7

Accounting for age- and sex-specific differences: population-projection models

> *For what is man? First, a child, soft-boned, unable to support itself on its rubbery legs, befouled with its excrement, that howls and laughs by turns, cries for the moon but hushes when it gets its mother's teat; a sleeper, eater, guzzler, howler, laugher, idiot, and a chewer of its toe; a little tender thing all blubbered with its spit, a reacher into fires, a beloved fool.*
>
> **Thomas Wolfe (1942:432), *You Can't Go Home Again***

> *If you can't generalize from data there's nothing else you can do with it either. A science without generalization is no science at all. Imagine someone telling Einstein, 'You can't say "E=mc^2." It's too general, too reductionist. We just want the facts of physics, not all this high-flown theory. Cuckoo.'*
>
> **Robert Pirsig (1992), *Lila***

Introduction

Bull elk, cowbird eggs, frog larvae, mother wallabies, turtle hatchlings. Often wildlife ecologists care about particular parts of a population as much as they do the population as a whole. Whether the applied goal is to harvest, recover, reduce, or reintroduce wildlife populations, one cannot long avoid the dynamics of particular ages, stages, and sexes. The last two chapters have described a foundation for how to predict and describe changes in wildlife populations, but thus far dynamics have been described by a single term (λ or r) applied to the total population size (N). In this chapter I will explore how particular groups of individuals, and their birth and death rates, affect population growth and the likely numbers of individuals of different classes.

Here is a story to transition us, adding the wrinkles of age and sex structure (Coulson et al. 2001). Soay sheep studied on the island of Hirta, off the coast of Scotland, fluctuate dramatically, more than expected based on weather or density dependence alone. Why? In large part because survival of lambs and older males is heavily influenced by winter weather, whereas yearlings and prime-aged females are most affected by rainfall at the end of winter. Meanwhile, negative density dependence affects lambs and older females more than prime-aged adults or yearlings. In turn, the changing proportions of different sex and age classes caused by weather and density dependence cascades into effects on population growth (see also Box 9.3). Not all sheep are equal (Gaillard et al. 2001). Counting the sheep as equivalent, ignoring age and sex, would tell us very little about how ecological stresses affect population fluctuations or population growth.

For humans and a few other species, age can be tracked as a meaningful descriptor of an individual. However, vital rates in wild populations often depend on developmental, morphological, or even behavioral stages more than calendar age. Consider, for example, larval forms and adults in amphibians, fish of different sizes, or big trees and saplings. Furthermore, different stages can often be distinguished more easily in the field than age classes can, and management often centers more on recognizable stages than on ages (e.g. ungulate males of different sizes or antler-development stages). The predominance of stage structure means that throughout this chapter (and the book), I will refer to **stage** instead of repeating age or stage.

In basic ecology classes, age or stage structure is typically covered using life tables. Although life tables are important for basic ecological understanding, most of the applied things that life tables can tell us about wildlife population dynamics (e.g. estimates of λ, stage structure, and reproductive value) can be better estimated using matrix-projection models[1]. Thus I will skip life tables and focus on less well known yet more versatile and practical tools for understanding how structure affects wildlife population dynamics.

Specifically, the aim of this chapter is to describe the wonders of matrix-projection models for understanding wildlife populations. If the thought of matrix math makes you nervous, think of a population-projection matrix as merely a box to help keep straight the bookkeeping of birth and survival, a mathematical representation of biological processes. That's it, really. Lots of bells and whistles can be added to matrix projections, but at their heart they are less intimidating than they may look. So let's look at what a matrix is, then we will quickly come back to the surface to gulp the air of application to wildlife population biology.

Anatomy of a population-projection matrix

Throughout the chapter, I will use as a tangible example the common frog, a species found throughout much of Europe. The projection matrix, **M**, is a square of k columns and k rows, where k is the total number of stage classes (Fig. 7.1). Each element (or cell) of the matrix contains a value that is used to project stage-specific reproduction or survival forward one time step. A time step can be anything:

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[1] For good overviews linking life tables to matrix models, see Noon and Sauer (1992) and Case (2000).

From this stage…

To this stage…

$$\begin{array}{r|ccc|}
 & \textbf{Pre-juvenile} & \textbf{Juvenile} & \textbf{Adult} \\
\text{Pre-juvenile} & 0 & 52 & 279.5 \\
\text{Juvenile} & 0.024 & 0.25 & 0 \\
\text{Adult} & 0 & 0.08 & 0.43
\end{array}$$

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.

for a yeast, the relevant time step of life and death might be an hour; for small mammals, it might be a month. For logistical and biological reasons, however, the most common time step for wildlife studies is a year, so throughout the book I will often use the terms year or annual as shorthand for the more general time step.

The elements of a matrix are described with subscripts that tell what row and column they are in (with the row first and the column second); for example, element $a_{2,1}$ is the element in row 2 and column 1. A handy way to decipher the biological meaning of any matrix element is to label the rows and columns of the matrix with the consecutive stages of your organism. Each element gives the transition – one time step later – from whatever column the number is in to whatever row the number is in. Another way to say the same thing is that $a_{i,j}$ represents the number of individuals contributed on average by each individual in class j at the current time step to class i at the next time step. For the common frog in Fig. 7.1, element $a_{2,1}$ is 0.024, meaning that on average 0.024 (or 2.4%) of the pre-juvenile frogs in the population survive to become juveniles the next year.

Notice in Fig. 7.1 that animals can remain in some stages for multiple time steps (for example 0.25 of the juveniles can remain as juveniles and 0.43 of the adults as adults). In a stage-based matrix, otherwise known as a **Lefkovitch matrix** (Lefkovitch 1965), transitions from any stage to any other stage can be accommodated. Stage-based matrices are more versatile than the original **Leslie matrix** (Leslie 1945), whereby vital rates depend on ages that are identifiable, and where the span of each age is the same as the length of the time step. In a Leslie matrix, an individual can only survive and transition to the next age, or die, so everything below the first row and not on the subdiagonal of the matrix must be zero. For practical purposes the distinction between Leslie and Lefkovitch matrices is only important to help you understand the terms in published papers.

With this brief lesson in projection-matrix anatomy, a few biological generalizations should become clear. First, each element of the top row of the matrix represents the reproductive contribution of each stage to the next time step. Second, the survival of individuals of any stage to the next time step (e.g. annual survival) can be determined from any matrix by adding up all the values for that column, excepting the first row[2]. For example, for the frogs in Fig. 7.1, annual survival of juveniles would equal 0.33, the sum of the proportion of juveniles that survive as juveniles (0.25) plus the proportion that survive and become adults (0.08). Third, the rates in the matrix must correspond to the stages you are interested in projecting. In particular, where the sexes have different survival rates, or where reproduction is known for females only, the vital rates are often female-based. In other cases, male-based models are most appropriate, as you will see for the red-cockaded woodpeckers in case study 1, below; two-sex matrix models are also possible, and you will see an example for ungulates in Chapter 14. The important thing is to be clear about which sexes are included in the projection, and how.

How timing of sampling affects the matrix

Because we are discussing applied population biology, let's think more about how to link the model to the field data, particularly to observable stages and to the timing of the surveys that produced counts of animals and estimates of vital rates (Fig. 7.2). Because each element of the top row contains the reproductive contribution of class j to the first stage class in the next time step, the top-row elements contain not only stage-specific fecundity (m_j), but also a term to advance the newborns to the next time step[3]. What does that mean? Well, newborns have to survive to be counted, or mothers counted last year have to survive to successfully bear their babies next year. So reproduction to the next time step depends on two terms: fecundity (m) and survival (P).

