# CHAPTER SIX

**DEMOGRAPHIC PVAs: USING DEMOGRAPHIC DATA TO BUILD STOCHASTIC PROJECTION MATRIX MODELS**

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INTRODUCTION

The methods we have discussed in previous chapters assume that all individuals are identical, so that the models only need to consider the total number of individuals. But for many organisms, particularly the long-lived ones that are often of special conservation concern, individuals differ in important ways that affect their current and future contributions to population growth. For example, larger individuals often have a greater chance of surviving and a higher reproductive rate than smaller individuals. As a result, two populations that differ in the proportion of larger vs. smaller individuals may have very different viabilities, even if they are of the same total size and experience the same sequence of environmental conditions. Populations in which individuals differ in their contributions to population growth are known as “structured” populations. The principal tool for assessing the viability of structured populations is the population projection matrix, which divides the population into discrete classes and tracks the contribution of individuals in each class at one census to all classes in the following census. Different variables describing the “state” of an individual, such as size, age or stage (e.g., seeds, seedlings, and adults for plants, or larvae, juveniles, and adults for fish or invertebrates), are most appropriate for different organisms as ways to classify individuals. As was true of the models for unstructured populations in Chapters 3, 4, and 5, projection matrix models must account not only for mean contributions of one stage to each of the others, but also for variability in these rates if they are to yield accurate assessments of population fate.

Projection matrix models have advantages and disadvantages relative to the simpler count-based models covered in the previous chapters. As we just indicated, one advantage is that structured models provide a more accurate portrayal of populations in which individuals differ in
their contributions to population growth. A second advantage is that structured models help us to make more targeted management decisions. For example, we can use a structured model to ask whether, say, increasing the survival of younger or smaller individuals will have a greater impact on a population’s growth rate than enhancing the reproductive rate of adults. Such questions are simply impossible to answer with an unstructured model. The principal disadvantage of structured models is that they contain more parameters than do simpler models, and hence require both more data and different kinds of data. Typically, the construction of a projection matrix model requires data from a demographic study of marked individuals, an endeavor that is both more time-consuming and more expensive than conducting a simple census of an unmarked population. Nevertheless, the advantages of incorporating population structure into viability assessments and management decisions will sometimes make more extensive data collection efforts worth the price, especially for keystone, indicator, or umbrella species, or for high-profile species for which it is easier to mount the necessary logistical and financial support.

In this and the subsequent three chapters, we discuss in some detail techniques for assessing and improving the viability of structured populations using stochastic projection matrix models. In this chapter we focus on the estimation of each year’s demographic rates, while in Chapters 7 and 8 we discuss how to put together these estimates to include environmental stochasticity into matrix model predictions. As we did for count-based PVAs, we begin with the simplest models for demographic PVAs, which include the effects of inter-individual differences and environmental stochasticity but omit density dependence, demographic stochasticity, temporal environmental autocorrelation, and catastrophes and bonanzas. While one or more of these factors are often included in matrix models, frequently the data needed to quantify them are lacking, and the issues of how to use demographic data to construct a matrix model are involved
enough without at first considering these added complications. However, once we have covered
the basics of how to construct and analyze simpler demographic models, we return to methods
for including these complicating factors at the end of Chapter 7 and in Chapter 8.

OVERVIEW OF PROCEDURES FOR BUILDING PROJECTION MATRICES

Individuals in structured populations may differ in any of three general types of
demographic processes, the so-called “vital rates”. First, the probability of survival may depend
upon an individual’s state. Second, given that an individual survives from one census to the
next, the probability that it will be in a particular state (e.g., a certain size class) will usually
depend upon its state at the beginning of the time period (the exception is age, because all who
survive one year must age one year). Third, an individual’s state may influence the number of
offspring it produces between one census and the next. Throughout this book, we will
consistently refer to these three vital rates as the "survival rate", "state transition rate" (or
"growth rate" for a size-structured population), and "fertility rate", respectively. The elements in
a projection matrix represent different combinations of these vital rates\(^1\). For example, the
probability that a small individual this year will be a medium-sized one next year equals the
probability it survives times the probability it grows. The projection matrix itself allows us to
integrate the contributions of individuals in different states, and the effects of different vital rates,
into an overall measure of population growth and viability. Even though matrix elements
typically combine several vital rates, it is still valuable to estimate the vital rates separately,
because particular threats or management actions may affect one particular vital rate and not

\(^1\) Some sources refer to actual projection matrix entries as vital rates. Here, we use the terms “matrix elements” to
indicate the matrix entries and “vital rates” to represent underlying survival, growth, and reproductive rates.
others, and that rate may contribute to multiple elements in the matrix. Thus understanding the underlying vital rates allows us to account for the full effect of changes in management throughout the matrix, as we describe in detail in Chapter 9.

The construction of a stochastic projection matrix model involves four general procedures:

1. Conduct a detailed demographic study of a representative set of marked individuals, measuring their survival, state, and rate of reproduction each year over several years;
2. Determine the best state variable (e.g. age, size, or stage) upon which to classify individuals, as well as the number and boundaries of classes;
3. Use the demographic data to estimate the vital rates for each class in each year; and
4. Use the class-specific vital rate estimates to build a stochastic projection matrix model.

In the remainder of this chapter, we flesh out each of these general procedures. If you are completely unfamiliar with projection matrices, you may wish to first read the section on Basic matrix structure below, so that you understand up front the goal toward which all the sections that precede it are aiming.

**STEP ONE: CONDUCTING A DEMOGRAPHIC STUDY**

Unlike the models in Chapters 3 through 5, which could be parameterized using data on simple counts of the total number of individuals in a population (or an identifiable subset of the population), to build a projection matrix model one must typically follow the states and fates of a set of known individuals over several years. Although conceptually simple, the collection of
such demographic data represents the greatest investment of effort and expense involved in performing a PVA for a structured population. Hence we devote attention here to the proper design of an informative demographic study.

At the outset of a demographic study, the individuals to be followed are “marked” in a way that allows them to be re-identified at subsequent censuses. Useful methods for “marking” individuals (e.g. numbered tags, colored leg bands, toe-clipping, notches in shells, unique morphological features, DNA markers, or even simple map coordinates) vary depending upon the morphology and vagility of the study organism. Ideally, the mark should be permanent but should not alter any of the organism’s vital rates (for example by making it more or less vulnerable to predation, or by affecting its mating success). At the time of the initial marking, the state of each individual should also be determined, for example by measuring its size (weight, height, girth, number of leaves or stems, etc.) and by determining its age (by tooth wear, annual growth rings, etc.) if possible. While sometimes you can conduct an entire demographic study using multiple measures of state, more commonly the best state variable to use is determined at the outset and used exclusively thereafter (see Step Two: Establishing Classes below).

Care should be taken to ensure that the individuals included in the demographic study are representative of the population as a whole (e.g. by including all individuals encountered along randomly located transects extended through a plant population, or by capturing animals to be marked at a variety of sites within the geographical area encompassing the study population). Some classes of individuals (e.g. the largest adults) may be relatively rare, yet may contribute disproportionately to population growth. Because a random sample of moderate size may include only a few or none of these individuals, a stratified random sampling scheme may be
needed to assure adequate representation of such individuals in the study (for example, one could mark only the largest individuals in every other transect through a plant population, or make special efforts to capture and mark old individuals in an animal population).

The marked individuals should then be censused at regular intervals. This same interval will be used for calculating the vital rates (e.g., survival over a year) and for projecting the future size and structure of the population. Because seasonality is ubiquitous, for most species and places, the best choice is to census, and hence project, over one year intervals. At each census, one simply records which of the marked individuals are still alive, and the current state of survivors (i.e., their age, size, or stage). In general, the census should be conducted at the time of year when individuals are most easily detected (for example, at a time when birds are making territorial displays, or when individuals are forming conspicuous groups prior to breeding or migration). However, the demographer also needs to estimate the number of offspring to which each individual gave birth over the previous inter-census interval. Consequently, it is also a good idea to consider the timing of reproduction while deciding when to conduct the census (see the section on Reproduction under Building the projection matrix from the underlying vital rates below). For many organisms, especially those in markedly seasonal environments, reproduction is concentrated in a small interval of time each year. These organisms have so-called “birth pulse” populations (Caswell 2001). In contrast, organisms with so-called “birth flow” populations reproduce continuously throughout the year. For animals with birth-pulse populations and short-term parental care, it may be best to conduct the census immediately after the birth pulse, while newborns are still associated with their mothers. For many plants, the release of seeds represents the birth pulse. For such populations, it makes sense to conduct the census just before the pulse, while the number of seeds produced by each parent plant can still be
determined. For birth flow populations, frequent checks of potentially reproductive individuals at time points within an inter-census intervals may be necessary to estimate annual per-capita offspring production, or more sophisticated methods (e.g. DNA fingerprinting) may be needed to identify the parents of newborn individuals observed at the next census.

For some organisms, special procedures other than a census of marked individuals may be needed to quantify some aspects of their life histories. Many plants produce seeds that lie dormant in a seed bank for years. To quantify all aspects of the life cycle of such organisms, the demographer may need to supplement a census of above-ground plants with additional experiments. For example, one could add known numbers of seeds to some plots and leave adjacent control plots unmanipulated. By quantifying seedling emergence in the addition plots over subsequent years, and correcting for background germination by subtracting the number of germinants in control plots, one could estimate the fraction of seeds that exhibit 0, 1, or more years of dormancy. Another common problem requiring special measures is the estimation of survival during juvenile dispersal. Dispersal often occurs over a short time period, can result in very low survival, and makes it very difficult to locate surviving individuals. Thus, quantifying survivorship over the dispersal period can require radio-tracking, marking a large number of potential dispersers and searching extensively for them later, or other extraordinary efforts.

