elements of the population matrix

**Fig. 7.2** General schematics of the birth and death processes captured when the sampling is either (a) before the birth pulse or (b) after the birth pulse. The animals sampled at times  $t$  and  $t+1$  are boxed, with  $N_j$  representing number of individuals in each stage class  $j$ . This example assumes that animals stay in each stage for only one time step, except that those in the last stage can survive and remain in that stage for multiple time steps. Fecundity for each age class ( $m_i$ ) represents the average number of offspring born to each individual of  $N_i$ . The probability of survival through one time step is represented by  $P_i$ . To the right of each schematic is the resulting projection matrix and population-size vector. In (a), note that newborns ( $N_0$ ) are not seen until they have survived through their first year ( $P_0$ ) to be counted as  $N_1$  at the next sample interval; likewise, individuals in age class 1 ( $N_1$ ) are just about to become 2 years old, and so on. The next batch of  $N_0$  individuals are born just after sampling. In (b), note that there is an extra column and row in the post-birth-pulse matrix (compared to the case of the pre-birth pulse) because post-birth sampling occurs just after reproduction, making  $N_0$  recognizable as its own class.



**Fig. 7.3** A real-life example of a female-based post-birth-pulse matrix model for the common frog (Fig. 7.1). Female eggs per adult female refers to fecundity (see Box 4.8). (a) A diagrammatic representation of the model; (b) the matrix (try plugging in the values and make sure you get the matrix in Fig. 7.1). Note that the matrix shows reproduction for juveniles (row 1, column 2) as well as adults (row 1, column 3) because a portion of the juveniles transition during the time step to become adults, at which point they reproduce. In general, for post-birth-pulse models for iteroparous species with  $n$  reproductive stages there should be  $(n+1)$  non-zero elements in row 1.



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Remember Exponential growth:

$$n(t+1) = n(t) * \lambda$$

Same holds here except we use matrices:

$$n(t+1) = n(t) * M$$



$$\begin{array}{l} \text{The matrix} \\ \begin{bmatrix} 0 & 52 & 279.5 \\ 0.024 & 0.25 & 0 \\ 0 & 0.08 & 0.43 \end{bmatrix} \end{array} * \begin{array}{l} \text{Population vector} \\ \text{in 2003} \\ \begin{bmatrix} 70 \\ 20 \\ 10 \end{bmatrix} \end{array} =$$

**Fig. 7.4** An example of how to project a matrix through time. The sample matrix comes from the common frog (see Figs 7.1 and 7.3). A matrix of mean vital rates is projected for three time steps, beginning in the year 2003. Initially, our population has 70 pre-juveniles, 20 juveniles, and 10 adults. At the bottom of each vector is the total population size ( $N$ ) for that year, rounded to the nearest whole female animal (as this is a female-based matrix).

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$$\begin{array}{l}
 \text{The matrix} \\
 \begin{bmatrix} 0 & 52 & 279.5 \\ 0.024 & 0.25 & 0 \\ 0 & 0.08 & 0.43 \end{bmatrix}
 \end{array}
 *
 \begin{array}{l}
 \text{Population vector} \\
 \text{in 2003} \\
 \begin{bmatrix} 70 \\ 20 \\ 10 \end{bmatrix}
 \end{array}
 =
 \begin{array}{l}
 \text{Population vector} \\
 \text{in 2004} \\
 \begin{bmatrix} (0 * 70) + (52 * 20) + (279.5 * 10) \\ (0.024 * 70) + (0.25 * 20) + (0 * 10) \\ (0 * 70) + (0.08 * 20) + (0.43 * 10) \end{bmatrix}
 \end{array}
 =
 \begin{array}{l}
 \begin{bmatrix} 3835.00 \\ 6.68 \\ 5.90 \end{bmatrix} \\
 N_{2004} = 3848
 \end{array}$$

**Fig. 7.4** An example of how to project a matrix through time. The sample matrix comes from the common frog (see Figs 7.1 and 7.3). A matrix of mean vital rates is projected for three time steps, beginning in the year 2003. Initially, our population has 70 pre-juveniles, 20 juveniles, and 10 adults. At the bottom of each vector is the total population size ( $N$ ) for that year, rounded to the nearest whole female animal (as this is a female-based matrix).

