4 Matrix Models for Primate Life History Analysis

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A major theme of this book is the analysis of primate life histories through broad interspecific comparisons of selected life history traits. In this chapter we present a complementary approach using demographic matrix models, which allow for a detailed analysis of the life history (the schedule of survival and reproduction across the life span) of a single species. This approach has not yet been used extensively for nonhuman primates, but as demographic and life history data accumulate on an increasing number of species, matrix models will offer a powerful means of exploring life history variation within species as well as alternative ways of exploring interspecific differences.

Demographic matrix models produce two results of major interest. The first is λ, an estimate of the population growth rate, which is also analytically equivalent to the relative fitness of the mean phenotype in the population (van Groenendael, de Kroon, and Caswell 1988; McDonald and Caswell 1993; Caswell 2001). The second is elasticity (or sensitivity), which estimates the effect of perturbations in life history parameters on λ. In an ecological context, elasticity analyses reveal how population dynamics change as individual life history parameters change. In an evolutionary context, elasticities measure the relative strength of selection on life history parameters. Thus, demographic models can provide evolutionary as well as ecological insights.

Demographic matrix models have several applications. First, they provide a method for evaluating the viability of populations that are threatened or endangered and for assessing management strategies for such populations. For example, Heppell, Walters, and Crowder (1994) used a matrix model and elasticity analysis to examine a declining population of endangered red-cockaded woodpeckers. They determined that a critical factor af-

fecting the population growth rate (λ) was the probability that a nonbreeding male woodpecker would become a breeder; perturbing their model by increasing the proportion of nonbreeding males that became breeders resulted in a relatively large increase in λ. They noted that the rate at which nonbreeders become breeders in this species is dependent on the availability of nesting cavities, and proposed that management efforts should focus on increasing the number of potential nesting cavities for woodpecker populations.

Second, the demonstration that λ is equivalent to fitness and that sensitivities are equivalent to selection gradients (Lande 1982a; McDonald and Caswell 1993; Caswell 2001) means that the strength of selection on life history parameters can be estimated. For example, McDonald (1993) used elasticity analysis to demonstrate that, for male long-tailed manakins, selection on survival is an order of magnitude stronger than selection on fertility, a somewhat counterintuitive result for a bird species with elaborate male displays and extreme variance in male reproductive success. McDonald also demonstrated that selection on prereproductive survival is much stronger for male manakins than it is for females and that male generation times are more than double those of females. The consequences of such sexual differences in demographic parameters have been little explored.

Third, while most uses of matrix demography have focused on within-population analysis, matrix methods can also be used to examine patterns across populations and even between species. For example, Pfister (1998) performed a broad interspecific comparison of phenotypic variance in life history traits and found that over a wide variety of taxa, ranging from annual plants to long-lived vertebrates, phenotypic variance tends to be lowest in traits with high elasticities (traits that have a large effect on fitness). This finding suggests that natural selection has resulted in the evolution of a suite of traits that minimizes temporal variation in fitness, which in turn supports the notion of bet hedging (i.e., that reduced phenotypic variance in fitness is selected for because it increases lifetime fitness: Stearns 1992; Benton and Grant 1999).

The purpose of this chapter is to provide an introduction to demographic matrix methods for the analysis of primate life histories, using examples from an analysis of baboon life histories. The wide applicability of matrix models makes them a useful tool for life history analyses from several perspectives. Their usefulness for conservation applications in particular is unequaled by other methods. Their use for analyzing fitness differences among individuals and for identifying selection pressures overlaps with that of the multivariate methods developed by Arnold and Wade

(1984a,b) and Brown (1988), and we therefore conclude this chapter with a brief comparison of matrix methods with these multivariate methods. For additional introductions to matrix methodology, the reader is referred to van Groenendael, de Kroon, and Caswell (1988), McDonald and Caswell (1993), and Morris and Doak (2002). For more detailed discussions of matrix models, the reader is referred to Caswell (2001).

Background

Life history theory describes the distribution of mortality and reproductive effort over the life span (Roff 1992; Stearns 1992). Life history traits include size at birth, pattern of growth, age at first reproduction, age-specific fertility, age-specific mortality, longevity, and number, size, and sex ratio of offspring. Life history theory asserts that these traits have evolved as a suite, with the target of selection being fitness over the lifetime rather than instantaneous fitness or maximization of any single trait.

The general approach for examining the life history of a particular species is to construct a model of the average life history in a given population, using age-specific rates of survival and reproduction. Collectively, these are known as vital rates, and in a real sense they define a life history: they encompass the probability of surviving for any given time period, the age at first reproduction, the rates of reproduction thereafter, and the average longevity. The model then generates a measure of population growth rate, as well as projected estimates of a population's size and its age distribution over specified time periods. The model can also serve as a point of comparison for variants of the mean life history, making it possible to compare the mean vital rates with a range of alternatives.