Once individuals have been marked and the census protocol established, data collection should be repeated as many times as researcher motivation, time, and financial constraints allow. If at all possible, the aim is to construct a stochastic model; hence enough censuses are needed to estimate the variability in the vital rates (see Building the Projection Matrix below). In order to estimate all vital rates in each year of the study, at each census a fresh group of newborns (or one-year olds, depending on when the census is conducted) must be marked and followed for at
least their first one or two years of life. In addition, because older individuals that were marked initially will eventually die out of the population, it may be necessary to add new marked individuals in other stages to maintain adequate sample sizes.

**STEP TWO: ESTABLISHING CLASSES**

As noted above, a projection matrix model classifies individuals into discrete classes. Yet two state variables, age and size, that are often correlated with an individual’s demographic contributions are continuous. Hence the first step in constructing the model is to use the demographic data to decide which state variable to use as the classifying variable, and if it is continuous, how to break the state variable into a set of discrete classes.

One possible way to begin classifying individuals is by sex, but most projection matrix models keep track of only a single gender, such as all individuals for hermaphroditic species or females in species with separate sexes. Tracking only females is usually justified by the assumption that (in promiscuously mating species) a single male can fertilize several females or that (in monogamous species) male and female numbers are similar. In either case, the number of females would closely correspond to the rate of offspring production. When these assumptions do not hold, structured population models that explicitly include more than one gender are sometimes used (e.g. for monogamous species with unequal sex ratios, or gynodioecious plants), but they require additional demographic information (such as how reproduction depends on the sex ratio, or the rates of seed production by females and hermaphrodites). We will not discuss two-sex models further here, but for more details, consult Chapter 17 in Caswell 2001.
Usually, we must decide whether to classify individuals by age, size, or stage. One important basis for making this decision is simple practicality. For many species, there is no way to determine non-destructively the age of individuals, precluding age as the classifying variable, whereas size can often be quickly measured in the field. Obvious morphological or life history stages (e.g. larval stages, dormant seeds, “juveniles”, etc.) that are easily recognized in the field are likely to be used when collecting demographic data, and should usually be retained in classifying individuals in the model. It is important to remember that it is possible to use combinations of classifying variables, such as stage and size (e.g. a dormant seed stage plus different sizes of above-ground plants) or age and stage (e.g. 1-, 2-, and 3-year olds plus all older individuals combined into an adult stage). The only requirement is that an individual can only be a member of one class at one time.

Basic features of an organism’s biology also help to determine how best to classify individuals. For example, for indeterminate growers (in which equal-aged individuals may differ dramatically in size, but size strongly determines rates of survival, growth, and fertility), size is almost always a better classifying variable than age. For determinate growers, it is often convenient to combine all full-sized individuals into a terminal “adult” stage, provided individuals in this stage do not show substantial changes in survival or reproduction with age (e.g., due to senescence), in which case it makes sense to break up the “adult” stage into several classes.

Apart from practicalities and biological rules-of-thumb, there are several other features to consider when choosing a state variable and deciding how to break it into discrete classes. An ideal state variable will be highly correlated with all vital rates for a population, allowing accurate prediction of an individual’s reproductive rate, survival and growth. A major problem
with some measures of size is that they do not accurately predict vital rates. For example, the future survival and growth rates of some plants with belowground storage organs may be only marginally predicted by, say, the current height of the stem, because aboveground height is not well correlated with belowground stores of carbohydrate. A second desirable feature in a state variable is accuracy of measurement. If repeatability of measurements is low, there will be little accuracy in estimates of growth, shrinkage, or stasis. Some measures of size, such as total leaf area, that would otherwise be excellent state variables, may be so difficult to measure accurately (at least with the amount of time that can be invested in measuring each plant when following hundreds or more individuals for a demographic study) that they are poor choices for a state variable. The best state variable is one that achieves a balance between accuracy and practicality.

When insufficient biological information is available to decide on a suitable state variable prior to the onset of a demographic study, graphical and statistical analysis of the study results can also help to identify state variables that have the best power to predict differences in vital rates among individuals. These same tools yield estimates of the vital rates that are used to construct the projection matrix (see Step Three: Estimating Vital Rates). The appropriate statistical tool to use depends upon whether the vital rate is a binary property of individuals (for example, individuals either survive or they do not) or a nearly continuous variable (for example, offspring number for fecund species may vary in an effectively continuous manner among individuals), and whether the prospective classifying variable is continuous (e.g. age or size) or discrete (stage). Table 6.1 lists appropriate statistical tools for various combinations of vital rates and classifying variables.
We now provide examples of three of the analyses in Table 6.1, using data from endangered populations.

**Example 1: Logistic regression of survival vs. size**

To determine whether survival is associated with a continuous classifying variable such as size or age, logistic regression is the appropriate analytical method to use. An example of such an analysis is provided by the mountain golden heather (*Hudsonia montana*), a federally-listed threatened plant found only in western North Carolina, USA. Mountain golden heather is threatened by increased competition with other plants caused by suppression of natural wildfires. Frost (1990) undertook a demographic study of tagged plants between 1985 and 1989. In an annual census conducted at the end of each summer, he determined which individuals were still alive, and their size (the plant is a ground-hugging species, and Frost measured size as the two-dimensional area of each individual). In this and the following three chapters, we will draw on Frost’s study extensively to illustrate how to conduct a PVA for a structured population.

To see if annual survival of mountain golden heather plants is related to size, we first assign to each individual that was alive at census \(i\) a binary survival variable (“1” if it lived to census \(i+1\) and “0” if it died). We then perform a logistic regression of the survival variable against size at census \(i\) (for example, using PROC LOGISTIC in SAS\(^2\)). Logistic regressions for

\(^2\) If you are using SAS and are coding death as “0” and survival as “1”, you must use the “descending” command to model the probability of survival, as the SAS default is to model the proportion of zeros. For example, if the variable “alive” contains the binary survival values, and “area” contains measures of plant size, the following SAS commands will fit a simple logistic regression model to the data:

```sas
proc logistic descending;
  model alive=area;
run;
```
survival vs. size are shown in Figure 6.1. Despite relatively small sample sizes, there was a significant or marginally significant increase in the probability of survival with plant size in three of four years (Table 6.2). Therefore, there is statistical justification for classifying individuals by size in the projection matrix.

Example 2: Log-linear model of survival vs. stage

When the potential classifying variable is discrete (i.e., stages), statistical association between survival and the classifying variable should be assessed using log-linear models (G tests; Bishop et al. 1975). Walters and colleagues (Walters et al. 1988, Walters 1990) conducted a long-term study of the federally-endangered red-cockaded woodpecker (*Picoides borealis*) in North Carolina. The red-cockaded woodpecker is a cooperative breeder, and Walters and colleagues classified male birds into stages according to their breeding status (fledglings, helpers-at-the-nest, floaters, solitary males (territorial birds without mates), and breeding males). The number of marked birds in each stage that survived or died over one year intervals in the period 1981-1986 are shown in Table 6.3 (data from Table 3.2 in Walters, 1990). The results of a G-test using these data ($G=182.86$ with 4 degrees of freedom, $p<0.001$) confirm a strong influence of stage on survival$^3$. On the basis of these and additional data, Heppell et al. (1994)

$^3$ In SAS, this analysis can be performed by creating a data set with the variables "stage" (i.e., type of male), "fate" (1 if alive and 0 if dead), and "count" (the number of males of each type experiencing each fate, from Table 6.3), and using the command:

```sas
proc freq;
  weight count;
  tables stage*fate/chisq;
run;
```

The output labeled "Likelihood ratio chi square" gives the desired result.
developed a projection matrix model for red-cockaded woodpeckers that followed the number of males rather than females, as is more typically done. Two reasons for this choice are that populations appear to be limited by the availability of suitable territories (and male numbers more closely follow territory availability than do female numbers) and that only males help at the nest (and helpers do increase the number of young fledged per nest; Walters 1990).

Example 3: Polynomial regression of seed production vs. size

Unlike survival which, at the level of the individual organism, either occurs or does not, reproduction often takes on a more continuous range of possible values\(^4\). Exceptions are common. For example, large mammals may produce either zero or one offspring in a given year; these cases can be analyzed by logistic regression or \(G\)-tests (Table 6.1), following the procedures used in Examples 1 and 2. Assessing relationships between more continuously varying reproductive output and continuous classifying variables such as size or age typically relies upon some form of regression analysis (linear, polynomial, or non-linear regression). For example, the number of seeds produced in 1987 and 1988 by mountain golden heather plants of different sizes in Frost’s (1990) study is shown in Figure 6.2. (Mountain golden heather produces all of its fruits at the end of the growing season, so it is possible to quantify total annual seed production by counting fruits only once at summer’s end, and then multiplying fruit number by the average number of viable seeds per fruit.) Because seed production is not necessarily a

\(^4\) Of course, actual offspring production per parent is always a discrete (i.e., integer) number. However, when the number of offspring is large and approximately normally distributed, little error is introduced by using familiar statistical analyses such as linear or polynomial regression that assume the dependent variable is continuous. An alternative that makes sense when analyzing offspring numbers that are more modest is to use a generalized linear model (also known as analysis of deviance) that assumes the response variable is Poisson-distributed. This analysis is not available in all statistical packages, but can be performed, for example, using the GENMOD procedure in SAS.
linear function of plant size, stepwise regressions of seed number against plant area, the square of area, and the cube of area were performed for the two years separately\(^5\). As plants with an area close to zero do not reproduce, and to prevent the regression equation from predicting negative seed numbers at small plant sizes, the regressions were forced to have a y-intercept of zero. The first-order terms are significant in the regression models chosen by the stepwise procedure for both years, indicating that there is a statistically significant (and positive) relationship between plant area and seed production. The squared and cubic terms in the regression were also significant in 1987, indicating that the relationship between seed production and size was non-linear in that year\(^6\) (Figure 6.2).