Exactly what we put into the elements of the top row depends on the kind of data collected. Suppose we were interested in projecting population growth for American bison, a species where most young are born at nearly the same time. For simplicity, assume all calves are born on May 31, and consider only the female portion of the population. If

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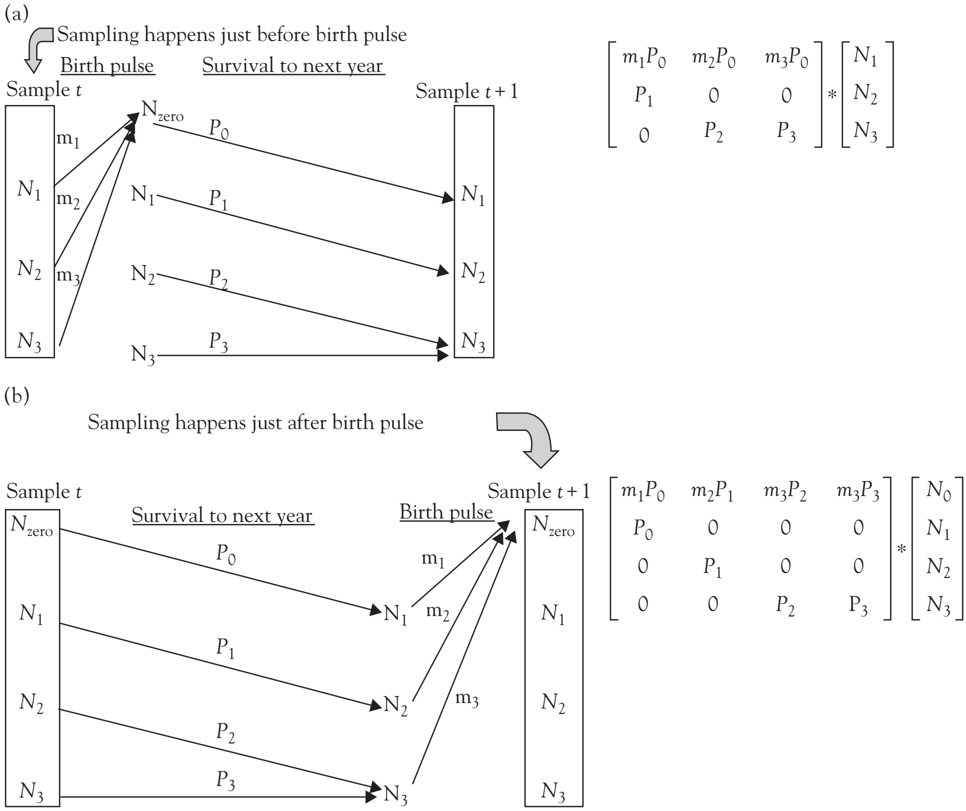
[2] When building a matrix from field-collected vital rates, one of many decisions is how to partition annual survival into the appropriate elements in a stage-based model. Crouse et al. (1987) give a nice, simple approach to partitioning survival into matrix elements for a stage-based model.

[3] Remember, **fecundity** (or m_j) refers to the average number of offspring an individual in stage j produces in a year (see Chapter 4); if you are familiar with life tables, then m_j is the same as the m_x or b_x. I use **reproduction to next time step** for the top-row matrix elements that include both the fecundity and survival terms needed to project the fecundity to the next time step; this is often called **fertility** by human demographers, but fertility has different meanings in the ecological literature so I will avoid the term here.



$$\begin{bmatrix} m_1P_0 & m_2P_0 & m_3P_0 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix} * \begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix}$$

$$\begin{bmatrix} m_1P_0 & m_2P_1 & m_3P_2 & m_3P_3 \\ P_0 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 \\ 0 & 0 & P_2 & P_3 \end{bmatrix} * \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \end{bmatrix}$$

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_j) represents the average number of offspring born to each individual of N_j. The probability of survival through one time step is represented by P_j. 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.

we sampled on May 30 (just before the birth pulse), then the youngest age class counted would be the calves born last May 31 that had lived to be counted just as they are about to become 1 year old. The reproductive contribution for each stage class, then, must include not only stage-specific fecundity (m_j; the average number of female calves born per year per female in stage j) but also the probability of newborns surviving to be counted at the end of their first year (call this P_0). Now, what if instead of sampling on

May 30 we sample on June 1, the day after the birth pulse? In this case we would sample newborns. We would know exactly how many female calves were born per female, but some of the mothers alive last year would have died during the year (remember again that the goal is to project the population forward through time). Thus the reproductive-contribution elements of the top row would include stage-specific fecundity (m_j) as well as survival of mothers in that stage to have the newborns (P_j).

People who spend a lot of time messing with population-projection matrices often denote as F_j each element of the top row, where each element is this composite of fecundity and survival of either the mothers or the newborns. Thus each element of the top row of the matrix represents the reproductive contribution to the next time step under either

- pre-birth-pulse sampling, $F_j = m_j P_0$, or
- post-birth-pulse sampling, $F_j = m_j P_j$.

So **post-birth** models have an extra stage class, because the newborns are recognizable as their own class (they were born just before sampling), whereas with **pre-birth**-pulse sampling we do not see newborns until they become class N_1 (as in Fig. 7.2a). I've been a little excruciating in detailing these two model types because it turns out to be a confusing topic in many ecology textbooks and published papers. If the accounting is kept straight, though, the two approaches give exactly the same population growth rate. And the strict pre- versus post-birth-pulse sampling can be relaxed to account for varying periods between the birth pulse and the sampling, or even to allow for continuous breeding (see Further reading). The development of the matrix for the common frog is shown in Fig. 7.3.

Projecting a matrix through time

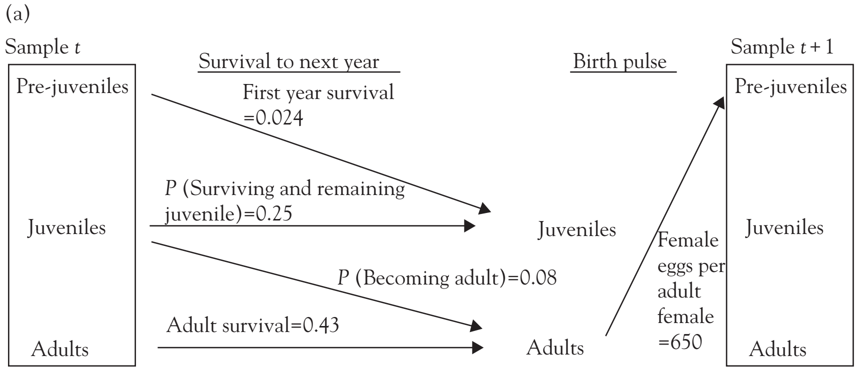
How to project the matrix

Once the matrix model is filled with vital rates, it can be projected through time. The advantage of a matrix approach over the nonstructured models of the previous two chapters is that it keeps track of not just the total population size but also the numbers in each stage. In matrix terms, we will project through time the population-size vector. A vector is a skinny matrix of one column and k rows that contains the number of individuals in each of the k stages. To determine the population-size vector next year [$\mathbf{n}(t+1)$], multiply the matrix $\mathbf{M}$ of vital rates by the vector of individuals at time t, $\mathbf{n}(t)$:

$$\mathbf{n}(t+1) = \mathbf{M} * \mathbf{n}(t) \tag{7.1}$$

By convention, matrices and vectors are shown in bold.

How do you multiply a matrix by a vector? Go across each row of the matrix, multiplying each element j by the same element of the vector (Fig. 7.4). Add up the products for one row to obtain the total number of individuals in that element of the vector. Again, if the math intimidates you, take a breath and realize that the projection



(b)

$$\begin{bmatrix} 0 & P\text{ (Juvenile becoming adult * eggs/adult)} & P\text{ (Adult survival * eggs/adult)} \\ P\text{ (First year survival)} & P\text{ (Remaining juvenile)} & 0 \\ 0 & P\text{ (Juvenile becoming adult)} & P\text{ (adult survival)} \end{bmatrix}$$

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 diagramatic 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.

of a matrix makes biological sense. The number of individuals in the first stage (newborns) next year comes from the reproductive contribution of each stage to the next time step (the top row of the matrix) multiplied by the number of individuals in each stage (the population vector). Likewise, the number of individuals advancing to a different stage or staying in the stage at the next time step are the product of survival (or other possible transitions below the first row) and the number of individuals in that stage.