Historically, most demographic models have taken the form of life tables, or $l_x m_x$ tables (see Sade et al. 1976; Altmann et al. 1977; Ricklefs 1983; Stearns 1992, chap. 2; Charlesworth 1994, chap. 1, for examples and discussions). In the last two decades, however, developments in demographic analysis have greatly extended classic life table analysis, overcoming some of its limitations and advancing methods for studying variation in vital rates (for excellent introductions, see van Groenendael, de Kroon, and Caswell 1988; McDonald and Caswell 1993). These developments have yielded several important results, three of which are particularly relevant to this chapter. First, life histories that are difficult to describe in terms of age-specific fertilities and mortalities (such as those in which size or social status is a better predictor of vital rates than age) can be analyzed using stage-specific vital rates. Second, perturbation analyses of demographic models provide a simple method for examining the consequences of changes in

vital rates, as exemplified by the red-cockaded woodpecker example (Heppell, Walters, and Crowder 1994). Finally, the analytic demonstration (Lande 1982a,b; see also McDonald and Caswell 1993; Caswell 2001) that λ, the measure of population growth rate, is equivalent to the relative fitness of a given life history (i.e., of a set of vital rates) means that matrix approaches can be used to describe the effects of life history changes at the level of the individual (in terms of the relative fitness of different phenotypes) and at the level of the population (in terms of effects on population growth).

Constructing the Model

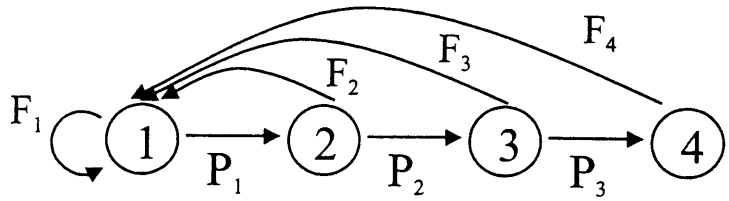
Projection Matrices and Life Cycle Graphs

A demographic analysis of life history can be formulated as a projection matrix (so called because it allows one to project estimates of population size) or as a life cycle graph. These are exactly equivalent formulations: the matrix representation is more traditional, while the life cycle graph is considered by many to be more intuitive. In the life cycle graph (fig. 4.1A), each age class is represented by a node, and arrows between the nodes represent the probabilities of moving from one age class to the next. Arrows back to the first age class represent age-specific fertilities. In the matrix formulation (fig. 4.1B), the vital rates are represented by the elements, a_{ij}, of the matrix. The first row of the matrix, with elements a_{1j}, represents the expected production of newborns by each age class (known as fertilities; see appendix 4.1), and corresponds to the arrows back to the first age class in the life cycle graph. Subsequent rows represent the probabilities of moving from one class to another. In general, rows can be thought of as representing demographic input to the corresponding age classes, with columns representing their demographic output (fig. 4.1B).

Multiplying the projection matrix by a vector representing the current numbers of animals in each age class (the census vector; see fig. 4.1B) yields an estimate of the population size and age distribution in the next time period (see Caswell 2001, appendix A, for a clear introduction to the rules of matrix manipulation). Repeated multiplication, then, gives the population size and age distribution after any arbitrary number of time units. The time unit over which population size is calculated is known as the projection interval.

Determining the Projection Interval

The first step in constructing a demographic model is determining the projection interval—the period over which one will measure vital rates and take



A

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}(t+1) = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix} * \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \end{bmatrix}(t)$$

B

FIG. 4.1. *(A)* Life cycle graph for a population with four age classes, in which reproduction occurs in each age class. *(B)* Projection matrix with census vectors corresponding to the life cycle graph in part A. Rows can be thought of as representing demographic input to the corresponding age classes, with columns representing their demographic output. For instance, the cell at the intersection of the first row and the third column (a_{13}) designates production of newborns by animals in the third age class (input to the first age class, output from the third). The cell at the intersection of the fourth row and the third column (a_{43}) designates the probability of surviving from the third age class to the fourth (input to the fourth class, output from the third).

censuses. To some extent this is an arbitrary choice, but the interval must be long enough to yield meaningful vital rates (for instance, daily survival and fertility measures will not yield reasonable values for vertebrates). Further, to ensure accurate estimates of vital rates, the interval should not be longer than the duration of the age classes (for instance, if the projection interval were two years, the resulting census data would allow estimation of survival from two to four years of age, but not from two to three years of age; thus, the age classes for such a model must be two years in duration). For primates and many other large-bodied animals, a projection interval of one year is convenient because it often encompasses a single birth season. Estimates of yearly survival and birth rate for each age class are then retrieved from yearly censuses or from continuous observations.

Age-Structured versus Stage-Structured Models

The next step is to determine whether the life history in question is best described by an age-structured model or a stage-structured model. Age-

structured models are appropriate if mortality or fertility changes with age, and if age can be accurately measured. For instance, a matrix representation of a population of female baboons in Amboseli, Kenya, is a 27 × 27 matrix describing survival and fertility for 27 age classes (fig. 4.2A); the 21 × 21 matrix for Amboseli males reflects the fact that males in this population have shorter life spans on average than females do (fig. 4.2B). Note that some life history characteristics, such as age at first reproduction and life span, are apparent in the matrix and that others, such as life expectancy, can readily be calculated by simple multiplication of the diagonal elements.