**Choosing among state variables**

When two or more potential classifying variables are statistically related to the vital rates, there are several methods to decide which of them to use. For example, a continuous measure of reproduction (e.g. seed production) might be significantly correlated with both age and size. If so, one could perform a stepwise regression, adding size to a regression model with age only, and age to a regression model with size only, to see which feature is a better predictor (for example, if adding age to a size-only regression does not improve \(r^2\) significantly, but adding

---

\(^5\) Specifically, a data set with the variables "year", "seeds", "area", "area2", and "area3" (the last two representing the square and cube of the area for each plant) was analyzed with the following SAS command:

```
proc reg;
   by year;
   model seeds=area area2 area3 / noint selection=stepwise;
run;
```

\(^6\) If we remove the largest plant in 1987, which could be having an undue influence on the results, the stepwise regression identifies the best model as \(y = 0.4828x + 1.38 \times 10^{-5}x^3\), which is still non-linear.

size to an age-only regression does, size is the better predictor). One can also test whether age or size better predicts a binary vital rate (e.g. survival) using log-linear models (for details, see Section 3.3 in Caswell 2001), although such analyses require that continuous state variables (age and size) be discretized first. Sometimes, age may continue to contribute explanatory power to a vital rate even after accounting for size, and vice versa. In such cases, matrix models that classify individuals by both size and age could be used (Law 1983). While the initial classification of such a model is more complicated, subsequent analysis is the same as for a single classifying variable. In Chapter 11, we will discuss multiple classifications of this kind that involve different habitats or populations, but we don’t pursue them further here.

If you are trying to choose between two or more different state variables (e.g. age vs. size, or several different ways of measuring size), then you should assess the ability of each state variable to predict both survival and fertility\(^7\). Most of the time the same state variable will prove the best predictor for both vital rates (or at least the best for one rate and as good as the alternatives for the other). Sometimes this will not be the case. If so, most researchers have picked the state variable that is the most convenient to use and seems to do a good (or at least adequate) job of predicting the two vital rates. An alternative (and less arbitrary) approach is to use Akaike Information Criteria to more formally determine which state variable is the best predictor over all vital rates. We introduced the use of \(AIC_c\) in Chapter 4, where we used it to

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\(^7\) Here we have deliberately omitted the third type of vital rate, the rate of transition among states (e.g., growth), for two reasons. First, state transitions are idiosyncratic to the state variable used (e.g. age can only increase, stages typically follow one another in a fixed sequence, and size can increase, remain the same, or decrease - it even might simultaneously increase by one measure (e.g. aboveground biomass) and decrease by another (e.g. number of stems)). In a sense, we are tracking these idiosyncratic changes in state only because state influences survival and fertility which (unlike state transitions) actually change directly the number of individuals in the population, the quantity we seek to predict. So we want to choose the state variable that best predicts survival and fertility, and then account for transitions in the chosen state variable in whatever way is appropriate. Second, we can only use \(AIC_c\) to compare models fit to the same data; that is, we cannot compare the ability of one model to predict changes in the number of stems to the ability of another model to predict changes in aboveground biomass.
distinguish between different density-dependent models of population growth (see Equation 4.8).

Now we wish to use this same method to combine the results of two different analyses for each state variable into a single measure of model fit. To make this comparison, we use the facts that the maximum log likelihood of the combined survival/fertility model is simply the sum of the maximum log likelihoods from the two analyses, and similarly that the total number of parameters is the sum over both analyses. Therefore, the $AIC_c$ for each state variable is

$$AIC_c = -2\left(\log L_{\text{max},s} + \log L_{\text{max},f}\right) + \frac{2p_s n_s}{n_s - p_s - 1} + \frac{2p_f n_f}{n_f - p_f - 1}$$  \hspace{1cm} (6.1)$$

where $\log L_{\text{max},s}$ is the maximum log likelihood of the best (i.e. smallest $AIC_c$) model from the analysis of survival, $\log L_{\text{max},f}$ is the maximum log likelihood of the best fertility model, $p_s$ and $p_f$ are the numbers of parameters in the best-fit models, and $n_s$ and $n_f$ are the numbers of data points in each analysis. For example, let's assume we have determined that a logistic regression best predicts survival vs. age, and a linear regression best predicts fertility vs. age. The former regression has two parameters (see Estimating Vital Rates below) and the latter three (slope, intercept, and residual variance). For a least-squares regression of fertility (and for analyses of variance using continuous fertility data), $\log L_{\text{max},f}$ can be calculated from the residual sum of squares and the sample size (see equation 4.7 and the explanation that accompanies it), while for a logistic regression of survival (and log-linear models of survival for discrete stages), the estimated maximum log likelihood $\log L_{\text{max},s}$ is a direct output on all standard statistical packages. We would thus have all the elements we would need to compute $AIC_c$ for an age-based analysis, using Equation 6.1. We could then compare the $AIC_c$ value for this age-based model to the $AIC_c$ value for a size-based model in which we used, say, a quadratic regression for fertility (four parameters) and a hazard function (three parameters; see footnote 1 to Table 6.1)
for survival. The state variable with the lowest $AIC_c$ provides the best predictive power over both vital rates. We could also use Akaike weights to decide how much better the fit of one state variable is than that of another (see Equation 4.9) – a variable that provides only slightly inferior predictive power can be better to use if it is cheaper and faster to measure in the field. One requirement of this analysis, though, is that we must fit all models to the same set of data (that is, we cannot compare the $AIC_c$ values of an age-based model fit to survival and fertility data for one set of individuals and a size-based model fit to data from a different set of individuals).

**Setting class boundaries**

Once we have determined an appropriate classifying variable, we must use it to divide the population into discrete classes. For an age-structured model, the widths of all classes must equal the inter-census (and therefore projection) interval (e.g., one year age classes for an annual census period, or 5-year age classes if we plan to project the population over 5-year increments). For a stage-based model, classes are synonymous with stages, so that in effect the choice of stages determines class boundaries. Defining classes is more complicated for a size-based matrix, because the width and number of classes are flexible. Thus we must decide both how many classes to use, and the exact boundaries between classes. Two considerations are important in deciding the number of classes. On the one hand, we want the number of classes to be large enough to reflect real differences in vital rates as a function of the classifying variable. If we use only a few, broad classes, we will be lumping individuals of very different sizes, and hence different vital rates, into a single class within which all individuals are assumed to be identical. Another reason to favor a larger number of narrower classes is that it more accurately
reflects real time delays caused by the processes of growth and maturation in structured populations, delays that can strongly affect some results of a viability analysis. For example, assume that a certain organism takes at least 10 years to grow to a size at which it can begin to reproduce. If we divide the population into 10 pre-reproductive size classes, and we only allow individuals to advance by at most one size class per year, then we can assure in the model that no individual can reproduce until it has survived for at least 10 time intervals. If instead we use only 2 pre-reproductive size classes, then our model will allow some individuals (albeit with small probability) to begin reproducing after only 2 time intervals.

Size-dependent changes in vital rates and time lags thus argue for a large number of classes. On the other hand, if we divide the population into too many classes, some classes will include few or none of the marked individuals in the demographic study that we are using to estimate the vital rates. This can be especially problematic in estimating growth probabilities; with many narrow classes there will be very few individuals ever observed to make any particular transition and hence poor estimates of most growth probabilities. To some extent, this problem is reduced by statistical procedures for estimating some vital rates (i.e. survival and fertility) using the data for individuals in all states simultaneously (see Estimating Vital Rates below). Nevertheless, standard estimation of size transitions (see below) requires that there be some individuals in each class, and more generally, it is prudent to avoid creating size classes about which we have no empirical information.

To balance the opposing pressures to create many classes with few individuals vs. few classes with many individuals, we advocate a practical approach to deciding the number and boundaries of size classes. Begin with a relatively large number of classes, and set the boundaries at sizes that are convenient for biological or management reasons. For example, we
might choose as the boundary between two classes the minimum size for reproduction, the maximum size at which individuals are vulnerable to a particular threat, or the size at which a particular management technique will begin to be effective. One should also examine scatter plots of survival, growth, and reproduction as functions of size to look for sharp discontinuities (if any); these values serve as natural break points between classes. Now check the data set to see that there are at least some marked individuals in each class. If not, reassign the class boundaries or combine adjacent classes until you achieve an adequate sample size in each class with which to estimate size transitions. While more formal procedures to make these decisions exist (Vandermeer 1978, Moloney 1986), they do not fully consider how particular choices of class boundaries affect all vital rates, and they are in practice rarely used (see Caswell 2001, p. 169-171, for a description and critique of these formal methods).

**STEP THREE: ESTIMATING VITAL RATES**

Once the number and boundaries of classes have been determined, we can use the demographic data to estimate the three types of class-specific vital rates.

**Survival rates**

The survival rate is simply the expected proportion of individuals in class $i$ at the last census that are still alive at the current census. How to best estimate survival depends on whether the classifying variable is inherently discrete (i.e., stage) or continuous (age or size). For stage-based estimates of survival, one simply sums the number of marked individuals in a
given stage at the previous census, determines the number of those individuals that are still alive at the current census regardless of their state, and divides the number of survivors by the initial number of individuals.