Stable stage distribution and reproductive value

Matrix-projection methods can start with any number of individuals in different stages, and keep track of the relative number in each stage as well as population growth over time. This feature makes an important tool for many applications, ranging from tracking the possible growth of a translocated population to predicting what

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

Repeat multiplying the matrix by the current vector to get

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

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).

might happen to certain stages during harvest. Although you can start with whatever number of individuals you want in each stage class, if vital rates stay relatively constant over time the population will converge on a population growth rate and stage distribution that is characteristic for that particular matrix. As a demonstration, Fig. 7.5 shows the projections for frogs from Fig. 7.4 for 14 years from the initial vector in 2003. By 2017 the population growth rate per year has become constant ($\lambda=1.46$; calculated by N_{t+1}/N_t). Also, the proportion of individuals in each class is constant, with about 98% of the population being pre-juveniles [e.g. $(306{,}931/313{,}490)*100=98\%$], 1.9% juveniles, and 0.2% adults (for practice, calculate the age distribution for the year 2016 from the information in Fig. 7.5). This constant proportion of individuals in each stage class is known as the **stable age distribution** (SAD) or, more generally, the **stable stage distribution** (SSD). Nearly any population matrix – whether it represents a declining, increasing, or stationary population – will converge on a constant population growth and SSD if the vital rates making up the matrix stay relatively constant[4]. (The time to SSD depends on factors such as the initial age structure and the characteristics of the matrix itself, but should be achieved within 20 time steps or so for most vertebrate populations.) The population growth rate at SSD, and the SSD itself, are characteristic of the matrix, and are independent of the initial age distribution.

Although the SSD and λ_{SSD} are independent of initial stage distribution, the distribution of animals across stages influences both the time to reach SSD and the population abundance in the future. Consider population growth curves for our frogs again,

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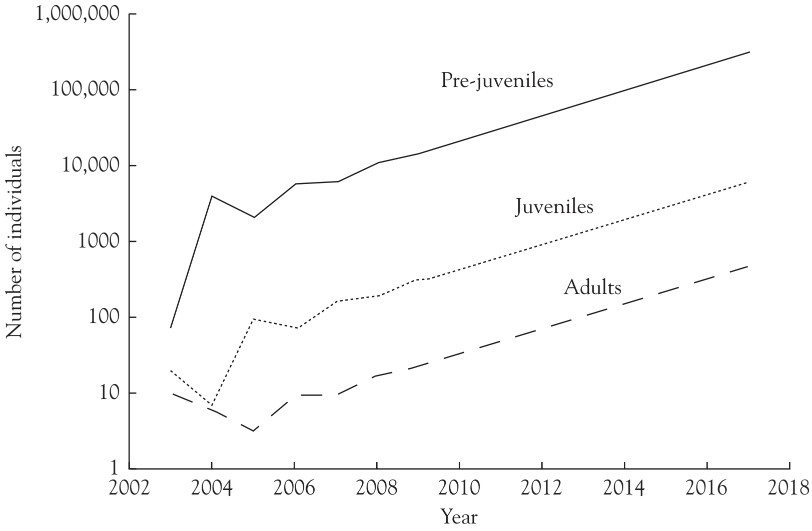
[4] There are matrices that will not converge to an SSD, including matrices that have only a single non-zero element in the first row, which can lead to stable oscillations (Leslie 1945, Caswell 2001).



$$n_{2015}=\begin{bmatrix}143{,}766\\2854\\221\end{bmatrix}\qquad n_{2016}=\begin{bmatrix}210{,}244\\4164\\323\end{bmatrix}\qquad n_{2017}=\begin{bmatrix}306{,}931\\6087\\472\end{bmatrix}$$

Total 146,842 214,732 313,490

$\lambda_{2015-16}=1.46$ $\lambda_{2016-17}=1.46$

$$\text{Distribution}\begin{bmatrix}97.9\%\\1.9\%\\0.15\%\end{bmatrix}$$

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 (λ) for the final 3 years. When the population reaches SSD, both the population growth rate (λ) and the proportion of individuals in each stage remain constant.

this time plotting total population size for 14 years with populations of 100 frogs that are seeded with all of one stage: 100 pre-juveniles, 100 juveniles, or 100 adults (Fig. 7.6). Even though all three populations start with the same initial number of frogs and the same constant set of vital rates, and after 14 years have all achieved the same growth rate at SSD, the numbers of frogs at time step 14 are vastly different for the three populations. Why? Because all stage classes are not created equal in their contribution to population growth, a phenomenon quantified by the concept of **reproductive value**. In Fig. 7.6 you can see that a population founded with 100 frogs, all adults, would reach a size of 2,125,660 frogs in 14 years, in contrast to the 477,171 individuals in the juvenile-seeded population and 7,843 in the population begun with 100 pre-juveniles. By convention, reproductive value is scaled relative to that of the first age

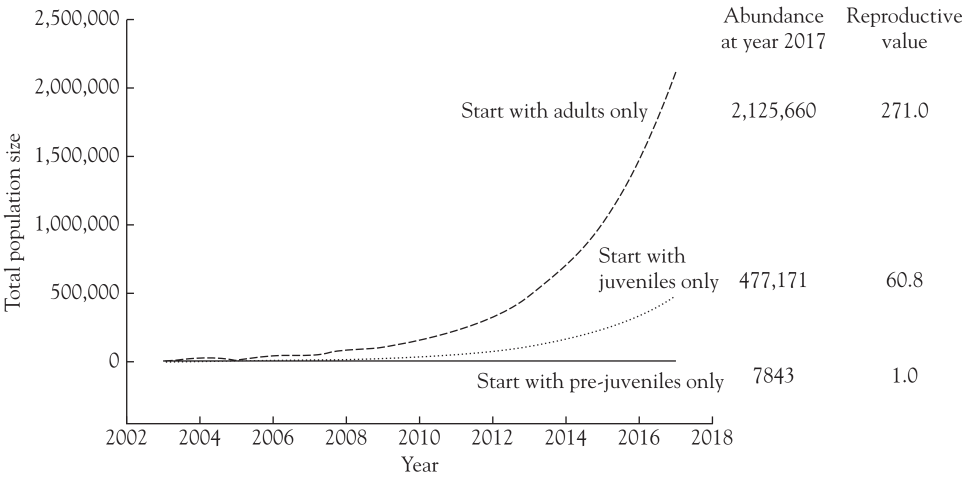


Fig. 7.6 A demonstration of reproductive value by projecting common frog population size beginning with 100 adults, 100 juveniles, or 100 pre-juveniles, with the constant vital-rate matrix from Fig. 7.1. Although the initial abundance, the projection matrix, and eventual population growth rate and SSD 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.)

class. Therefore, for the frogs, adults have a reproductive value of 271.0, and juveniles of 60.8, compared to the reproductive value of 1.0 for pre-juveniles (Fig. 7.6).

Because the reproductive value quantifies how much each stage acts as a seed for future population growth (Caswell 1989:67), it has immense yet under-appreciated applications in wildlife population biology. Reproductive value is not a synonym for fecundity, or reproduction in the top row of the matrix. Rather, it takes into account reproductive output at that stage, as well as future reproduction, the likelihood to survive to those stages, and the population growth rate. In other words, reproductive value is a weighted average of present and future reproduction, accounting for population growth rate, that provides us with a practical way to assess contribution of different stages to future population growth (see Lanciani 1998, Case 2000).

So, here's what we've got so far on projecting matrices: Because all stages are not equal in their effects on population growth – that is, they have different reproductive values – the initial age distribution affects future abundance and the time required to reach SSD[5]. It also causes the population size to bounce around early on (as the age

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[5] Look back at Fig. 1.3, showing how population momentum would cause the global human population size to increase even if women had only replacement numbers of children. The momentum is caused by an age structure leading to lots of babies even though modified vital rates would lead one to expect stationary population growth.

Box 7.1 How to calculate reproductive value, SSD, and the expected population growth at SSD

Because any constant population-projection matrix attains a constant SSD and λ, with each stage having a characteristic reproductive value, these are called **asymptotic matrix properties**. In the text I showed an approach to calculating each of the asymptotic matrix properties. For SSD and λ, project any initial population vector out by a number of times, say 100 time steps, and then calculate at time step 100 the proportion of individuals in each stage and the growth rate ($\lambda = N_{100}/N_{99}$). For reproductive value, you could use the seeding method (as in the frog example in Fig. 7.6).

Although these projection-based approaches are perfectly legitimate, intuitively transparent, and pretty easy to accomplish with simple multiplication that could be done, for example, in a Microsoft Excel spreadsheet, there are more elegant approaches to calculating the asymptotic matrix properties. For example, the **dominant eigenvalue** of the matrix, calculated using matrix math, equals λ, and its associated **right eigenvector** equals the SSD vector. Likewise, the **left eigenvector** of the dominant eigenvalue gives the vector of reproductive values.

distribution settles down to a SSD), and this is in the absence of any demographic or environmental stochasticity. However, the SSD and corresponding growth rate are a function of the matrix values and not the initial age distribution, so a population of any composition will eventually reach SSD and its associated λ as long as the matrix rates are relatively constant. Various ways to estimate reproductive value, SSD, and its associated λ value are described in Box 7.1.