In many cases, however, such fine-grained age classifications are not possible. Instead, researchers identify individuals only as infants, young juveniles, older juveniles, young adults, and so forth. In such cases, stage-based models may be employed, as illustrated by a stage-based life cycle graph for female elk in Yellowstone National Park, USA (fig. 4.3; Dixon et al. 1997). Some cautions are required in constructing stage-based models of this sort, and these will be described in more detail below.

Finally, for some species, an individual's reproductive status and survival probabilities depend more on its position in the social group than on its age (among primates, callitrichids are the best example). In these cases, a stage-based model may be most appropriate, as illustrated by a stage-based model for male red-cockaded woodpeckers, cooperatively breeding North American birds (fig. 4.4; Heppell, Walters, and Crowder 1994).

Cautions for Constructing Stage-Based Models

While age-based matrices (Leslie matrices; after Leslie 1945) are historically most common, stage-based matrices (Lefkovitch matrices; after Lefkovitch 1965) are increasingly popular because their flexibility makes them applicable to a wide range of species and data sets. We have described two types of stage-based models: those in which vital rates are better predicted by social status than by age (as in red-cockaded woodpeckers), and those in which vital rates are age-specific but the data are not sufficiently fine-grained to generate age-based models (as in Yellowstone elk).

In constructing stage-based models, two points bear emphasis. First, the duration of the stage class is independent of the length of projection interval, the period over which vital rates are measured. Regardless of the length of the projection interval and the duration of the stage classes, vital rates are calculated as the number of events per interval (Caswell 2001). For instance, in the model of Yellowstone elk (see fig. 4.3), some classes cover one-year durations while others cover several years (e.g., class 4 comprises three- to seven-year-olds). In both cases, survival and fertility are calculated yearly

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\begin{pmatrix}
0 & 0 & 0 & 0 & 0.128 & 0.272 & 0.275 & 0.265 & 0.260 & 0.224 & 0.198 & 0.231 & 0.262 & 0.260 & 0.284 & 0.301 & 0.266 & 0.217 & 0.244 & 0.184 & 0.240 & 0.322 & 0.131 & 0.214 & 0 & 0 & 0 \\
0.794 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.888 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.937 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.969 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.953 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.944 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.948 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.948 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.943 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.923 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.891 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.894 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.942 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.916 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.870 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.873 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.788 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.633 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.628 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.865 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.746 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.552 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.609 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.417 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.380 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.5 & 0
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\begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 0.373 & 0.776 & 0.779 & 0.766 & 0.742 & 0.722 & 0.707 & 0.665 & 0.647 & 0.595 & 0.475 & 0.433 & 0.625 & 0.586 & 0.213 & 0 \\
0.782 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.912 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.934 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.917 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.959 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.943 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
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0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.942 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.931 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.911 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.894 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.882 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.846 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.830 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.782 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.667 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.625 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.800 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.750 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.333 & 0
\end{pmatrix}
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FIG. 4.2. Demographic matrices for wild-foraging baboons in Amboseli, Kenya (birth-flow model): *(A)* females, *(B)* males.

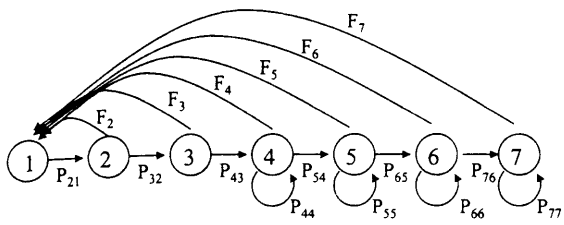
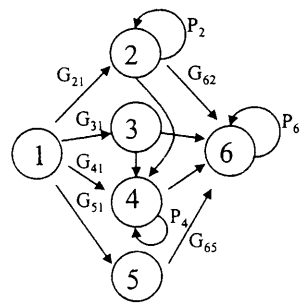


FIG. 4.3. Life cycle graph for female elk in Yellowstone National Park. Stage classes: 1, newborns; 2, yearlings; 3, 2-year-olds; 4, 3–7 years; 5, 8–15 years; 6, 16–20 years; 7, 20+ years. (After Dixon et al. 1997.)

$$\begin{pmatrix} F_1 & F_2 & F_3 & F_4 & F_5 & F_6 \\ G_{21} & P_2 & 0 & 0 & 0 & 0 \\ G_{31} & 0 & 0 & 0 & 0 & 0 \\ G_{41} & G_{42} & G_{43} & P_4 & 0 & 0 \\ G_{51} & 0 & 0 & 0 & 0 & 0 \\ 0 & G_{62} & G_{63} & G_{64} & G_{65} & P_6 \end{pmatrix}$$

A



B

FIG. 4.4. *(A)* Projection matrix for male red-cockaded woodpeckers. Stages: 1, fledgling; 2, helper; 3, floater; 4, solitary; 5, 1-year-old breeder; 6, older breeder. *(B)* Life cycle graph for male red-cockaded woodpeckers; no fertilities and only some transition probabilities are shown. *P*s represent survival probabilities; *G*s represent probabilities of transition from one stage to another. (After Heppell, Walters, and Crowder 1994.)

(i.e., the projection interval is one year). The projection interval is independent of the duration of stages, and must be the same for all classes.