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$$\begin{array}{l}
 \text{The matrix} \\
 \begin{bmatrix} 0 & 52 & 279.5 \\ 0.024 & 0.25 & 0 \\ 0 & 0.08 & 0.43 \end{bmatrix}
 \end{array}
 *
 \begin{array}{l}
 \text{Population vector} \\
 \text{in 2003} \\
 \begin{bmatrix} 70 \\ 20 \\ 10 \end{bmatrix} \\
 N_{2003} = 100
 \end{array}
 =
 \begin{array}{l}
 \text{Population vector} \\
 \text{in 2004} \\
 \begin{bmatrix} (0 * 70) + (52 * 20) + (279.5 * 10) \\ (0.024 * 70) + (0.25 * 20) + (0 * 10) \\ (0 * 70) + (0.08 * 20) + (0.43 * 10) \end{bmatrix} \\
 = \begin{bmatrix} 3835.00 \\ 6.68 \\ 5.90 \end{bmatrix} \\
 N_{2004} = 3848
 \end{array}$$

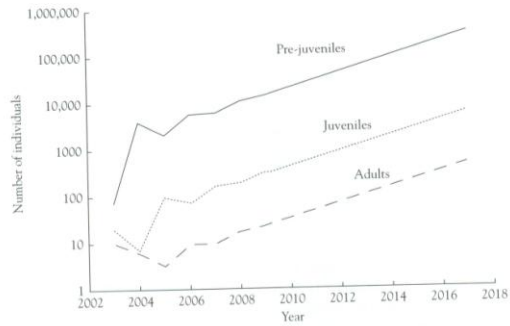
Repeat multiplying the matrix by the current vector to get

$$\begin{array}{l}
 \text{Population vector in 2005} \\
 \begin{bmatrix} 0 + 347.36 + 1649.05 = 1996.41 \\ 92.04 + 1.67 + 0 = 93.71 \\ 0 + 0.53 + 2.54 = 3.07 \end{bmatrix} \\
 N_{2005} = 2093
 \end{array}
 \rightarrow
 \begin{array}{l}
 \text{Population vector in 2006} \\
 \begin{bmatrix} 5731.38 \\ 71.34 \\ 8.82 \end{bmatrix} \\
 N_{2006} = 5812
 \end{array}$$

**Fig. 7.4** An example of how to project a matrix through time. The sample matrix comes from the common frog (see Figs 7.1 and 7.3). A matrix of mean vital rates is projected for three time steps, beginning in the year 2003. Initially, our population has 70 pre-juveniles, 20 juveniles, and 10 adults. At the bottom of each vector is the total population size ( $N$ ) for that year, rounded to the nearest whole female animal (as this is a female-based matrix).

### Stable stage distribution (SSD)

After enough time, if matrix is stable, the population will reach a stable state where the distribution among age classes is stable and so is the growth rate.



$n_{2015} = \begin{bmatrix} 143,766 \\ 2854 \\ 221 \end{bmatrix}$	$n_{2016} = \begin{bmatrix} 210,244 \\ 4164 \\ 323 \end{bmatrix}$	$n_{2017} = \begin{bmatrix} 306,931 \\ 6087 \\ 472 \end{bmatrix}$
Total 146,842	214,732	313,490
$\lambda_{2015-16} = 1.46$		$\lambda_{2016-17} = 1.46$
Distribution $\begin{bmatrix} 97.9\% \\ 1.9\% \\ 0.15\% \end{bmatrix}$		Stable stage