For wildlife population management the implications of these population dynamics properties are profound. First, a set of vital rates represented as a projection matrix, coupled with a count of animals by stage class, provides insights into the inherent growth rate to be expected and the proportion of individuals eventually expected in each stage class over time. Second, the effect of age distribution means that a newly reintroduced population can be wildly erratic in its population growth – even without any stochasticity occurring – if the initial composition of the population is far from the expected SSD. Third, the reproductive value itself conveys the consequences of losing individuals of certain stages through harvest, or gaining them through translocations.

Before leaving this discussion on projecting matrix models through time, I should emphasize that I have only talked about density-independent matrix models. Density dependence can be added to matrix models (see the Further reading section of this chapter). I have also limited the discussion so far to the case where vital rates in the matrix are constant through time. Next I will briefly show how random variation (demographic and environmental stochasticity) can be incorporated into matrix projections.

Adding stochasticity to a matrix model

Although asymptotic properties such as the reproductive value, SSD, and population growth at SSD are useful, they are based on vital rates in the matrix being constant, or nearly so. But we know that vital rates are seldom constant for any length of time. And as we saw in Chapter 5, stochasticity has important implications, including the fact that it will decrease the likely future growth of a population compared with that expected from λ at the SSD[6].

Fortunately, computers make it quite easy to project a stage-structured model incorporating both environmental and demographic stochasticity (Chapter 5), assuming you have a specified starting population vector, and estimated means and variances for vital rates. To incorporate environmental stochasticity over time for a population, the computer builds a new matrix each time step, where each element in the matrix is chosen from a set of random numbers with a specified mean and process variance. The distribution of random numbers may be from a uniform distribution (all values equally likely to be chosen between a high and low value) or – more usually – from a distribution with central tendency, such as lognormal, normal, or beta (see Morris & Doak 2002). An alternate approach randomly picks one of several vital rates measured in the field (or even entire matrices of vital rates from field data; Bierzychudek 1982, Akçakaya 2000). Box 7.2 gives an example of environmental stochasticity in action for a population projection for the red-legged frog.

Demographic stochasticity in survival can be modeled to capture the real-world phenomenon whereby animals live or die as whole animals and not as fractions (Chapter 5). A common way to model demographic stochasticity in survival using the computer is to determine the fate of each individual in a stage based on the mean survival rate. Specifically, for each individual the computer picks a random number between 0 and 1; if the random number is less than the mean survival probability (also between 0 and 1) then the animal lives, if not, it dies. For example, suppose that your population vector has six yearlings, and the mean survival probability for yearlings is 0.8. Without demographic stochasticity, the expected number of subadults next time step is $(0.8*6=4.8)$. With demographic stochasticity, the computer might pick the following six random numbers: 0.32, 0.89, 0.51, 0.11, 0.94, 0.70. Thus, four of the animals would live, but two would die (the second and fifth). At small numbers the proportion of survivors can deviate greatly from that expected from the mean survival rate, just as a small number of coin tosses can lead to a big deviation from 50:50 heads/tails (see Chapter 5).

Sensitivity analysis

As we have seen, all stage classes are not created equal in their management importance, their effects on population growth, or in their relative abundance. Similarly, it

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[6] Specifically, stochasticity will decrease population growth by an amount depending on which rate varies, how much it varies, and the sensitivity of λ to changes in that rate (Morris & Doak 2002:239). We will look at how to quantify sensitivity in the next section.

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.

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

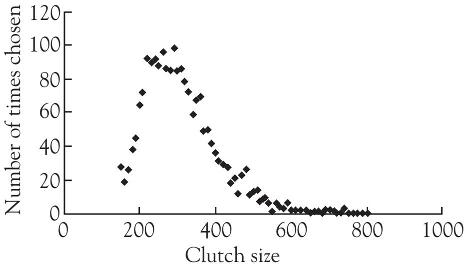
Step 2: environmental stochasticity for the two emboldened vital rates (clutch size and adult survival) is as follows.

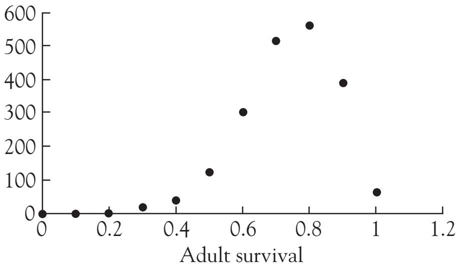
	Clutch size	**Adult survival**
Mean	303	0.69
SD	95	0.13
Distribution for random numbers	Lognormal	Beta

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

Time step	**Clutch size**	**Adult survival**
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.





should not be surprising to learn that the vital rates themselves also vary widely in their effects on population growth and structure: all vital rates are not created equal. Intuition alone is insufficient to predict how changes in individual life-history components will affect population growth. Although one commonly hears conclusions like "forest fragmentation affects adult survival" or "acid rain affects clutch size," such statements do not indicate how the expected changes in vital rates affect population growth.

This simple demographic fact – that different vital rates do not have equal impacts on population growth rate – has been known for a long time (e.g. Cole 1954). But it was Hal Caswell's book on *Matrix Population Models* (1989), arriving on the heels of unprecedented access to desktop computers, that irrevocably convinced ecologists of the importance of a formal framework evaluating the effects of changes in vital rates. Sensitivity analysis provides that framework in the form of analytical and simulation-based tools to evaluate how past or future changes in life-history attributes or demographic vital rates affect population growth or persistence.

One of the earliest and most influential uses of sensitivity analysis in animal population biology targeted loggerhead sea turtles, which had been declining in the Atlantic by 3–5% per year for a long time. On the east coast of the USA enormous public sentiment built up concerning mortality of the eggs on the beach and the tiny (and adorable) hatchlings that were killed by predators, crushed by vehicles, and disoriented by lights as they tried to make their way from the nest to the ocean. Therefore, management focused on what seemed to be the obvious solution: increasing the survival of eggs and hatchlings. But in 1987 Deborah Crouse and colleagues published a sensitivity analysis that showed that even large increases in egg or hatchling survival would do little to reverse the population decline: the key was to increase survival of young adults in the ocean. It turned out that roughly 50% of loggerhead mortality in the Atlantic was due to young adult turtles becoming entangled in shrimp nets. The paper by Crouse et al. (1987) was key to the development of legislation requiring turtle-excluder devices to be installed by shrimpers (Crowder et al. 1994). In this case, sensitivity analysis of a matrix-projection model showed that intuition focusing on eggs and hatchlings alone to recover the species was wrong, and that a different management action would be much more beneficial and efficient for recovery.

Three main approaches are used by applied wildlife population ecologists to conduct sensitivity analyses (see Mills & Lindberg 2002 for more details). I will give a brief overview of these approaches, followed by a peek into the range of questions that can be answered with sensitivity analysis of matrix population models.

How to do a sensitivity analysis

Manual perturbation

The most basic approach to sensitivity analysis is to manually perturb, or change, the input to a population model and observe how the change affects the output[7].

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[7] Output could be population growth rate, or it could be probabilities of quasi-extinction (see Chapter 14).

For example, one could ask how the deterministic population growth rate (λ) of a matrix model changes when adult survival is increased by 10% compared with an increase in fecundity. Management options can be explored by comparing the expected effects on population growth or persistence when each option changes certain vital rates by any pre-determined amount. The approach is infinitely flexible; sensitivity analysis via manual perturbations is not limited to investigating the importance of vital rates alone, but rather can explore a range of factors including density dependence, inbreeding depression, and movement among populations (Chapter 12). Also, manual-perturbation sensitivity analysis can incorporate different age or stage structures, quantifying the effect of age structure on population growth.