Second, choosing the durations of the stages is a critical step. If stages of long duration are chosen, one runs the risk of pooling together ages that have very different vital rates (Vandermeer 1978; Benton and Grant 1999). For instance, if three-year-old elk have much lower survival rates than four- to seven-year-old elk, then grouping them into a single class of three- to seven-year-olds will inflate their survival, and will consequently inflate λ—the model will, in essence, project that three-year-olds will remain alive and reproduce for longer than they really do. A good rule of thumb is to avoid grouping the early age classes, which often have high and rapidly decreasing mortality rates. Employment of this rule often coincides with available data, as researchers typically have more fine-grained age estimates (and thus survival data) for infants and young juveniles than they do for adults. In the case

of Yellowstone elk, the first three classes each represent one-year intervals, and grouping is not employed until well into adulthood, when mortalities are likely to be less variable over larger age spans (see fig. 4.3, Dixon et al. 1997).

Obtaining Vital Rates

Initial Decisions about the Matrix

Vital rates, the elements a_{ij} of the projection matrix, may be obtained from continuous observational data or from periodic census data. In constructing a matrix model, several key decisions must be made prior to beginning. These decisions include (1) which sex will be modeled, (2) whether the population will be modeled as a birth-flow or a birth-pulse population, and (3) whether the censuses (either actual or taken from a long-term database) will occur before the birth season (a prebreeding census) or after (a postbreeding census). The implications of each decision are described below.

Males versus females. Unless females and males exhibit the same vital rates (generally not the case for primates), separate models will be constructed for the two sexes. Within any population, the sexes will vary in their age distributions, in their reproductive patterns, and in how changes in these parameters affect fitness. However, models for each sex should yield roughly equivalent values of λ; this must be the case unless one sex is increasing in frequency relative to the other. For questions of general population dynamics, females are typically modeled (e.g., Yellowstone elk: Dixon et al. 1997), both because of the relative ease of measuring female fertility rather than male fertility and because, particularly among mammals, females are often the nondispersing sex, leading to better data on female survival rates. In some cases, conservation issues may be highly sex-specific, so that one sex rather than the other becomes the focus of demographic models (e.g., male red-cockaded woodpeckers: Heppell, Walters, and Crowder 1994). In evolutionary studies in which selection pressures on life history are likely to be different for the two sexes, both sexes are modeled if possible (e.g., McDonald 1993). Reproductive data for males are often difficult to obtain, but if paternity data come from genetic studies or behavioral data have been validated with genetic data (both of which are being accomplished for a number of primate populations; e.g., de Ruiter, van Hooff, and Scheffrahn 1994; Altmann et al. 1996; Bercovitch and Nürnberg 1996; Borries et al. 1999), the task is somewhat less onerous.

Birth-pulse versus birth-flow populations. Many primate species reproduce seasonally, so that all births occur within a fairly short period. Such species

are termed birth-pulse populations. Species such as baboons and the great apes, which reproduce throughout the year, are termed birth-flow populations. In both cases, the matrix model makes the simplifying assumption that age classes are discrete and that population growth is a discrete rather than a continuous process. This assumption is less troublesome for birth-pulse populations than it is for birth-flow populations. Birth-flow methods for calculating matrix elements are designed to mitigate the effects of assuming discrete population processes, and so are more complex than birth-pulse methods. Below we present a birth-pulse model for a hypothetical population of seasonally breeding monkeys, as well as birth-pulse and birth-flow models for female baboons in Amboseli. In some cases, the results of birth-flow and birth-pulse models for the same population may be quite different (Caswell 2001). However, the results of our birth-flow and birth-pulse models for Amboseli baboons are very similar, suggesting that in some cases a birth-pulse model provides an adequate description of population processes, even for birth-flow populations.

Prebreeding versus postbreeding censuses. For a birth-pulse population, if the census takes place before the birth season each year (a prebreeding census), it includes pregnant females and nearly-one-year-olds, but not newborns. Hence, survival during the first year of life is not observed directly, although it can be inferred by taking the difference between the number of pregnant females each year and the number of one-year-olds each subsequent year. In contrast, if the census takes place immediately after the birth season (a postbreeding census), newborns are counted each year, and survival during the first year of life can be observed directly by censusing each newborn cohort both immediately after birth and immediately after its first birthday. Prebreeding and postbreeding censuses yield exactly equivalent estimates of population growth (Caswell 2001). In the birth-pulse models presented here, we employ postbreeding censuses (i.e., we count newborns). We do not cover methods for employing prebreeding censuses, as many of the principles are the same. However, care must be taken to make explicit which type of census is being taken, as it affects calculations of both survival and fertility. We recommend Morris and Doak (2000) and Caswell (2001) to interested readers.