One could use this same approach if the underlying state variable used to make the classes is continuous. Specifically, one could use the class boundaries to first divide the marked population at the previous census into size or age classes, and then estimate survival separately for each class. An important limitation of this approach is that estimates of survival for classes into which few marked individuals happen to fall will be based on a small sample size. Small sample size means that our survival estimate will be especially sensitive to chance variation around the true value. For example, assume the true survival probability for a given class is 0.5. If only four individuals in the data set fall into that class, we would not consider it to be unusual if either all or none of those individuals happened to survive over a particular inter-census interval, whereas such outcomes are very unlikely if the sample size is 100. A second problem with small sample size is precision; with only four marked individuals we can only estimate survival to the nearest 25% (i.e., the estimate would be 0, 25, 50, 75, or 100 percent if 0, 1, 2, 3, or 4 individuals survive; this is the same problem – here in a sample of individuals rather than a whole population – that creates demographic stochasticity; see Table 2.2). An example of this problem is for estimates of age-specific survival of Yellowstone grizzly bears. Eberhardt et al. (1986) had data for so few animals in most age groups that the estimated survival rates were usually either 0 or 1. These sample size limitations can seriously constrain our choice of the number and boundaries of classes if we plan to divide the marked population into classes before estimating survival.
To get around this problem, we advocate a two-step procedure for age- or size-based models that effectively uses all of the data to estimate survival for each class, thus reducing sample size limitations. First, use the entire demographic data set to perform a logistic regression of survival against age or size. This is precisely the regression we performed earlier to determine whether survival was associated with age or size (see Step Two: Establish Classes), the only difference being that here we will use it to estimate vital rates rather than as a simple statistical test for association. The second step is to use the fitted regression equation to calculate survival for each class. Because the regression equation is estimated from the entire data set, problems of chance variation and precision are less important. This procedure also yields smooth changes in survival among classes, which in most cases is probably more biologically realistic than the large upward or downward jumps in survival among adjacent classes that can result from small within-class sample sizes. But note that frequently we do want to allow one or more discontinuities, estimating a smooth survival function for most classes but doing a separate, stage-based calculation for others. This is especially true for the youngest age classes (weanling mammals, fledgling birds, seedling plants), which often have much lower survival than do the next oldest classes. In this case, we can estimate survival of the youngest age class as for a stage-based model above, and then perform a logistic regression using the data for older age classes separately to estimate their survival rates.

There are at least three ways to perform the second step in the above procedure. The simplest is to take the midpoint of each size class, substitute it into the best-fit logistic regression equation as the independent variable, and use the resulting value of the dependent variable as the estimated survival for that class. This method assumes that the actual sizes of individuals within a class are tightly clustered around the class midpoint. In reality, the actual sizes might be
broadly distributed within the class, and the distribution might even be skewed toward sizes above or below the midpoint (for example, because on average individuals must survive longer to reach a larger size, there may be more individuals at the smaller end of a given size class than at the larger end). If there is a distribution of sizes within the class, the survival at the class midpoint may not accurately reflect the survival of the average individual in the class, particularly if the logistic regression equation is strongly non-linear across the range of sizes in the class. A second option that better accounts for skewness in the distribution of sizes within a class is to use the median size from a sample of individuals from the population that fall within the class. A third option is to use the actual sizes of individuals in the sample in the regression equation to calculate an expected value of survival for each individual, and then average those values to estimate survival for the entire class. The sample should reflect the distribution of sizes or ages of individuals that are in the class, and might simply be the subset of marked individuals that fall within the class. If there are few such individuals or the sampling was stratified so that this distribution doesn’t reflect the distribution of the population as a whole, we might supplement the detailed demographic data with additional information on the frequency distribution of sizes or ages in the population, data that are easier to obtain than detailed demographic information because they do not require us to mark and follow individuals over time.

To illustrate the estimation of class-specific survival, we return to the data for mountain golden heather. We first chose class boundaries that yield a reasonable number of plants in each of 4 size classes (Table 6.4). The equation for a logistic regression (see Figure 6.1) is:

\[
y = \frac{e^{b_0 + b_1 x}}{1 + e^{b_0 + b_1 x}}
\]

(6.2)
where in this case, $y$ is the predicted survival probability for plants with area $x$. For each year, we substitute the appropriate estimates of the regression coefficients $b_0$ and $b_1$ from Table 6.2 into Equation 6.2, and then calculate the survival probabilities using all three methods discussed in the preceding paragraph (Table 6.4). In this case, the three methods yield broadly similar estimates of survival probabilities, with the maximum difference in survival between methods averaging only 0.015 across years and classes. Such similarity is not guaranteed, however, and we recommend that you use the class medians or the distribution of sizes if you suspect that sizes are strongly skewed within classes or that survival is a highly non-linear function of size. But for the purpose of illustrating methods in this book, we will use the estimates of survival for mountain golden heather based on the simple class midpoint method. Note that regardless of the estimation procedure used, large plants have a high probability of surviving every year, whereas survival of smaller plants is lower and more variable from year to year (Table 6.4).

**State transition rates, or growth rates**

If individuals are classified by size or stage, then in addition to estimating the chance that individuals in each class survive, we must also estimate the probability that a surviving individual undergoes a transition from its original class to each of the other potential classes (for age-structure populations, survival and state transition are one and the same, as all survivors must age). The simplest way to estimate state transition rates is to first place survivors from the marked population into a class transition table (Table 6.5). The columns of the table represent a survivor’s class at the previous census, and the rows represent its class at the current census. Dividing each element in the table by the corresponding column total yields the estimated class
transition probabilities. Note that this procedure also yields an estimate of the probability that a survivor remains in its original class from one census to the next.

This procedure suffers from the same sample size problems that affect the procedure for estimating survival by first dividing the population into size classes, especially for rarely seen transitions such as rapid growth or shrinkage (see above; for example, note the small sample sizes for some size classes in Table 6.5). More sophisticated methods that make use of the entire data set to get around these problems are available, but they are even more complex than similar methods for estimating survival and have hardly been used to date. Details of these procedures are provided by Easterling et al. (2000). Until it is clearer how well these methods can deal with different patterns of growth, stasis, and shrinkage, we suggest sticking with the simpler procedure outlined above, which is unlikely to result in serious errors unless the numbers of observed individuals in some classes are extremely small.

A note on alternative methods for estimating survival rates and class transition rates using capture-recapture data and size vs. age relationships

In the preceding discussion, we have assumed that it is possible to find every marked individual at each census, so that its fate (survival and state) can be determined unambiguously. The ability to locate with certainty all marked individuals is routine in demographic studies of sessile organisms (e.g. plants, fungi, many aquatic invertebrates), and may also be achieved for mobile organisms if they are large, occupy structurally simple habitats, and do not move far between censuses. However, for smaller and more mobile species in complex habitats, we will often fail to observe some proportion of the marked individuals at a given census even if they are
still alive. This same problem introduces observation error into estimates of total population size that are based on capture-recapture studies, and so can complicate the interpretation of census data used in count-based PVAs (see Chapter 5). In the context of demographic PVAs, to accurately estimate both the survival rates and the rates of transition among classes, we must also estimate the probability that a live, marked individual failed to be "resighted" in a given census. Fortunately, maximum likelihood methods have been developed to estimate survival rates and rates of class transition, as well as resighting probabilities, using data from capture-recapture studies. The literature on parameter estimation using capture-recapture data is too extensive for us to review here. Methods for estimating survival are described by Lebreton et al. (1992), and Nichols et al. (1996) describe how to estimate class transition rates. An overview of the use of capture-recapture models in the specific context of PVA in presented by White et al. (2002). Examples of the use of these methods in demographic PVAs are Hitchcock and Gatto-Trevor (1997) and Caswell et al. (1999). Another good source of information is Gary White's website (http://www.cnr.colostate.edu/~gwhite/mark/mark.htm), from which users can obtain the program MARK which implements maximum likelihood parameter estimation using capture-recapture data. As any viability analyst who intends to estimate vital rates for a demographic PVA based on a capture-recapture study will need to become familiar with the use of MARK (or similar programs), we refer readers to the original sources rather than attempt to describe here how the programs work.

Another method to estimate class transition rates from capture-recapture data was used to parameterize the influential demographic PVA for the loggerhead sea turtle (Crouse et al. 1987; also see Chapter 1). Briefly, this method uses data on the average number of years individuals require to grow from one benchmark size to another (i.e., the boundaries of a size class), as well
as the estimated probability of surviving over those years, to calculate the rate of transition from one size class to the next. A plot of size vs. age for recaptured individuals gives the average length of time an individual will reside in a size class, and the fraction of marked individuals in that size class in one year observed alive in subsequent years provides an estimate of the survival rate. One then calculates the probability that a survivor advances to the next size class at the next census in such a way that the projection matrix predicts the same average residence time in a size class as is observed in the actual size vs. age data. For more details on this method, see pages 159-165 in Caswell (2001).

**Fertility rate**

Finally, we must estimate the average number of offspring that individuals in each class produce during the interval from one census to the next. Note that the fertility rate is simply the number of new individuals to which an adult in a given size class has given birth over the interval, *regardless of whether those offspring survive to the next census* (we will account for offspring survival when calculating the actual matrix elements). If properly designed, the demographic study should yield an estimate of total offspring production for each marked individual, as either the sum of offspring observed in repeated checks of marked individuals throughout an inter-census interval (if reproduction is spread out over the interval) or as the number produced during a brief reproductive pulse.

If individuals are classified by stage, the stage-specific rate of fertility is simply the arithmetic mean offspring number for all individuals in a given stage at the previous census\(^8\).