Analytical sensitivity and elasticity analysis

You have learned that different age classes may have very different relative abundances at SSD, and different effects on future population size (i.e. different reproductive values). Therefore, a vital rate for a certain age class will influence λ more if there are proportionately more of that age class (larger SSD) and if each individual of that age class has a larger impact (bigger reproductive value). Analytical **sensitivities** and **elasticities** elegantly combine the reproductive value of an age class with its expected SSD to evaluate how infinitesimal changes in individual vital rates will affect λ. Specifically, sensitivity for a vital rate that makes up matrix element $a_{i,j}$ (remember this is the matrix element in row i and column j) is a function of the reproductive value of the age class (v_i) and the SSD (w_j)[8]:

$$\text{Sensitivity of matrix element } a_{i,j} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\left(\sum_{k=1}^{\text{Last stage class}} v_k w_k \right)} \tag{7.2}$$

A larger reproductive value (v_i) or SSD (w_j) leads to a larger sensitivity. Notice that sensitivity is a partial derivative, defined as the infinitesimal absolute change in population growth rate given an infinitesimal absolute change in a vital rate or matrix element, while all other vital rates are held constant. As an alternative to the calculus in eqn. 7.2, you can also estimate sensitivity by making a tiny manual change to the vital rate of interest, and quantify how λ at SSD changes before and after the perturbation. For example, increase the element $a_{i,j}$ by 0.01, leaving everything else unchanged, and estimate λ before and after, as follows.

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[8] If you prefer to think about equations graphically, consider that as a partial derivative, the sensitivity of matrix element $a_{i,j}$ equals the slope of the tangent to the curve relating population growth rate to the matrix element, evaluated at the mean element.

$$\text{Sensitivity of matrix element } a_{i,j} = \frac{\lambda_{a_{i,j}+0.02} - \lambda_{\text{original}}}{0.01} \tag{7.3}$$

So, for the red-legged frogs in Box 7.2, analytical sensitivity would quantify how a tiny change in juvenile survival (say, from 0.69 to 0.70) would affect population growth compared with the same tiny change in another vital rate, such as clutch size (from 303 to 303.01). Although this may be useful for some applications, you can see immediately that from a practical perspective we have a scaling problem; the same absolute change of 0.01 in the mean of these two rates is very different for survival (a 1.4% change) compared with clutch size (a 0.003% change). That's where elasticity becomes useful. Elasticity is sensitivity's cousin, a metric that rescales the sensitivity to account for the magnitude of the vital rate. Thus elasticities are **proportional sensitivities** that describe the proportional change in λ given an infinitesimal one-at-a-time proportional change in a vital rate[9]:

$$\text{Elasticity of matrix element } a_{i,j} = (\text{sensitivity of } a_{i,j}) * \frac{a_{i,j}}{\lambda} \tag{7.4}$$

When matrix elements are composed of more than one vital rate (e.g. where each element of the top row of a projection matrix contains both reproduction and survival components), or when a particular vital rate shows up in more than one matrix element, component sensitivities and elasticities can be calculated for each vital rate that appears in one or more matrix elements. Although the analytical formula for component sensitivities requires chain-rule differentiation for each $a_{i,j}$ that contains a particular vital rate x, in many cases the procedure is pretty simple[10].

As a proportional measure of sensitivity, analytical elasticities are more widely used in applied population biology than sensitivities. Elasticities can be added together to predict the joint effect of changes in multiple rates (assuming the changes in vital rates and λ are linearly related). Elasticities of all matrix elements sum to one; elasticities of component vital rates do not add up to one but can still be ranked. Based on analysis of measured vital rates from hundreds of studies of different bird and mammal species, predictable patterns link life-history traits to the relative elasticities of different vital rates (Box 7.3).

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[9] Analogous to sensitivity, elasticity is the slope of the tangent to the curve relating proportional changes in λ to proportional change in matrix elements.

[10] Assuming that each matrix element is a simple linear combination of different vital rates, here is a simple translation of the chain rule to calculate sensitivity for a vital rate x that is a component of more than one matrix element, where each element containing x has sensitivity $s_{i,j}$.

$$\sum_{1}^{\text{Elements containing } x} [(s_{i,j}) * (\text{product of components other t}$$

You can also use eqn. 7.3 to tweak a component vital rate and calculate sensitivity. Either way, the

$$\text{elasticity of vital rate } x = (\text{component sensitivity of vital rate } x) * \left(\frac{x}{\lambda}\right).$$

Box 7.3 How might we predict which vital rates will have highest elasticities for a wildlife species?

Although the best way to assess elasticity of a vital rate is to conduct analysis on a complete set of field-derived vital rates for a particular population, it is useful to know that some coarse generalizations can support general principles. For example, species with early maturation and large litters tend to have elasticities that are higher for reproduction (litter size and offspring survival) and lower for adult survival; conversely, in species with late maturation, fewer offspring, and higher survival rates, population growth is affected more by adult survival than by reproduction (Heppell et al. 2000, Sæther & Bakke 2000, Oli & Dobson 2003). Survival of all stages will tend to have higher elasticities than reproductive output for most taxa with lifespans longer than a year (Crone 2001). The implication is that "in any sharp change of population growth rate for a long-lived species, one should first suspect a change in adult survival" (Lebreton & Clobert 1991:108).

Although these life-history general principles give us first-cut insights into which rates will have the highest elasticities, that does not mean that those rates are most important. Remember, vital rates with low elasticities but that change a large amount could actually affect the growth rate more than rates with high elasticities but that change little.

Analytical sensitivities and elasticities are easily applied, comparable across studies, and can be calculated from a single population matrix constructed from average or even best-guess vital rates. However, we should keep in mind their fundamental assumptions (Mills et al. 1999, 2001). First, they are asymptotic, relying on the population being at SSD (although this assumption can be relaxed; see Fox & Gurevitch 2000, Grant & Benton 2000, Caswell 2001). Second – and perhaps most importantly – analytical sensitivities and elasticities by themselves say nothing about how much vital rates change in nature or under management.

A classic case in point (Gaillard et al. 1998, Raithel et al. 2006) is that for ungulates in general, adult survival would be expected to have the highest elasticity by far. However, juvenile survival will be much more variable than adult survival, because juveniles are less buffered against density-dependent influences or environmental factors such as predation, bad weather, and so on. The fact that juvenile survival may easily vary from 0.1 to 0.7, whereas adult survival will tend to be much less variable, means that the rate with relatively low elasticity that changes a lot (e.g. juvenile survival) may affect population growth more than a rate with high elasticity that doesn't vary much (e.g. adult survival). Elasticities based on a mean matrix cannot capture how much a vital rate, and therefore population growth, can change in nature or under management.

An extension of analytical sensitivity and elasticity analysis, called **life-table-response experiments** (or LTREs for short), does explicitly account for variation with an analytical equation (Caswell 2001). For practical purposes, changes simulated on the computer are a more versatile way to the same end, so I will discuss such an approach next.

Life-stage simulation analysis

Wisdom and Mills (1997) developed a simulation-based approach to sensitivity analysis that might be considered a hybrid of the manual perturbation and analytical sensitivity/elasticity-based methods. The approach is called **life-stage simulation analysis** (LSA; Wisdom et al. 2000)[11] because it uses simulations to evaluate the impact of changes in different vital rates on elasticity rankings and λ. For the purposes of conservation decision-making, the user obtains (from the field if possible) both means and variances for vital rates. The variance should be based on process variance, uninflated by sample variance (Mills & Lindberg 2002). For projecting what might happen in the future, you can couple information from the past with specified changes in means and variances that are considered biologically, politically, and logistically possible under management in the future[12]. Correlations among vital rates are specified, if possible, as are the distribution functions for each vital rate (i.e. uniform, lognormal, beta, etc.). A computer program constructs many matrices with each rate in each matrix drawn from the specified distributions. Population growth rate is calculated for the matrix (usually asymptotic λ at SSD, although stochastic λ could also be calculated).

Output metrics in LSA include elasticity-based measures (e.g. the proportion of replicates where the vital rates shift rankings of elasticities, or the differences in elasticity values whenever the rankings of elasticities change across the replicates; Wisdom et al. 2000), as well as other metrics that avoid elasticity entirely. For example, one LSA output could be the percentage of replicates having positive population growth under different scenarios (Fig. 7.7).

Another way that LSA has commonly been used to evaluate the importance of vital rates for management is to regress λ on each vital rate as all rates change simultaneously (including the vital rate of interest) in 1000 or so simulated matrices (e.g. Wisdom & Mills 1997, Crooks et al. 1998, Cross & Beissinger 2001). The coefficient of determination (R^2) represents proportion of the variation in population growth rate that is explained by environmental variation in that vital rate, with all other vital rates varying simultaneously. When all main effects and interactions are included, the R^2 values sum to one. When λ is a linear function of the vital rates, the slope of the line equals the analytical sensitivity and R^2 is a function of both the slope (i.e. analytical sensitivity) and the proportionate variation in that vital rate, adjusted for covariance among vital rates. The same relationships hold for elasticity if the regression is done on log-transformed data (Brault & Caswell 1993, Horvitz et al. 1997). Therefore, the

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[11] Morris & Doak (2002:344–8) refer to this approach as a "simulation-based sensitivity analysis."