A Birth-Pulse Model for a Hypothetical Population of Seasonally Breeding Monkeys

Here we present a birth-pulse model that employs a postbreeding census for females in a hypothetical monkey population that reproduces seasonally (table 4.1 and fig. 4.5). We have made some simplifying assumptions to make

Table 4.1 Female matrix data for a hypothetical seasonally breeding monkey population

A	B	C	D	E	F	G	H	I	J[a]	K[b]	L[c]
Age	Age class (i)	Census took place when?	Females in this age class gave birth when?	Number of females that entered the age class	Number of age class members that died during the age class (i.e., did not give birth)	Number of age class members that survived to the next age class but did not give birth in the current age class	Number of female offspring born to the age class	$l(i)$ (survivorship)	$P_i = l(i)/l(i-1)$	Birth rate, m_i	$F_i = P_i m_i$
Newborn	—	—	—	1000	—	—	—	1.00	—	—	—
Newborn to 1	1	Just after birth	—	1000	200	800	0	0.80	0.80	0.00	0.00
1 to 2	2	Just after 1st birthday	—	800	300	500	0	0.50	0.63	0.00	0.00
2 to 3	3	Just after 2nd birthday	—	500	100	400	0	0.40	0.80	0.00	0.00
3 to 4	4	Just after 3rd birthday	On 4th birthday	400	80	60	260	0.32	0.80	0.81	0.65
4 to 5	5	Just after 4th birthday	On 5th birthday	320	60	30	230	0.26	0.81	0.88	0.72
5 to 6	6	Just after 5th birthday	On 6th birthday	260	110	40	110	0.15	0.58	0.73	0.42
6 to 7	7	Just after 6th birthday	On 7th birthday	150	100	10	40	0.05	0.33	0.80	0.27
7 to 8	8	Just after 7th birthday	On 8th birthday	50	50	0	0	0.00	0.00	0.00	0.00

[a] P_i is also equal to 1 − hazard, where hazard = (column F/column E).
[b] Birth rate, m_i = column H/(column G + column H).
[c] F_i is also equivalent to column H/column E (births/entering females).

$$\begin{pmatrix} 0.00 & 0.00 & 0.00 & 0.65 & 0.72 & 0.42 & 0.27 & 0.00 \\ 0.80 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.63 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.80 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.80 & 0.00 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.81 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.58 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.33 & 0.00 \end{pmatrix}$$

FIG. 4.5. Demographic matrix for the hypothetical seasonally breeding monkey population in table 4.1.

the process of calculating vital rates clear. In particular, we assume (1) that all females gave birth to a single offspring at the same time each year (and hence gave birth on or near their own birthdays), (2) that yearly census data are available, (3) that the censuses were taken immediately after the births occurred, (4) that all newborns were counted, and (5) that the population is now extinct, so that no population processes were ongoing when the model was constructed. In table 4.1, the numbers of individuals in each age class represent census data that are pooled over a number of years.

Survival (P_i). In the case of a postbreeding census, survival, P_i, is the probability of surviving from age class $(i - 1)$ to age class i. For each age class, the fate of all animals that ever entered that class must be determined; that is, animals must be designated as having survived through the age class or died in it. Survival for each age class can be calculated as simply (1 − hazard), where the hazard is defined, in this simple case, as the proportion dying in the age class (table 4.1, column J).

It is also valuable to calculate survivorship, $l(i)$, which is the probability of surviving from birth to the ith birthday (i.e., to the end of age class i in the case of a postbreeding census: table 4.1, column I). Matrix models begin with age class 1 (there is no 0 age class), but survivorship of newborns, $l(0)$, is retained as a placeholder, and is set to 1.00 (see tables 4.1 and 4.2). Survivorship, $l(i)$, is calculated as the number of females that survive to the ith birthday divided by the number of females ever born. Thus, survivorship is a cumulative measure of survival (the proportion of all animals born that survive to the ith birthday), while survival, P_i, is a conditional one (the proportion that survive age class i, given that they entered age class i). In most presentations of matrix methodology, survival is presented as

$$P_i = \frac{l(i)}{l(i-1)},$$

and it can be seen in table 4.1 that this yields the same values for P_i as does (1 − hazard).

Birth rate (m_i) and fertility (F_i). The calculation of fertility can be a source of confusion in matrix models, even though it may seem intuitively straightforward. The desired fertility rate for age class i is the expected number of female offspring born to a female *entering* the ith age class. In the case of the birth-pulse population presented in table 4.1, F_i can be calculated directly by dividing the number of female offspring produced by females in age class i by the number of females that ever entered age class i (column H/column E; see notes to table 4.1).

Care must be taken here to distinguish fertility, F_i, from the birth rate, m_i, which is the average number of offspring produced by a female who *reaches her* i*th birthday* (Caswell 2001, p. 27). More females *enter* the ith age class than reach their ith birthday unless survival for the age class is 1.00 (which will be rare). Thus, the age-specific birth rate, m_i, will be higher than the age-specific fertility, F_i. In table 4.1, age-specific birth rate, m_i, is calculated as the number of female offspring born to females in age class i (column H), divided by the number of females that gave birth in age class i (column H again, assuming all births are singletons) *plus* the number of females that survived through age class i but did not give birth (column G).

In most descriptions of how to produce vital rates, fertility for post-breeding censuses is described as

$$F_i = P_i m_i.$$

In table 4.1 it can be seen that this equation produces exactly the same value of F_i that is produced by dividing number of births by number of females entering the age class (see notes to table 4.1).

A Birth-Flow Model for Female Baboons in Amboseli

Three things distinguish the birth-flow model we constructed for baboons from the birth-pulse model presented above. First, the Amboseli baboons reproduce year-round, so that no clear birth season occurs. This reproductive pattern both makes the population better suited to a birth-flow than a birth-pulse model and makes the calculation of the vital rates less obvious.