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\(^8\) Hence the demographic study must include enough individuals in each stage to estimate mean offspring number accurately.
For age- or size-classified models, we advocate using all individuals in the data set to estimate reproduction simultaneously for all classes, as we did when estimating survival. For example, we can substitute either the class midpoints, the median, or the distribution of individual sizes or ages within the class into the equation for a regression of offspring number vs. adult size. Again using mountain golden heather as the example, substituting the class midpoints from Table 6.4 into the regression equations for seed number vs. plant size (Figure 6.2) yield the class-specific seed production values in Table 6.6 (as for survival, fertility estimates based on median sizes and the within-class distribution of sizes yielded similar estimates).

Some organisms have multiple modes of reproduction. For example, many plants have both sexually produced seeds and vegetatively produced daughter ramets. Because seeds and daughter ramets may have quite different survival and growth rates, and hence make different contributions to population growth, it may be valuable to explicitly include each type of reproduction in the projection matrix. For such organisms, we can use the procedures we have just outlined to obtain class-specific estimates of reproduction via each mode. For example, matrix models for wild leeks were constructed to incorporate both sexual reproduction and asexual bulb division (Nault and Gagnon 1993, Nantel et al. 1996). (Note that mountain golden heather does not reproduce vegetatively.)

STEP FOUR: BUILDING THE PROJECTION MATRIX

Having conducted a demographic study, divided the population into classes, and estimated class-specific vital rates, we are finally ready to build the projection matrix.
Basic matrix structure

Here is a typical projection matrix:

$$A = \begin{bmatrix}
  a_{11} & a_{12} & a_{13} \\
  a_{21} & a_{22} & a_{23} \\
  a_{31} & a_{32} & a_{33}
\end{bmatrix} \quad (6.3)$$

Both the number of rows and the number of columns in the matrix equal the number of classes into which we have chosen to divide the population. Matrix elements are indexed first by row and then by column. For example, $a_{ij}$ is the element in row $i$ and column $j$ of the matrix $A$. The element $a_{ij}$ indicates the number of individuals in class $i$ at the next census that will be contributed by each individual in class $j$ at the current census. Typically, we index the classes in the order in which they occur in the organism’s life cycle, so that class 1 individuals are the most recently-born members of the population. As a result, $a_{1j}$ is the number of new, live individuals at the next census produced by each individual in class $j$ at the current census. The first row of the projection matrix therefore represents reproduction. Elements along the diagonal of the matrix (e.g. $a_{22}$, $a_{33}$, etc.) represent survival of pre-existing individuals without a change in state; elements below the diagonal represent survival with an “advance” in state; and elements above the diagonal represent survival with “reversion” to a “lower” state (e.g. a smaller size).

Population projection matrices have stereotyped structures depending on whether individuals are classified by age, size, or stage, as the following matrices indicate:
The three matrices each include four classes, but they differ in the distribution of non-zero elements within the matrix. Matrix $A_1$ is a typical age-structured matrix; $F_j$ and $P_j$ represent, respectively, reproduction and the probability of survival of individuals in class $j$. In age-structured matrices, an individual that survives from one year to the next must advance to the next age class; hence the only non-zero elements in the matrix are on the principal subdiagonal (survival plus aging) and in the first row (reproduction). In a size-structured matrix, such as $A_2$, the $F_j$’s again represent reproduction, but $P_{j, j}$, $P_{j+1, j}$, and $P_{j-1, j}$, represent, respectively, the probabilities that an individual in class $j$ will survive without growing, survive and grow to the

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9 The notation $a_{ij}$ in Equation 6.3 refers to any matrix element, even ones that must equal zero (e.g. transitions to younger age classes). In contrast, the $F$ and $P$ notation that follows is used to refer to non-zero elements representing, respectively, the production of new members of the population (i.e., reproduction) and class transitions of existing members.

10 Age-structured matrices are often called Leslie matrices, after the British ecologist P.H. Leslie who pioneered their use (Leslie 1945). Similarly, size- and stage-structured matrices are often called Lefkovitch matrices, after their originator L.P. Lefkovitch (Lefkovitch 1965).
next-largest size class, and survive but revert to the next-smallest size class (because an individual in size class \( j \) can wind up in any of three classes next year (if it survives), the \( P \)'s must have two subscripts). Note that individuals in class 2 can contribute to class 1 at the next census both by reproducing and by shrinking. In matrix \( A_2 \), individuals can advance or revert by at most 1 size class in a year, but matrices that allow larger changes in size are easily constructed. Matrix \( A_3 \) represents an organism with three pre-reproductive stages (classes 1-3) and an adult stage (class 4). Each year, individuals in the pre-reproductive stages can stay in the same stage or advance to the next stage (or die if \( P_{jj} + P_{j+1,j} < 1 \)). Surviving adults can only remain in the adult stage. For some stage-based models, it might be sensible to allow individuals to revert to an "earlier" stage (e.g. reproductive individuals that lose a breeding territory may rejoin a "pre-reproductive" class). As we will see below, it is also possible to construct matrices that combine age-based, size-based, and stage-based classes. Regardless of how the classes are defined, to put specific numbers into the matrix we must express the \( F \)'s and \( P \)'s in terms of the estimated vital rates, as we now describe.

**Building the matrix from the underlying vital rates**

We begin by describing how to use estimated vital rates from a single inter-census interval to build a single projection matrix. We then describe how data from multiple censuses are used to estimated means, variances, and covariances of vital rates and of matrix elements, the key components of a stochastic projection matrix model. We use these components to assess population growth and extinction risk in Chapters 7 and 8, and to explore management options in Chapter 9.
In describing both the construction of a matrix from the underlying vital rates and methods for analyzing matrix models, it is useful to represent the three types of vital rates by the following symbols:

- \( s_j \) is the survival rate for class \( j \)
- \( f_j \) is the fertility rate for class \( j \)
- \( g_{ij} \) is the probability that an individual in class \( j \) at one census makes the transition to class \( i \) at the next census, given that it survives.

To keep clear the distinction between vital rates and matrix elements, we will consistently use the above symbols for the vital rates and either \( F \)'s and \( P \)'s (as in the matrices \( A_1, A_2, \) and \( A_3 \) above) or \( a_{ij} \) for the matrix elements. Moreover, we will consistently refer to the \( F \)'s as "reproduction" (not "fertility", which we reserve for a vital rate\(^{11}\)) and the \( P \)'s as "class transition probabilities".

\[ Class\ transition\ probabilities\ in\ age-structured\ models\]

In an age-structured model, an individual that survives an inter-census interval must be one age class older than it was at the last census. Thus survival is all we need to estimate class transitions for individuals alive at the previous census. We simply put the class-specific survival estimates, \( s_j \), along the principal sub-diagonal of the matrix (i.e. \( a_{j+1,j} = P_{j} = s_j \); see the matrix \( A_1 \) above). Note that all individuals currently in the oldest age class are assumed to die before the next census.

\(^{11}\) The terms "fertility", "fecundity", and "reproduction" have all been used for both matrix elements and vital rates, and human demographers tend to use these terms differently than do ecologists, who cannot seem to agree among themselves what these words mean. Rather than trying to sort out this semantic morass, we will choose one set of definitions and apply them consistently.
In contrast with age-classified populations, survivors in a size- or stage-classified model may or may not undergo a transition to another class. Individuals making a transition can advance in state, but they can also regress. For example, some of the mountain golden heather plants in Frost’s (1990) study became smaller from one year to the next (Table 6.5), perhaps due to dieback or consumption by herbivores. In a size- or stage-structured matrix, the entry \( P_{ij} \) (see the matrix \( A_2 \) above) represents the product of two vital rates: \( s_j \), the probability that an individual in size class \( j \) at the current census survives to the next census, and \( g_{ij} \), the probability that a survivor from class \( j \) makes a transition to class \( i \). Hence to estimate \( P_{ij} \), we simply multiply these two vital rates (i.e. \( a_{ij} = P_{ij} = s_j g_{ij} \)).

**Reproduction**

As with class transitions in a size- or stage-based model, the reproduction terms in the matrix combine two or more underlying vital rates, the fertility rate plus the survival rate of adults and/or offspring, depending on the timing of reproduction relative to the census. The key idea here is that all matrix elements, including those for reproduction, must account for the passage of time from one census to the next, with the accompanying chance that some individuals will die over that time. Therefore, the reproductive elements of the matrix must
include not only fertility (e.g. the number of cubs per interval), but also survival (e.g., the fraction of newborn cubs that survive to the next census). The three scenarios for the timing of the census relative to reproduction (birth pulse with a pre- and post-breeding census and birth flow) necessitate different procedures to calculate the reproduction terms in the matrix, as we now describe.

i. Birth pulse populations with a pre-breeding census:

If we census the population immediately before a birth pulse, the youngest (i.e., class 1) individuals in the population will be those that were produced in the previous birth pulse, and they will be nearly an entire census interval in age (Figure 6.3A). Thus to contribute to class 1 at the next census, an adult in the current census must produce newborns during the birth pulse immediately after the census, and those newborns must survive for an entire inter-census interval. That is, the reproduction term \( F_j \) in a birth pulse population with a pre-breeding census is the number of newborn offspring an individual in class \( j \) produces during the pulse times the survival of newborns for one inter-census interval; i.e., \( a_{1j} = F_j f_j s_0 \), where \( s_0 \) is the one-year survival rate of newborns. In practice, the design of the demographic study frequently does not allow the initial number of newborns and their survival over the first year of life to be estimated separately. That is, if the population is censused only before the birth pulse, the best we can do is to use the number of surviving offspring associated with a female at the next census to estimate her net reproduction (i.e., her total offspring number times their survival) over the previous interval. One disadvantage of such a procedure is that it does not allow us to investigate whether changing offspring production or newborn survival would have a greater effect on population growth (see Chapter 9). If such an investigation is worth doing, we would need to census the population (or at least females in the reproductive classes) both before and
immediately after the birth pulse, or if biological circumstances allow, use a post-breeding census design instead.