[12] I avoid use of the terms prospective and retrospective sensitivity analysis (Caswell 2001) because these terms have been used to imply that the inclusion of variation in a sensitivity analysis prohibits one from asking what might occur under future management. When conducting a sensitivity analysis of potential management scenarios, it seems more constructive to simply make explicit whether or not variation is included, the origin of the estimates of both variation and mean rates, and the rationale for potential future changes in vital rates (Mills et al. 2001, Wisdom et al. 2000, Mills & Lindberg 2002).

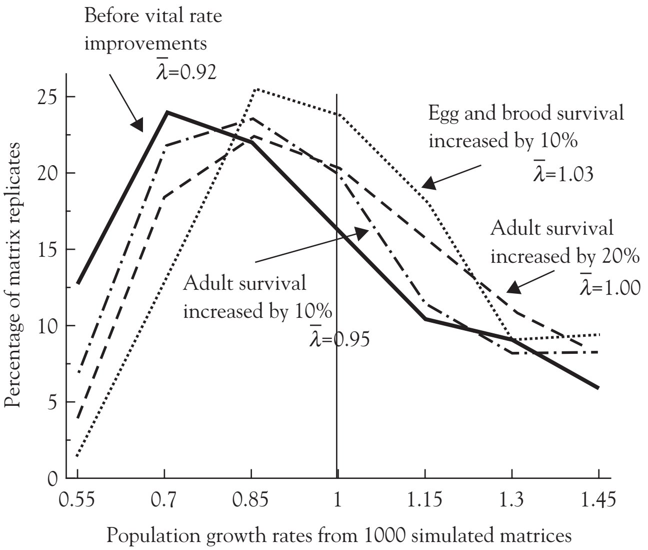

Fig. 7.7 An example of one form of LSA output for greater prairie-chickens, a species whose populations are declining, scattered, and potentially vulnerable to extirpation (see Wisdom & Mills 1997). The potential consequences to expected population growth (λ) for different potential management strategies are derived from simulations of mean (and variances) of vital rates using a LSA. The expected distribution of λ in 1000 simulated matrix projections before vital-rate improvements is shown by the solid line; dashed and dotted lines show how the distribution of expected growth rates change as particular vital rates are improved by increasing their means by specified amounts (and decreasing their variation by 20%). $\bar{\lambda}$ gives the mean of the λ for that distribution. Increasing by 10% the average survival during part of the first year (egg and brood survival) gives the biggest increase in the expected population growth (dotted line). Increasing by 10% the average adult survival gives much less improvement (dotted/dashed line). To get about the same increase in population growth as the 10% increase in first-year survival, average adult survival would need to be increased by 20% (dashed line). Modified from Wisdom et al. (2000). Reproduced with permission of the ESA.

simulation-based LSA R^2 can be compared with analytical life-table-response experiment approaches, in that both account for infinitesimal effects (e.g. elasticity) as well as the range in variation of different rates (Wisdom et al. 2000). However, LSA is more flexible than life-table-response experiments because any sort of change can be simulated, and a variety of output metrics are possible.

Case studies

To end the chapter, I will consider four case studies that used the application of matrix projections and sensitivity analysis to inform management, often in nonintuitive ways.

Case study 1: what are the best management actions to recover an endangered species?

Red-cockaded woodpeckers are an endangered species endemic to mature pine forests of the southeastern USA. They are cooperative breeders, with males staying on natal territories as nonbreeding helpers to the breeding pair for up to 11 years before inheriting natal territories or dispersing. How should managers decide which management strategies are most likely to increase the population growth of this endangered species? Detailed field studies provided critical insights into vital rates, behavior, and potential effects of management actions (Walters 1991), which could then be extended with population models exploring how population growth and persistence could be most efficiently increased through management.

Selina Heppell and colleagues (1994) used an innovative matrix-modeling approach based on male red-cockaded woodpeckers and using behavioral transitions associated with helping in addition to the usual size or age transitions (Fig. 7.8a). For example, fecundity in the top row was defined as the number of fledglings produced by individuals that survived the year and were helpers or breeders in that time step. Four management techniques with specific predicted effects on one or more vital rates were evaluated using the manual-perturbation approach coupled with elasticity analysis. Each of these actions targeted specific vital rates, thereby affecting one or more elements $a_{i,j}$ of the matrix in Fig. 7.8(a). The management options were as follows.

1. Remove invaders: remove cavity invaders such as flying squirrels and other woodpecker species that inhabit red-cockaded woodpecker nest cavities, increasing woodpecker fecundity (all elements of top row).
2. Female translocation: capture and relocate female red-cockaded woodpecker fledglings to solitary male territories, causing more solitary males to become breeders (increase $a_{6,4}$ and $a_{1,4}$).
3. Cavities in occupied territories: drill cavities in existing territories, increasing the fecundity of breeders (increasing all of the top row) and the probability that fledglings become helpers ($a_{2,1}$) while decreasing the chance that fledglings become breeders ($a_{5,1}$).
4. Cavities in unoccupied territories: increase new territories by drilling artificial cavities in unused yet suitable habitat and by reducing hardwood understory. This action should increase both fledgling-to-breeder and helper-to-breeder transitions (top row, and $a_{5,1}$ and $a_{6,2}$) while decreasing fledgling mortality (all of first column).

What would be the predicted relative effect of these management actions? Creating new territories through cavity construction in unoccupied territories (management option 4) had the biggest benefit (Fig. 7.8b) through its effects on two vital rates with relatively high elasticity (fledgling-to-breeder and helper-to-breeder transitions). Removing cavity invaders and placing more cavities in unoccupied territories were also potentially reasonable approaches, whereas female translocation (option 2) seems a waste of money. Importantly, Fig. 7.8 also underscores a recurring theme: the best strategy ultimately depends on how much rates could be changed. For example, a 25% change by removing invaders (option 1) would increase red-cockaded woodpeckers more than a smaller (10%) change via the best strategy of installing cavities in unoccupied territories.

(a)

Transition	From fledglings	From helpers	From floaters	From solitary males	From 1-year-old breeders	From ≥2-year-old breeders
Fledglings produced	0.080	0.266	0.324	0.275	0.486	0.522
To helpers	0.294	0.494	0.000	0.000	0.000	0.000
To floaters	0.031	0.000	0.000	0.000	0.000	0.000
To solitary males	0.043	0.020	0.172	0.216	0.000	0.000
To 1-year-old breeders	0.074	0.000	0.000	0.000	0.000	0.000
To ≥2-year-old breeders	0.000	0.257	0.483	0.410	0.725	0.800

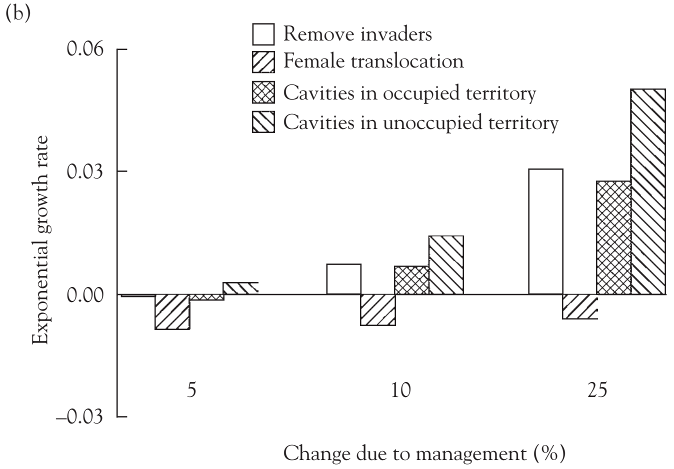

Fig. 7.8 Male-based population-projection modeling to inform management of the endangered red-cockaded woodpecker (from Heppell et al. 1994; reproduced by permission of The Wildlife Society). (a) The stage-based matrix model; (b) expected growth rates expected following implementation of the four management alternatives, each of which was expected to influence different vital rates.