Second, for the baboons, we had continuous data rather than yearly censuses. In principle, we could have easily constructed, post hoc, the equivalent of yearly censuses from the continuous data. This would be a reasonable approach to the use of continuous data. However, we wanted the more accurate survival estimates obtainable from continuous data.

Finally, the population was still extant at the time we constructed the matrix, so our analysis included many incomplete life histories (i.e., many females were still alive and contributing to population growth at the time of

the last census). Data on incomplete life histories are termed censored data, since the fate of each animal alive at the time of the last census (will it die in its current age class? survive to the next age class? reproduce in the current or future age classes?) is unknown. Including censored data is important, particularly in studies of long-lived species, because the sample of completed life histories is often biased toward animals that died young.

There are several methods for handling censored data, some of which can be used with either yearly census data or continuous data. For instance, Proc Lifetest, a computational program in SAS, produces age-specific survival estimates using numbers of animals that died or were censored in each age class. (For a clear description of how to produce survival estimates manually or using SAS, see Kalbfleisch and Prentice 1980; Lee 1992; Allison 1995.)

Birth-flow survival using continuous data. Survival, P_i, is the probability that an individual in age class i will survive from time t to $t + 1$. To calculate this probability for birth flow populations, the first step, for each age class, is to designate all animals that ever entered that age class as having survived, died, or been censored in that age class. For studies with continuous data on survival, we recommend the following method, which we employed for the Amboseli baboons. We calculated the age-specific hazard rate, H_i, as

$$H_i = N_i/T_i,$$

where N_i = the number of individuals that died in the ith age class and T_i = the total "exposure" time in the ith age class—the cumulative length of time that all individuals that entered the ith age class, including those that died, survived, or were censored in it, spent in it. For instance, in Amboseli, five females died while they were between eighteen and nineteen years of age (i.e., while they were in the nineteenth age class), and exposure time in the nineteenth age class totaled 4091 female-days (11.2 female-years). Some of this exposure time was contributed by the five females that died during the age class, some by females that survived through it, and some by females that were censored during it. The resulting hazard rate for the nineteenth age class is thus 5/11.2, or 0.4464 (table 4.2).

In the case of the birth-pulse model, it was helpful, but not critical, to calculate survivorship, $l(i)$, but for the birth-flow model, both survival and fertility values depend on estimates of survivorship, the probability of surviving from birth to the ith birthday (Caswell 2001, chap. 2). We estimated survivorship, $l(i)$, as follows:

$$l(i) = (1 - H_i)l(i - 1)$$

Table 4.2 Matrix data for female baboons in Amboseli

A	B	C	D	E	F	G	I	J	K	L	M	N	O	P
Age	Age class	Females that entered the age class	Females that died in the age class	Females born to mothers in age class $= B_i$	Denominator for m_i[a]	$m_i = B_i$/ColF	Exposure time (days)	Hazard[b]	1−Hazard	$l(i)$	Birth-flow survival	Birth-flow fertility	Birth-pulse survival	Birth-pulse fertility
Newborn	(0)									1.0000				
0–1	1	274	59	0	195	0.0000	81536	0.2643	0.7357	0.7357	0.7938	0.0000	0.7357	0.0000
1–2	2	195	22	0	164	0.0000	63146	0.1273	0.8727	0.6421	0.8884	0.0000	0.8727	0.0000
2–3	3	164	14	0	138	0.0000	54577	0.0937	0.9063	0.5819	0.9366	0.0000	0.9063	0.0000
3–4	4	138	4	0	132	0.0000	48684	0.0300	0.9700	0.5645	0.9688	0.0000[c]	0.9700	0.0000
4–5	5	132	4	1	120	0.0083	45106	0.0324	0.9676	0.5462	0.9529	0.1284	0.9676	0.0081
5–6	6	120	7	33	108	0.3056	41033	0.0623	0.9377	0.5121	0.9439	0.2727	0.9377	0.2865
6–7	7	107	5	35	100	0.3500	36843	0.0496	0.9504	0.4868	0.9481	0.2755	0.9504	0.3327
7–8	8	96	5	29	94	0.3085	33539	0.0545	0.9455	0.4603	0.9483	0.2647	0.9455	0.2917
8–9	9	89	4	28	86	0.3256	29906	0.0489	0.9511	0.4378	0.9427	0.2598	0.9511	0.3097
9–10	10	83	5	22	74	0.2973	27636	0.0661	0.9339	0.4088	0.9233	0.2237	0.9339	0.2777
10–11	11	74	6	17	70	0.2429	24900	0.0880	0.9120	0.3729	0.8910	0.1981	0.9120	0.2215
11–12	12	68	8	15	61	0.2459	22135	0.1320	0.8680	0.3236	0.8943	0.2310	0.8680	0.2134
12–13	13	58	4	18	55	0.3273	19402	0.0753	0.9247	0.2993	0.9419	0.2615	0.9247	0.3026
13–14	14	54	2	15	50	0.3000	18469	0.0396	0.9604	0.2874	0.9160	0.2596	0.9604	0.2881
14–15	15	50	6	14	42	0.3333	16819	0.1303	0.8697	0.2500	0.8701	0.2842	0.8697	0.2899
15–16	16	42	5	14	37	0.3784	14113	0.1294	0.8706	0.2176	0.8731	0.3010	0.8706	0.3294
16–17	17	37	4	10	27	0.3704	11785	0.1240	0.8760	0.1907	0.7880	0.2656	0.8760	0.3245