**ii. Birth pulse populations with a post-breeding census:**

In contrast with a pre-breeding census, if we census a population immediately after a birth pulse, the youngest individuals we will see will have just been born (Figure 6.3B). The reproduction terms in the matrix now represent the number of such newborns that each adult in the current census will contribute to the next census. To make such a contribution, however, the adult itself must survive for nearly an entire inter-census interval and then reproduce. The reproduction term $F_j$ in a birth pulse population with a post-breeding census is thus the survival of class $j$ adults for one inter-census interval times the number of offspring an individual in class $j$ produces during the pulse; i.e., $a_{ij} = F_j = s_j f_j$.

**iii. Birth pulse populations with an intermediate census:**

In some cases, it may be necessary to census a population at a point in time that lies between successive birth pulses. For example, if females go into hiding to give birth (as is true of bears, whose cubs are born in winter dens), a pre- or post-breeding census might be impractical. If so, offspring would be first observed at the next census. The reproduction element for class $j$ would then be the average of the number of offspring at the next census attributable to each individual in class $j$ at the previous census. Note that the number of offspring would be zero for individuals who died before the birth pulse, who produced no offspring, or whose offspring died before the next census. In principle, one could also parameterize a projection matrix model with a birth pulse occurring at an intermediate point between two censuses if one had the data to estimate both the probability that each adult survives from one
census to the next pulse and the probability that an offspring survives from birth to the following census (see equation 2.42 in Caswell 2001). In practice, such data can only be obtained by actually censusing the population near the time of the birth pulse, in which case it would be simpler to assume a pre- or post-breeding census when constructing the projection matrix.

Another useful approach in some cases is to "pretend" that the birth pulse occurs later than it actually does. For example, for demographic studies of songbird species, a sensible time to conduct the census might be just at the time of fledging, when offspring are still in (or near) the nest but are then large enough to band. Thus even though fledglings were actually born several weeks earlier, and some eggs or chicks may have died before they could fledge, we might treat fledglings as newborns (i.e. class 1) in constructing the matrix. If so, the reproduction terms in the matrix would represent the survival rate of an individual observed at the current census (including the fledglings, if it is possible for them to breed in the following summer) times the number of fledglings that individual can be expected to produce at the next census, given that it survives. That is, we might adapt the procedure for a post-breeding census of a birth-pulse population (see above), even though the time of fledging is not, strictly speaking, the birth pulse.

iv. Birth flow populations:

When reproduction occurs continually over an interval, the simplest approach to calculating the reproduction matrix elements is to pretend that all offspring are born at the midpoint of the inter-census interval. Reproduction for class $j$ individuals is then the product of three things:

(1) The probability that a class $j$ individual survives from one census to the midpoint of the succeeding inter-census interval. If the survival rates are more or less constant over the
course of a year, then six month survival can be approximated as the square root of annual survival, \( \sqrt{s_j} \).

(2) The average number of offspring to which each surviving class \( j \) individual gives birth over an inter-census interval (summed over repeated checks performed throughout the interval), \( f_j \).

(3) The probability that an offspring produced at the midpoint of an interval survives to the next census. If the most recently-born individuals at a census have an annual survival probability of \( s_0 \), the probability that an offspring born at the midpoint of an interval survives to the next census is approximately \( \sqrt{s_0} \).


PUTTING IT ALL TOGETHER: ESTIMATING PROJECTION MATRICES FOR MOUNTAIN GOLDEN HEATHER

We now illustrate the entire procedure of building a projection matrix using the data for mountain golden heather. This example highlights two important points about estimating matrix elements in a world of limited data. First, as noted above, we will often need to rely on information beyond that obtained in the annual census of marked individuals in order to estimate all the matrix entries. Second, data on certain vital rates will often be missing for one or more years; if so, we may have no other option than to use average values for those years.

In Tables 6.4 and 6.5, we divided the plants from Frost’s census into four size classes. For our projection matrix to accurately reflect the plant’s life cycle, we must add two additional classes. First, mountain golden heather has a persistent seed bank (as indicated by the
appearance of seedlings after a fire in locations far from potential seed sources). Seeds in the seed bank would not be observed in the census of above-ground plants but could nevertheless contribute to population persistence, so we need to include them in our matrix. The second class we must add to the matrix is seedlings, which represent seeds that have germinated since the last census and which are smaller than any of the marked plants in Frost’s census. It is important to include the seedling class because it reflects a realistic delay of at least one year between germination and the onset of flowering and because seedlings are unlikely to survive as well as already established plants. Our matrix will thus have six classes: (1) seeds in the seed bank (really more of a stage than a size class); (2) seedlings (really an age class, since by definition seedlings do not remain so if they survive beyond one year after germination); (3) tiny plants (plants older than seedlings but between 0 and 25 cm\(^2\) in area); (4) small plants (25-50 cm\(^2\)); (5) medium plants (50-100 cm\(^2\)); and (6) large plants (greater than 100 cm\(^2\)). We will use these class numbers (1-6) in presenting the construction of the matrix. Note that the widths of the larger size classes exceed those of the smaller classes; we did this to achieve better sample sizes in order to more accurately estimate class transitions for the larger classes. In Frost’s study, plants were censused near the end of the growing season, when all of the fruits produced that season were present on the plants but had not yet released their seeds. Hence we will construct our matrix to reflect a pre-breeding census of a birth-pulse population.

Because all seeds do not germinate in the spring after they are produced, our matrix will need to have two types of reproduction terms: (1) contributions of above-ground plants to seeds in the seed bank (which appear in the first row of the matrix); and (2) contributions by above-ground plants to seeds that germinate the following spring to become seedlings (which appear in

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\(^{12}\) These class definitions differ slightly from those used by Gross et al. (1998), who combined seedlings and tiny plants into a single size class, and used different boundaries for the other classes.
the second row of the matrix). Contributions to the seed bank (class 1) by individuals in class $j$, $a_{1j}$, are given by the product of: (1) $f_j$, the average number of seeds produced by plants in class $j$ (from Table 6.6); (2) $g_{11}$, the fraction of those seeds that do not germinate the following spring; and, (3) $s_1$, the probability that a seed survives one year in the soil to be present in the population at the time of the next census. Knowledge of the plant’s natural history suggests that only about 1% of the viable seeds dispersed at the end of the summer germinate the following Spring (thus the fraction $g_{11}$=0.99 do not germinate), and that viability of seeds in the seed bank declines by about 50% per year, so $s_1$=0.50 (for details on how these estimates were obtained, see Gross et al. 1998). For example in 1987, the estimated contribution of each large plant (class 6) to the seed bank, $a_{16}$, equals 97.08 seeds (Table 6.6) times 0.99 times 0.5, or 48.0546 seeds.

Contributions to the seedling class (class 2) by individuals in class $j$, $a_{2j}$, are products of four terms: (1) $f_j$, the average number of seeds produced by plants in class $j$; (2) the fraction of seeds that survive the winter in the soil; (3) the fraction of surviving seeds that germinate the following Spring, which equals $(1- g_{11})$ or 0.01; and (4) the probability that a seedling survives its first summer. To estimate the second component, we assume (in the absence of data needed to do otherwise) that the rate of survival does not change from month to month, so that the fraction of seeds surviving the 7 month winter period from dispersal to spring germination is $(0.5)^{7/12} = 0.6674$, where 0.5 is the annual survival rate of seeds in the soil. In a set of plots separate from his census plots, Frost (1990) observed that newly-emerged seedlings had a probability of 0.4681, 0.4444, and 0.9810 of surviving their first summer of life in 1987, 1988, and 1989, respectively (because Frost did not measure seedling survival in 1985 or 1986, we use the average of these three numbers for those years). For example in 1987, the estimated contribution of each large plant (class 6) to the seedling class $a_{26}$ equals 97.08 seeds times 0.6674
times 0.01 times 0.4681, or 0.3033 seedlings. Repeating these steps for other size classes yields the reproduction terms in Table 6.7.

A seed remains in the seed bank at the next census if it survives (probability 0.5) and does not germinate (probability 0.99); hence \( a_{11} \) equals \( 0.5 \times 0.99 = 0.4950 \) (note that we have no way to estimate annual variability in this matrix element). A seed will become a seedling at the next census if it survives the winter (probability 0.6674), germinates (probability 0.01), and survives the summer (probabilities given in the preceding paragraph). Thus, for example, in 1987, \( a_{12} = 0.6674 \times 0.01 \times 0.4681 = 0.0031 \).

Next we estimate the survival probabilities of seedlings. In his seedling plots, Frost (1990) found that seedlings still alive at the time of the census in 1987 and 1988 had a probability of 0.4545 and 0.5000, respectively, of surviving to the following census. In the absence of additional data, we use the average of these two numbers in the other years. Because a seedling cannot remain so for more than one year, all surviving seedlings automatically advance to the tiny plant class.

Finally, we estimate the size transition probabilities for plants older than seedlings by multiplying the size transitions in Table 6.5 by the survival probabilities in Table 6.4. For example, the estimated probabilities that individuals in size class 5 in 1987 are in size classes 3 through 6 in 1988 are 0.1425, 0.1425, 0.4985, and 0.2137, respectively. The results for all classes are given in Table 6.7.