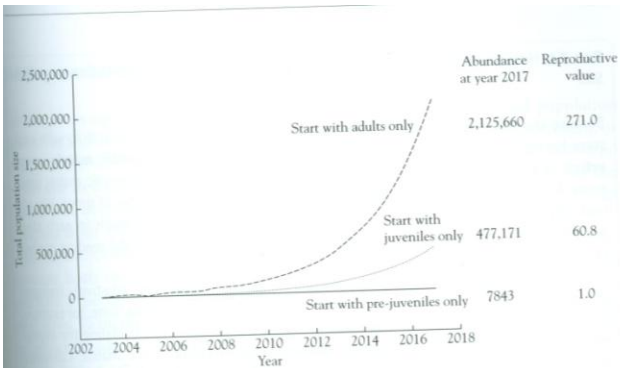


**Fig. 7.5** Convergence to a SSD for the common frogs considered in previous figures. Population numbers over 14 years (from 2003 to 2017) are shown by stage class. The number of frogs is plotted on a logarithmic scale to accommodate the huge numbers of pre-juveniles, and because at SSD the trajectories become linear. Below the graph are the vectors ( $n$ ), total population sizes, and geometric growth rates ( $\lambda$ ) for the final 3 years. When the population reaches SSD, both the population growth rate ( $\lambda$ ) and the proportion of individuals in each stage remain constant.

### Reproductive Value

Quantifies how important each stage is to current and future population growth.

Allows for assessment of which stages are of most conservation concern.



**Fig. 7.6** A demonstration of reproductive value by projecting common frog population size beginning with 100 adults, 100 juveniles, or 100 pre-juveniles, with the constant vital-rate matrix from Fig. 7.1. Although the initial abundance, the projection matrix, and eventual population growth rate and SSD are identical in each case, the initial stage distribution causes bounce in population growth early on, and leads to drastic differences in abundance. Reproductive value is typically scaled relative to the first age class. The right side of the graph shows how reproductive value can be calculated based on relative abundances at SSD, dividing each abundance by that of the population begun with the first age class. (I used abundances in year 2017, after 14 years had passed, but you could use abundances any time after SSD was achieved.)



**Box 7.2** An example of how to model environmental stochasticity, based on a population-projection matrix for red-legged frogs (*Rana aurora*)

Notice that this is a different frog species than the one discussed previously in this chapter. Data come from Biek et al. (2002).  
 Step 1: here is the matrix of vital rates.

$$\begin{pmatrix}
 0 & \left[ \begin{array}{l} \text{Probability of juvenile} \\ \text{becoming adult * probability} \\ \text{of laying * clutch size} \end{array} \right] & \left[ \begin{array}{l} \text{Adult survival *} \\ \text{probability of laying} \\ \text{* clutch size} \end{array} \right] \\
 \left[ \begin{array}{l} \text{Embryo survival *} \\ \text{larval survival *} \\ \text{metamorph survival} \end{array} \right] & \left[ \begin{array}{l} \text{Probability of} \\ \text{remaining a juvenile} \end{array} \right] & 0 \\
 0 & \left[ \begin{array}{l} \text{Probability of} \\ \text{juvenile becoming} \\ \text{adult} \end{array} \right] & \left[ \text{Adult survival} \right]
 \end{pmatrix}$$

Step 2: environmental stochasticity for the two emboldened vital rates (clutch size and adult survival) is as follows.

	<b>Clutch size</b>	<b>Adult survival</b>
Mean	303	0.69
SD	95	0.13
Distribution for random numbers	Lognormal	Beta

### Adding stochasticity to the models

Step 3: for five time steps, the vital rates chosen randomly from the specified distributions might, for example, be as follows.

<b>Time step</b>	<b>Clutch size</b>	<b>Adult survival</b>
1	287.6	0.66
2	326.8	0.71
3	252.0	0.93
4	382.9	0.55
5	251.9	0.60

Step 4: the distribution of vital rates chosen many times would look like the graphs below.