17–18	18	27	7	6	19	0.3158	8181	0.3125	0.6875	0.1311	0.6329	0.2169	0.6875	0.2171
18–19	19	15	5	3	10	0.3000	4091	0.4464	0.5536	0.0726	0.6278	0.2440	0.5536	0.1661
19–20	20	9	2	3	7	0.4286	3066	0.2383	0.7617	0.0553	0.8648	0.1838	0.7617	0.3265
20–21	21	7	0	0	7	0.0000	2562	0.0000	1.0000	0.0553	0.7455	0.2398	1.0000	0.0000
21–22	22	7	3	3	4	0.7500	2153	0.5089	0.4911	0.0271	0.5517	0.3216	0.4911	0.3683
22–23	23	4	1	0	3	0.0000	1124	0.3250	0.6750	0.0183	0.6090	0.1306	0.6750	0.0000
23–24	24	3	1	1	2	0.5000	747	0.4890	0.5110	0.0094	0.4174	0.2144	0.5110	0.2555
24–25	25	2	1	0	1	0.0000	477	0.7657	0.2343	0.0022	0.3796	0.0000	0.2343	0.0000
25–26	26	1	0	0	1	0.0000	365	0.0000	1.0000	0.0022	0.5000	0.0000	1.0000	0.0000
26–27	27	1	0	0		0.0000	193	0.0000	0.0000[c]	0.0000	0.0000[c]	0.0000	0.0000[c]	0.0000

[a]Denominator for m_i = females that gave birth in the age class plus those that survived the age class without giving birth.

[b]Hazard = column D/(column J/365.25).

[c]An asterisk next to the value means the value was forced to zero. In the case of F_4, this was because no wild-feeding female below the 5th age class had ever been observed to become pregnant. In the case of P_{27}, this was because, even though our oldest age class was not the oldest possible, it is both close to it and associated with zero fertility, suggesting that it does not contribute to population growth.

Thus, $l(19) = (1 - H_{19})l(18)$, or $(0.5536)(0.1311) = 0.7256$ (table 4.2). Note that $l(0)$, the survivorship of newborns, is by definition 1.0 (table 4.2).

Survival values, P_i, for birth-flow models (Caswell 2001, chap. 2) can then be estimated as

$$P_i = \frac{l(i) + l(i+1)}{l(i-1) + l(i)}.$$

(For other possible estimates, see Caswell 2001, chap. 2.)

Birth-flow birth rates (m_i) and fertilities (F_i). Recall that the birth rate, m_i, is the average number of offspring produced by a female who *reaches her ith birthday* (Caswell 2001, p. 27), or

$$m_i = \frac{B_i}{N_i},$$

where B_i is the number of births to females in age class i and N_i is the number of females that survived to their ith birthday without giving birth plus the number that gave birth in the ith age class (i.e., on their ith birthday in the hypothetical case presented above). Because females in birth-flow populations do not reproduce on their birthdays, it is less obvious in this case which animals should be included in the denominator.

For the Amboseli birth-flow model, we included four classes of females in the denominator for m_i: (1) females that survived through the ith age class without giving birth in that age class, (2) females that survived through the ith age class and gave birth in that age class, (3) females that gave birth in the ith age class and then died without surviving through the entire age class, and (4) females that gave birth in the ith age class and then were censored before their fate was known (i.e., on 31 December 1999, the last census date we included in the analysis, these females had produced an infant and were still alive in the age class). Females that were censored without giving birth in the ith age class might eventually contribute to the birth rate in that age class, but we deemed it incorrect to include them in the denominator of m_i if they had not yet done so. For instance, in Amboseli, three female offspring were born to females in the nineteenth age class, and ten females either gave birth in that age class or survived childless through it, yielding a value of $m_{19} = 3/10$, or 0.30 (table 4.2).

Fertility in birth-flow models may be estimated as

$$F_i = l(0.5)\left(\frac{m_i + P_i m_{i+1}}{2}\right)$$

(Caswell 2001). This formula reflects the fact that in forming age classes from a continuous age distribution, we have given up all knowledge of age

within each age class. Thus, to account for fertility over the entire projection interval, we must take into account the fact that some reproductive females in age class i will transition to age class $i + 1$ with probability P_i. Further, their offspring may be produced at any time during the projection interval, and must survive for varying lengths of time to be included in the next census; on average, they must survive half the projection interval. Thus, birth-flow fertilities depend on an estimate of $l(0.5)$ as well as estimates of m_i. $l(0.5)$ may be estimated directly from the continuous data or by interpolation from the values of $l(0)$ and $l(1)$ as follows (Caswell 2001, chap. 2):

$$l(0.5) = l(0)\sqrt{l(1)}.$$

We recommend that those interested in employing birth-flow estimates of survival and fertility read Caswell (2001, chap. 2) for a full description of the logic behind them.