The second through fifth columns in Table 6.7 give the estimates of the matrix entries for particular years. In Chapter 7, we will envision the projection matrix as changing from year to year due to changes in environmental conditions that affect the population’s vital rates. To reflect this annual variation, we will represent the projection matrix by the short-hand \( A(t) \),
which indicates that this matrix only applies in the interval between census $t$ and census $t+1$.

Table 6.7 also shows the means and variances across years for each matrix element. We can also use the matrix element values in Table 6.7 to compute the covariance between each possible pair of matrix elements, which measures the similarity between the patterns of temporal fluctuation in the two elements. In Chapter 7, we will say more about how to calculate and interpret these covariances. More importantly, we will see that the means, variances, and covariances of matrix elements play an important role in analyzing the viability of structured populations in a variable environment. We could also compute means, variances, and covariances of the vital rates themselves, and we will discuss in Chapter 8 how to make use of them in a vital-rate-based PVA.

**Summary**

In this chapter we’ve gone through the basics of how to take field data from a demographic study and turn them into a set of vital rate estimates than can in turn be used to construct a projection matrix model. In doing so, we have emphasized how to construct a single matrix using the data from a single inter-census interval. We have done this in part because a single annual transition may be all the data you have. Even if data for only a single transition are all that are available, many useful analyses can still be done with a matrix model, as we will see when we discuss deterministic results in the beginning of Chapter 7. However, with only a single matrix, we cannot assess the effect of environmental stochasticity on population viability, so ideally we would have access to data from a demographic study conducted long enough to allow the estimation of vital rates and matrix elements over multiple years. In either case, the task ahead is to use the estimated matrices to predict population growth and extinction.
probabilities. That is the topic of Chapters 7 and 8. We will also discuss how to treat several complications that we have ignored here, in particular demographic stochasticity, density dependence, and catastrophes and bonanzas. Then in Chapter 9, we will focus on the use of projection matrix models to identify the causes of low viability and to guide effective management of threatened populations.
Table 6.1: Appropriate statistical tools for testing associations between vital rates and potential classifying variables.

<table>
<thead>
<tr>
<th>Classifying variable:</th>
<th>Vital rate:</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Survival or reproduction (binary)</td>
<td>Reproduction (discrete but not binary)</td>
<td>Reproduction or growth (continuous or nearly so)</td>
<td></td>
</tr>
<tr>
<td>Age or size (continuous)</td>
<td>Logistic regression (or hazard functions)¹</td>
<td>Generalized linear models (e.g. Poisson regression)²</td>
<td>Linear, polynomial, or non-linear regression</td>
<td></td>
</tr>
<tr>
<td>Stage (discrete)</td>
<td>Log-linear models (G-tests)</td>
<td>Log-linear models (G-tests)</td>
<td>ANOVA (or non-parametric analogs)</td>
<td></td>
</tr>
</tbody>
</table>

¹ Simple logistic regression models predict steadily increasing or decreasing survival probabilities as a function of size or age, but logistic models can also include more complex patterns, such as survival rates that rise from young to middle-aged animals and then fall as animals senesce. If age is $A$ and $a$, $b$, and $c$ are constants, a logistic equation that can include such effects is: $\text{survival}(A) = \exp(a + bA + cA^2)/(1 + \exp(a + bA + cA^2))$. If $b$ is positive and $c$ is negative, survival will reach a maximum at an intermediate age. In spite of the flexibility of adding higher order terms to a logistic function ($A^2$, $A^3$, etc), for some groups, it may be more natural to use a different equation to predict age- or size-dependent survival. In particular, a “proportional hazards function” (Eberhardt and Siniff 1988) has been formulated to flexibly model the usual patterns of age-dependent survival (or fertility) of large mammals that include juvenile, mature and senescent phases. If you are fitting this or other functions to survival data using a nonlinear fitting routine in a statistical package, be sure to require that the fitting procedure uses binomial probabilities to calculate log likelihoods (this is exactly the way maximum-likelihood fitting of logistic regression models is done and is well-described in Sokal and Rohlf 1995).

² See Footnote 4 in the text.
Table 6.2: Results of logistic regressions of survival vs. size using data for *Hudsonia montana* in Figure 6.1. $b_0$ and $b_1$ are the coefficients in the logistic regression (Equation 6.2), and $P$ is the probability that the true value of $b_1$ is zero (i.e. that size has no effect on survival).

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Dependent variable</th>
<th>$b_0$</th>
<th>$b_1$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size in 1985</td>
<td>Survival from 1985 to 1986</td>
<td>0.7434</td>
<td>0.0734</td>
<td>0.0521</td>
</tr>
<tr>
<td>Size in 1986</td>
<td>Survival from 1986 to 1987</td>
<td>0.7336</td>
<td>0.0477</td>
<td>0.0602</td>
</tr>
<tr>
<td>Size in 1987</td>
<td>Survival from 1987 to 1988</td>
<td>-0.8144</td>
<td>0.0883</td>
<td>0.0076</td>
</tr>
<tr>
<td>Size in 1988</td>
<td>Survival from 1988 to 1989</td>
<td>-0.6981</td>
<td>0.2968</td>
<td>0.1847</td>
</tr>
</tbody>
</table>
Table 6.3: Survival data for red-cockaded woodpeckers in different reproductive stages, from Walters 1990.

<table>
<thead>
<tr>
<th>Stage:</th>
<th>Total number of bird-years:</th>
<th>Fate at the end of a one-year interval:</th>
<th>Proportion surviving one year:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Dead</td>
<td>Alive</td>
</tr>
<tr>
<td>Fledglings</td>
<td>616</td>
<td>345</td>
<td>271</td>
</tr>
<tr>
<td>Solitary males</td>
<td>131</td>
<td>50</td>
<td>81</td>
</tr>
<tr>
<td>Helpers-at-the-nest</td>
<td>273</td>
<td>60</td>
<td>213</td>
</tr>
<tr>
<td>Breeding males</td>
<td>838</td>
<td>201</td>
<td>637</td>
</tr>
<tr>
<td>Floaters</td>
<td>29</td>
<td>11</td>
<td>18</td>
</tr>
</tbody>
</table>
Table 6.4: Estimated survival of *Hudsonia montana* plants in 4 size classes in 4 years, using data from Frost (1990). Survival probabilities were obtained by substituting values of the regression coefficients $b_0$ and $b_1$ from Table 6.2 into the logistic regression Equation 6.2, and calculating the predicted survival using the midpoint, median, or distribution of plant size.

<table>
<thead>
<tr>
<th>Plant area (cm$^2$)</th>
<th>Class midpoint</th>
<th>Class median in 1985</th>
<th>Number of plants in 1985</th>
<th>Survival probabilities estimated using:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Class midpoints:</td>
</tr>
<tr>
<td>0 – 25</td>
<td>12.5</td>
<td>10.95</td>
<td>30</td>
<td>0.8404</td>
</tr>
<tr>
<td>25 – 50</td>
<td>37.5</td>
<td>34.85</td>
<td>16</td>
<td>0.9706</td>
</tr>
<tr>
<td>50 – 100</td>
<td>75</td>
<td>65.85</td>
<td>24</td>
<td>0.9981</td>
</tr>
<tr>
<td>&gt;100</td>
<td>135(^1)</td>
<td>134.8</td>
<td>5</td>
<td>1.0000</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Class medians in 1985:</td>
</tr>
<tr>
<td>0 – 25</td>
<td>12.5</td>
<td>10.95</td>
<td>30</td>
<td>0.8245</td>
</tr>
<tr>
<td>25 – 50</td>
<td>37.5</td>
<td>34.85</td>
<td>16</td>
<td>0.9645</td>
</tr>
<tr>
<td>50 – 100</td>
<td>75</td>
<td>65.85</td>
<td>24</td>
<td>0.9962</td>
</tr>
<tr>
<td>&gt;100</td>
<td>135(^1)</td>
<td>134.8</td>
<td>5</td>
<td>1.0000</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Distribution of plant sizes within each class in 1985:</td>
</tr>
<tr>
<td>0 – 25</td>
<td>12.5</td>
<td>10.95</td>
<td>30</td>
<td>0.8247</td>
</tr>
<tr>
<td>25 – 50</td>
<td>37.5</td>
<td>34.85</td>
<td>16</td>
<td>0.9600</td>
</tr>
<tr>
<td>50 – 100</td>
<td>75</td>
<td>65.85</td>
<td>24</td>
<td>0.9957</td>
</tr>
<tr>
<td>&gt;100</td>
<td>135(^1)</td>
<td>134.8</td>
<td>5</td>
<td>1.0000</td>
</tr>
</tbody>
</table>

\(^1\) Because it is difficult to define an upper boundary for plant size, we use the median of all size measurements over 100 cm$^2$ in the first year of Frost's demographic study as the midpoint of the largest size class.
Table 6.5: Size transitions for mountain golden heather over 4 years (data from Frost 1990).

The table shows the number of plants making each size transition and in parentheses, the proportions across the cells in each column of the table; these are the estimated size transition probabilities.