A critical part of red-cockaded woodpecker life history not incorporated into this model is the spatial structure among multiple groups. Because helper males do not disperse far to fill a breeding vacancy, the new territories established with cavities need to be close to currently occupied territories. Although matrix models can be built to incorporate multiple populations with specified movement among them, individual-based models provide an alternative framework to matrix models for population projections. Using an individual-based model that was also spatially explicit, Walters et al. (2002) extended the findings of Heppell et al. (1994) to conclude that new artificial cavity sites need to be aggregated, or clumped near current territories, emphasizing not only density but also spatial distribution of the managed cavities; even quite small local populations could be supported if the territory groups were aggregated. Importantly, these recommendations about cavity establishment – born of a union of excellent field work coupled with thoughtful population modeling – have been incorporated into the new federal recovery plan for red-cockaded woodpeckers (US Fish and Wildlife Service 2003).

Case study 2: what are the most efficient management actions to reduce a pest population?

Brown-headed cowbirds are a nest parasite native to the short-grass Great Plains of North America. Although scattered populations may have been present historically throughout much of North America (Morrison & Hahn 2002), their numbers and distribution increased with landscape fragmentation associated with European settlement and agriculture during the 19th and 20th centuries. Because cowbirds exist at high densities in many agricultural areas, and each female can lay up to 40 eggs per season in the nests of other species, cowbirds can reduce nest success of their passerine hosts. To reduce the effects of cowbirds on native and threatened species, land managers have implemented control efforts since at least the early 1970s. For example, trapping efforts in Texas have removed 3000–5000 female cowbirds per year, and in Michigan control programs to protect Kirtland's warblers have removed 3000 or more cowbirds and eggs each year (Kelly & DeCapita 1982). Given limited funds, is the most efficient way to decrease cowbird population growth to remove eggs, to remove adults on the breeding or wintering range, or some other action?

Citta and Mills (1999) used both analytical sensitivity analysis and LSA to examine the consequences of cowbird control efforts. The LSA scatterplots of the variation in λ explained by each vital rate in 1000 simulated cowbird matrices indicate that egg survival alone explains a preponderance (61%) of the variation in λ (Fig. 7.9a). By contrast, fecundity and survival of other stages all explain less than 15% of variation in λ (Fig. 7.9b–f). Why? It turns out that the proportional infinitesimal effect of each rate (i.e. analytical elasticity) is equal for egg, nestling, and yearling survival, but egg survival probably varies a lot more (see the range on the *x* axis in Fig. 7.9) and so has a greater opportunity to affect λ. Thus LSA captured the fact that both elasticity – the infinitesimal effect – and the variation in a rate determine the merit of altering certain vital rates.

So, the next question is how easy it would be to change egg survival, which is normally highly variable. Killing certain stages (adults or eggs) may be more or less palatable to the public, and more or less feasible under field conditions, both of which affect how much a rate can be changed. At SSD, 92% of the cowbirds would be eggs, so that in a population of 5000 cowbirds you would have to destroy more than 400 eggs to change survival enough to cause λ to be less than 1.0; to remove that many eggs would involve intense effort, making it not only expensive but also prone to disrupting the host species that are innocently caring for the cowbird's eggs (Citta & Mills 1999).

The conclusion of the modeling was that management-induced changes in neither fecundity nor egg survival alone would easily affect population growth. Likewise, adult survival on the breeding grounds would have to be reduced by a lot to cause λ to decline, an option limited by the compensation that occurs via replacement by floaters and immigrants; reducing survival on wintering grounds is logistically daunting. Thus, although local cowbird reductions can successfully protect sensitive host species on a local scale (Rothstein & Cook 2000), the sensitivity analysis clarified that easy fixes in the form of removals of one stage would not reduce long-term population growth of the parasitic pest. Instead, multiple vital rates would have to be hammered simultaneously, probably by managing land use across a landscape.

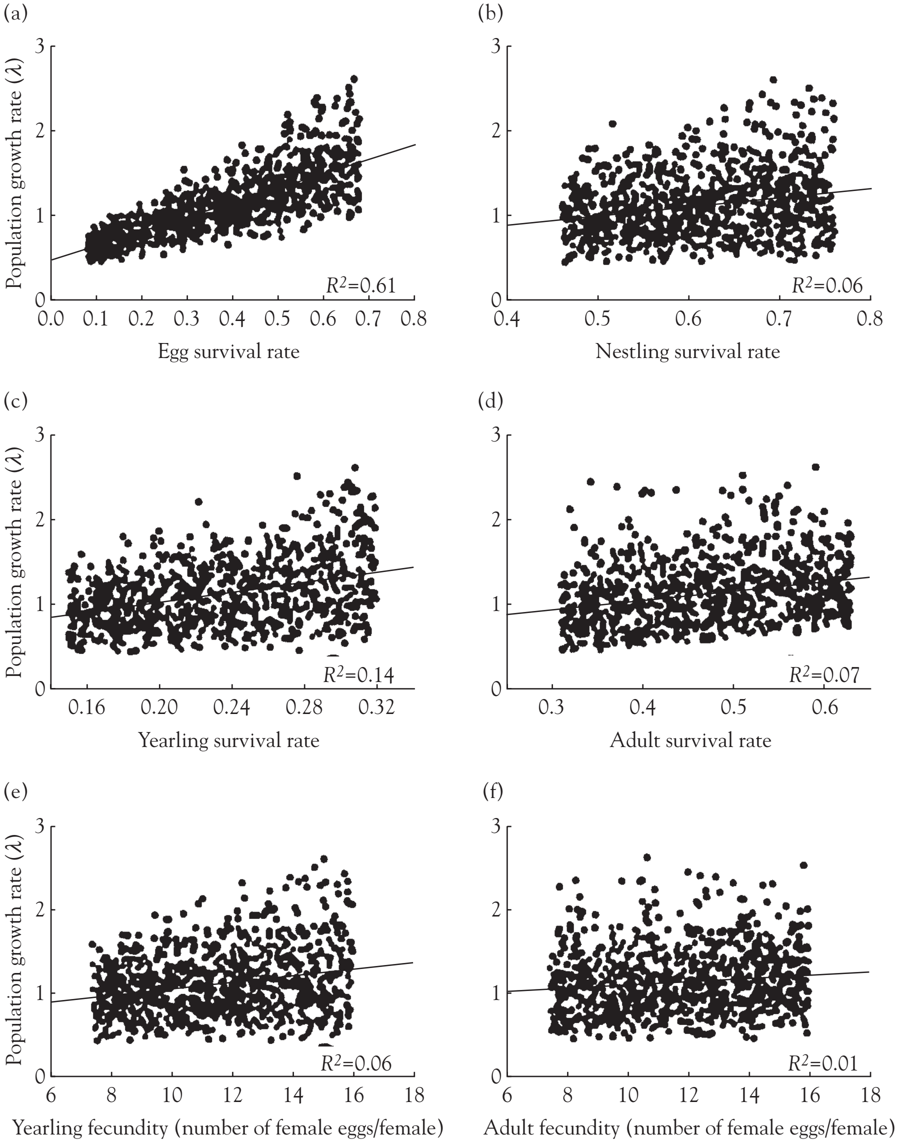

Fig. 7.9 An LSA-based approach to evaluating the relative importance of different vital rates to population growth in brown-headed cowbirds. The R^2 value describes the proportion of variation in λ explained by variation in a vital rate, based on 1000 simulated matrices where vital rates were chosen from the range of variation determined from published studies. Notice that egg survival alone accounts for 61% of the variation in λ. From Citta & Mills (1999)

Case study 3: how should a harvested species be managed?

Migratory waterfowl have been intensively studied and managed, to both protect populations and provide compatible hunting opportunities. In the USA about $50 million in migratory bird conservation funds (primarily funded by duck stamps bought by hunters) are dispersed each year to protect and enhance wetlands and grasslands for waterfowl habitat. Traditionally, less than 40% of these funds has been apportioned to breeding areas. An ongoing debate has centered on how much effort (and money) should be dedicated to protection and enhancement of habitats on breeding areas (especially wetlands and nesting habitat) compared with non-breeding areas (especially wetlands for migratory and wintering waterfowl).

Hoekman et al. (2002) used LSA to assess the effects of management and environmental variation on population growth of the North American mid-continent mallard population, considering both the infinitesimal effect of each vital rate, and the observed variation in each. The LSA indicated that vital rates on breeding grounds (hen survival during the breeding season, clutch size and nest success, and survival of ducklings) collectively explained about 84% of the variation in λ, compared to only 9% explained by nonbreeding survival on migration and wintering areas[13] (Fig. 7.10).

The finding that the contribution to duck population growth of nonbreeding survival is dwarfed by vital rates on breeding grounds has profoundly influenced waterfowl management. An expert panel assembled in 2004 by the US Fish and Wildlife Service came to a striking science-based conclusion based largely on the sensitivity analysis: given that variation in vital rates on breeding grounds explains the vast majority of the variation in λ for mid-continent mallards, and given the general absence of strong differences in the ability to change vital rates on breeding compared with nonbreeding areas through habitat management, the panel recommended that approximately 90% of the waterfowl conservation funds should go to breeding areas (Cox et al. 2004). This suggestion has been elevated to the top levels of the US Fish and Wildlife Service, and although politics will certainly play a role, it appears likely that proportionately more management funding will shift to the breeding grounds. Simultaneously, current adaptive harvest management for waterfowl (see Chapter 14) is recognizing the need to incorporate breeding-area processes to optimize harvest management. Thus, a matrix population model has distilled a nonintuitive insight (that breeding-ground dynamics drive population growth) that is changing the trajectory of waterfowl funding and management. These results have also been useful in reassessing research priorities, with increased funding directed toward sources of variation in nest and duckling survival.

Case study 4: what research is needed to understand global amphibian declines?

Beginning around 1990, researchers from around the world sounded an alarm that amphibian numbers seemed to be declining. The call to action came from monitoring studies, and for the last decade or so the question has been how the declines would best be reversed. Work on a variety of species has shown how various vital rates might be affected by ultraviolet radiation, pH, disease, habitat destruction, or other factors. But there has been a missing link between the data showing declines and the data

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[13] The final 7% can be thought of as statistical noise, accounted for by interactions among rates and the nonlinear response of λ to the changes in vital rates.

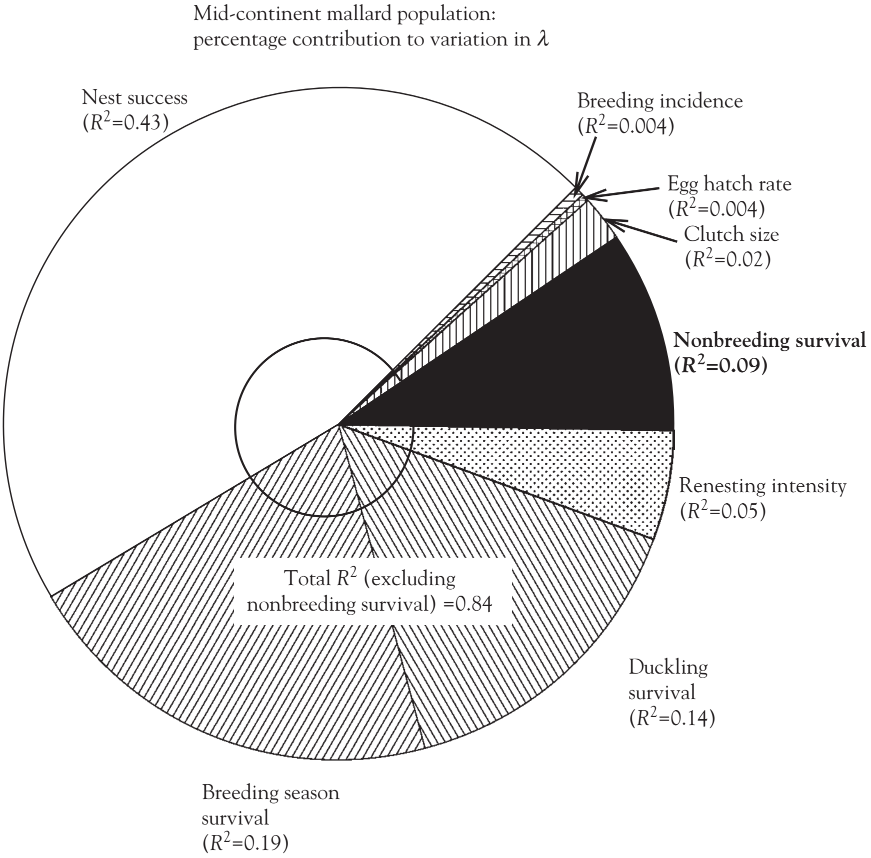

Fig. 7.10 Results of an LSA analysis for female mid-continent mallards in North America (Hoekman et al. 2002). Each pie slice shows the proportion of variance in population growth rate explained by that vital rate in 1000 simulations of vital rates drawn from field studies. In other words, the plot shows the R^2 from regression plots of vital rates against population growth determined as in the cowbird example (Fig. 7.9). Approximately 84% of the variation in population growth rate is expected to arise from breeding-ground vital rates. The 7% not accounted for in the pie can be thought of as statistical noise, accounted for by interactions among the rates and the nonlinear responses of population growth to the changes in vital rates.

showing that vital rates have changed by certain amounts: would those changes in vital rates be likely to cause the observed declines?

Biek et al. (2002) conducted sensitivity analysis for three potentially declining amphibian species for which there were reasonable vital-rate estimates and purported mechanisms driving reduced vital rates: western toads, red-legged frogs, and common frogs (the latter two species formed the basis for the matrix examples in this chapter). In all three species, post-metamorph survival (juvenile or adult) had the highest elasticity, indicating that λ was most likely to be decreased by a given reduction in these rates compared with others (such as embryonic or larval survival) that have been the target of most experimental studies. Manual perturbation and LSA enriched the conclusions by reinforcing (as in other case studies) that if rates with low elasticities vary a lot, then they can affect λ even more than rates with higher elasticities.

Summary

Understanding the effects of age or stage structure on population processes is critical for wildlife population ecologists, both because different stages are important to management decision-making (e.g. bull elk compared with fawns, or turtle eggs compared with ocean-going juveniles) and because structure affects population growth. Matrix population models are certainly not the only way to account for population structure, but they are popular due to their relative simplicity and straightforward links to vital rates measured in the field.

The fact that different stages are not equal in their influence on population growth means that a saavy population ecologist will quantify the reproductive values of each stage to help inform translocations, harvest strategies, or control of pest species. If vital rates remain relatively constant over time, a population will achieve a SSD and a population growth rate characteristic of those vital rates.

Because both reproductive values and proportions in the population will differ between stages, survival and reproduction in different stages do not have the same effects on population growth. In other words, just as different stages are not equal in their effects on population growth, neither are vital rates equal. The broad and important field of sensitivity analysis seeks to quantify the relative importance of different vital rates and the expected efficacy of different management actions on population growth or persistence. Analytical sensitivity and elasticity show how much an infinitesimal change in each vital rate might affect population growth. As useful as this insight is, remember that the amount that a rate can change in nature or under management will also affect how important a vital rate is to population growth.

The two sensitivity analysis methods that do the best job of specifically and intuitively incorporating a specified range of variation in vital rates include manual perturbations and LSA. Manual perturbations of vital rates can contrast specific predictions from management actions that are expected to have specific effect, an approach that identified useful steps for managers to take in the recovery of red-cockaded woodpeckers. LSA can simulate many possible matrices from user-specified means and variances. Its output can be variable, including assessment of the stability of elasticity rankings across variation in vital rates as well as direct insight into how changes in certain rates are expected to affect population growth. Management of pest species (e.g. cowbirds), harvested species (e.g. mallards), and other species of concern (e.g. declining amphibians) would be more efficiently directed using LSA to evaluate the effects of management scenarios on expected population growth rate.

I will end with an apt metaphor borrowed from Ron Reynolds of the US Fish and Wildlife Service. A good general always goes into battle with a thoughtful focus on achieving the most with the resources at hand; troops are not scattered randomly across the battlefield or positioned according to political whims. Likewise, a good wildlife manager should use the insights from population-projection models and sensitivity analysis to see how proposed actions could ripple through to affect population growth in ways that are not obvious, revealing which actions will be a waste of time and money and which would be cost-effective. Population-projection models frame the biological context to help win the management battle.

Further reading

Caswell, H. (1989/2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 1st and 2nd edns. Sinauer Associates, Sunderland, MA. The single most important reference for the mathematics of matrix models.

Noon, B.R. and Sauer, J.R. (1992) Population models for passerine birds: structure, parameterization, and analysis. In: *Wildlife 2001: Populations* (eds. D.C. McCullough and R.H. Barrett), pp. 441–64. Elsevier Applied Science, London. Although specifically focused on birds, this is one of the most readable and practical discussions of building and analyzing matrix populations.