<table>
<thead>
<tr>
<th>Size in 1986 (cm²)</th>
<th>Size in 1985 (cm²)</th>
<th>0-25</th>
<th>25-50</th>
<th>50-100</th>
<th>&gt;100</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-25</td>
<td>0-25</td>
<td>21 (0.84)</td>
<td>2 (0.1333)</td>
<td>2 (0.0833)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>25-50</td>
<td>25-50</td>
<td>4 (0.16)</td>
<td>7 (0.4667)</td>
<td>5 (0.2083)</td>
<td>1 (0.2)</td>
</tr>
<tr>
<td>50-100</td>
<td>50-100</td>
<td>0 (0)</td>
<td>5 (0.3333)</td>
<td>15 (0.625)</td>
<td>1 (0.2)</td>
</tr>
<tr>
<td>&gt;100</td>
<td>&gt;100</td>
<td>0 (0)</td>
<td>1 (0.0667)</td>
<td>2 (0.0833)</td>
<td>3 (0.6)</td>
</tr>
<tr>
<td>TOTAL:</td>
<td>TOTAL:</td>
<td>25</td>
<td>15</td>
<td>24</td>
<td>5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Size in 1987 (cm²)</th>
<th>Size in 1986 (cm²)</th>
<th>0-25</th>
<th>25-50</th>
<th>50-100</th>
<th>&gt;100</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-25</td>
<td>0-25</td>
<td>12 (0.6316)</td>
<td>4 (0.2353)</td>
<td>1 (0.05)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>25-50</td>
<td>25-50</td>
<td>7 (0.3684)</td>
<td>8 (0.4706)</td>
<td>3 (0.15)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>50-100</td>
<td>50-100</td>
<td>0 (0)</td>
<td>5 (0.2941)</td>
<td>9 (0.45)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>&gt;100</td>
<td>&gt;100</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>7 (0.35)</td>
<td>6 (1)</td>
</tr>
<tr>
<td>TOTAL:</td>
<td>TOTAL:</td>
<td>19</td>
<td>17</td>
<td>20</td>
<td>6</td>
</tr>
</tbody>
</table>
Table 6.5 (continued)

<table>
<thead>
<tr>
<th>Size in 1987 (cm²)</th>
<th>Size in 1988 (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-25</td>
<td>25-50</td>
</tr>
<tr>
<td>0-25</td>
<td>8 (0.8)</td>
</tr>
<tr>
<td>25-50</td>
<td>2 (0.2)</td>
</tr>
<tr>
<td>50-100</td>
<td>0 (0)</td>
</tr>
<tr>
<td>&gt;100</td>
<td>0 (0)</td>
</tr>
<tr>
<td>TOTAL:</td>
<td>10</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Size in 1988 (cm²)</th>
<th>Size in 1989 (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-25</td>
<td>25-50</td>
</tr>
<tr>
<td>0-25</td>
<td>10 (0.7692)</td>
</tr>
<tr>
<td>25-50</td>
<td>3 (0.2308)</td>
</tr>
<tr>
<td>50-100</td>
<td>0 (0)</td>
</tr>
<tr>
<td>&gt;100</td>
<td>0 (0)</td>
</tr>
<tr>
<td>TOTAL:</td>
<td>13</td>
</tr>
</tbody>
</table>
Table 6.6: Estimated number of seeds produced annually by mountain golden heather plants in four size classes. Data from Figure 6.2 (Frost 1990).

<table>
<thead>
<tr>
<th>Size of parent (cm²):</th>
<th>Class midpoint, x</th>
<th>Estimated seed production in 1987</th>
<th>Estimated seed production in 1988</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-25</td>
<td>12.5</td>
<td>8.86</td>
<td>9.48</td>
</tr>
<tr>
<td>25-50</td>
<td>37.5</td>
<td>23.49</td>
<td>25.13</td>
</tr>
<tr>
<td>50-100</td>
<td>75</td>
<td>43.17</td>
<td>46.19</td>
</tr>
<tr>
<td>&gt;100</td>
<td>140</td>
<td>97.08</td>
<td>103.88</td>
</tr>
</tbody>
</table>
Table 6.7: Estimated projection matrix elements for mountain golden heather for 4 years, using data from Frost (1990) and Gross et al. (1998). Matrix elements not listed in the table were zero in each of the 4 years.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>a_{11}</td>
<td>0.4995</td>
<td>0.4995</td>
<td>0.4995</td>
<td>0.4995</td>
<td>0.4995</td>
<td>0.0000</td>
</tr>
<tr>
<td>a_{13}</td>
<td>4.5782</td>
<td>4.5782</td>
<td>4.4234</td>
<td>4.7330</td>
<td>4.5782</td>
<td>0.0120</td>
</tr>
<tr>
<td>a_{14}</td>
<td>12.1425</td>
<td>12.1425</td>
<td>11.7319</td>
<td>12.5531</td>
<td>12.1425</td>
<td>0.0843</td>
</tr>
<tr>
<td>a_{15}</td>
<td>22.3167</td>
<td>22.3167</td>
<td>21.5620</td>
<td>23.0714</td>
<td>22.3167</td>
<td>0.2848</td>
</tr>
<tr>
<td>a_{16}</td>
<td>50.1895</td>
<td>50.1895</td>
<td>48.4923</td>
<td>51.8867</td>
<td>50.1895</td>
<td>1.4403</td>
</tr>
<tr>
<td>a_{21}</td>
<td>0.0004</td>
<td>0.0004</td>
<td>0.0003</td>
<td>0.0003</td>
<td>0.0004</td>
<td>0.0000</td>
</tr>
<tr>
<td>a_{22}</td>
<td>0.0039</td>
<td>0.0039</td>
<td>0.0028</td>
<td>0.0028</td>
<td>0.0033</td>
<td>0.0000</td>
</tr>
<tr>
<td>a_{23}</td>
<td>0.0102</td>
<td>0.0102</td>
<td>0.0073</td>
<td>0.0075</td>
<td>0.0088</td>
<td>0.0000</td>
</tr>
<tr>
<td>a_{24}</td>
<td>0.0188</td>
<td>0.0188</td>
<td>0.0135</td>
<td>0.0137</td>
<td>0.0162</td>
<td>0.0000</td>
</tr>
<tr>
<td>a_{25}</td>
<td>0.0423</td>
<td>0.0423</td>
<td>0.0303</td>
<td>0.0308</td>
<td>0.0364</td>
<td>0.0000</td>
</tr>
<tr>
<td>a_{26}</td>
<td>0.4773</td>
<td>0.4773</td>
<td>0.4545</td>
<td>0.5000</td>
<td>0.4773</td>
<td>0.0003</td>
</tr>
<tr>
<td>a_{32}</td>
<td>0.7059</td>
<td>0.4995</td>
<td>0.4575</td>
<td>0.7331</td>
<td>0.5990</td>
<td>0.0148</td>
</tr>
<tr>
<td>a_{33}</td>
<td>0.1294</td>
<td>0.2178</td>
<td>0.3079</td>
<td>0.1429</td>
<td>0.1995</td>
<td>0.0051</td>
</tr>
<tr>
<td>a_{34}</td>
<td>0.0831</td>
<td>0.0493</td>
<td>0.1425</td>
<td>0.0000</td>
<td>0.0687</td>
<td>0.0027</td>
</tr>
<tr>
<td>a_{35}</td>
<td>0.1345</td>
<td>0.2913</td>
<td>0.1144</td>
<td>0.2200</td>
<td>0.1900</td>
<td>0.0050</td>
</tr>
<tr>
<td>a_{41}</td>
<td>0.4530</td>
<td>0.4356</td>
<td>0.5544</td>
<td>0.4286</td>
<td>0.4679</td>
<td>0.0026</td>
</tr>
<tr>
<td>a_{42}</td>
<td>0.2079</td>
<td>0.1480</td>
<td>0.1425</td>
<td>0.0000</td>
<td>0.1246</td>
<td>0.0058</td>
</tr>
<tr>
<td>a_{43}</td>
<td>0.2000</td>
<td>0.0000</td>
<td>0.0769</td>
<td>0.0000</td>
<td>0.0692</td>
<td>0.0067</td>
</tr>
<tr>
<td>a_{44}</td>
<td>0.3235</td>
<td>0.2722</td>
<td>0.0616</td>
<td>0.4286</td>
<td>0.2715</td>
<td>0.0179</td>
</tr>
<tr>
<td>a_{53}</td>
<td>0.6238</td>
<td>0.4440</td>
<td>0.4985</td>
<td>0.6154</td>
<td>0.5454</td>
<td>0.0059</td>
</tr>
<tr>
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Figure 6.1: Survival vs. size for mountain golden heather (data from Frost 1990). Points show fates of individual plants (0=dead, 1=alive). Best-fit lines were obtained by logistic regression (for regression coefficients, see Table 6.2).

Figure 6.2: Seed production vs. size for mountain golden heather in two years (data from Frost 1990). Seed number was estimated by counting fruits in photographic images of census plants, and multiplying by the average number of viable seeds per fruit (for details, see Gross et al. 1998).

Figure 6.3: Graphical representation of how to calculate, for three temporal patterns of fertility, the matrix elements representing reproduction. Black bars represent the number of newborns produced per live adult in class \( j \); hatched bars represent offspring alive at the next census. For birth flow populations, fertility is represented by summing newborns produced throughout the inter-census interval and assuming their birth date is the same as that of the average newborn. See text for definitions of vital rate symbols.
Figure 6.1

- **Size in 1985 (cm^2)**
- **Probability of surviving to 1986**

- **Size in 1986 (cm^2)**
- **Probability of surviving to 1987**

- **Size in 1987 (cm^2)**
- **Probability of surviving to 1988**

- **Size in 1988 (cm^2)**
- **Probability of surviving to 1989**
Figure 6.2

**Top graph:**
- Number of seeds vs. Plant area in 1987 (cm$^2$)
- Equation: $y = 0.764x - 0.00483x^2 + 3.09 \times 10^{-5} x^3$

**Bottom graph:**
- Number of seeds vs. Size in 1988 (cm$^2$)
- Equation: $y = 1.07x$
Figure 6.3

A. Birth-pulse, pre-breeding census

B. Birth-pulse, post-breeding census

C. Birth-flow

“Averaged” fertility

“Actual” fertility