Female Baboons in Amboseli Modeled as a Birth-Pulse Population

In order to explore the differences between modeling a continuously breeding population as a birth-pulse population and modeling it as a birth-flow population, we developed a birth-pulse model for the Amboseli females, assuming postbreeding censuses.

Birth-pulse survivals were taken directly from the hazard rate, $P_i = (1 - H_i)$, as described for the hypothetical population in table 4.1. Similarly, we estimated birth-pulse fertility, F_i, as for the hypothetical population in table 4.1, as

$$F_i = P_i m_i.$$

We estimated m_i in the same manner for the birth-pulse model as for the birth-flow model.

Our resulting birth-pulse estimates of survival and fertility for the Amboseli population are presented in table 4.2 for easy comparison with the birth-flow estimates. Birth-flow estimates of vital rates show less variation over age classes, which reflects the fact that they are like moving averages. That is, in the birth-flow model, the vital rates for each age class include contributions from the birth rate and survivorship estimates of previous and successive age classes.

Survival and Fertility for Males

Survival and fertility calculations for male baboons (and males of many mammal species) are less straightforward than those for females. Survival estimates are complicated by the facts that males disperse from their natal group and that some dispersing animals have unknown fates, so that the du-

ration of their lives is uncertain. (In species with female dispersal, this problem will apply to females rather than, or in addition to, males, but the principles are the same.) Fertility estimates are complicated by the difficulty of establishing paternity. Here we present methods for estimating both survival and fertility for males. Using these methods, we constructed a birth-flow model for male baboons in Amboseli so that we could compare its output to that of the female model.

Male survival. In the case of baboon males, we estimated P_i for the predispersal age classes (1–6) in the same manner as for females (table 4.3). We estimated survival after the age of dispersal by examining the age distribution. The age distribution gives exact measures of survival from one age class to the next, assuming (1) that the population produces and receives migrants at the same rates, (2) that if the population includes age-biased groups (such as all-male bands in which old or juvenile males are overrepresented), such groups are included in the census in proportion to their representation in the population, and (3) that the population is at equilibrium and is neither growing nor shrinking. If these assumptions are met, then any drop in numbers from one age class to the next will represent mortality in a stable population. In a growing population, however, the age distribution will underestimate survival. That is, in a growing population, the drop in numbers between age class 1 and age class 2 will reflect not only mortality from age class 1 to 2, but also the fact that the cohort represented by age class 1 was larger to begin with than that represented by age class 2. Before equilibrium is reached, population growth will be reflected in the age distribution at successive time periods as a wave that is moving through the population from younger to older age classes over time. Similarly, in a declining population, the age distribution will overestimate survival.

Our analysis of female baboons suggested that the population in Amboseli was growing. Consequently, when we constructed survival estimates for males based on their age distribution, we adjusted those estimates by examining the relationship between age distribution and survival for females. We reasoned that the female and male populations were growing at the same rate and, because both age distribution and survival were known exactly for females, that the female data would provide us with a measure of the extent to which the age distribution overestimated mortality. In particular, we regressed observed female survival (l_x) on the observed female age distribution and used the slope and intercept of the resulting line as a correction factor for our male survival estimates (fig. 4.6, table 4.3). We did not employ this correction for the oldest age classes (16–20), as both

Table 4.3 Matrix data for male baboons in Amboseli

Age	Age class	Exposure time (days)	Males that died in the age class	Hazard	Survivorship ($l(i)$), based on observed hazard	Survivorship ($l(i)$), based on age distribution	Flow survival for predispersal classes	Flow survival for dispersing classes	Birth rate (m_i)	Flow Fertility
Newborn					1.0000					
0–1	1	62735	47	0.2736	0.7264		0.7825		0.00000	0.0000
1–2	2	49480	19	0.1403	0.6245		0.9122		0.00000	0.0000
2–3	3	40963	3	0.0267	0.6078		0.9337		0.00000	0.0000
3–4	4	34146	10	0.1070	0.5428		0.9167		0.00000	0.0000
4–5	5	32108	5	0.0569	0.5119		0.9588		0.00000	0.0000
5–6	6	29717	2	0.0246	0.4993	0.5217	0.9427		0.00000	0.3734
6–7	7	28170	7	0.0908	0.4540	0.4849		0.9390	0.00000	0.7759
7–8	8					0.4603		0.9416	0.06669	0.7791
8–9	9					0.4297		0.9311	0.57542	0.7663
9–10	10					0.3990		0.9112	0.81552	0.7423
10–11	11					0.3561		0.8944	0.64931	0.7221
11–12	12					0.3193		0.8820	0.81757	0.7074
12–13	13					0.2764		0.8456	0.55429	0.6652
13–14	14					0.2273		0.8295	0.49193	0.6467
14–15	15					0.1906		0.7816	0.30070	0.5950
15–16	16					0.1361		0.6665	0.33257	0.4747
16–17	17					0.0816		0.6251	0.07760	0.4334
17–18	18					0.0544		0.8002	0.06467	0.6252
18–19	19					0.0544		0.7500	0.04850	0.5859
19–20	20					0.0272		0.3333	0.07760	0.2131
20–21	21					0.0000		0.0000	0.00000	0.0000

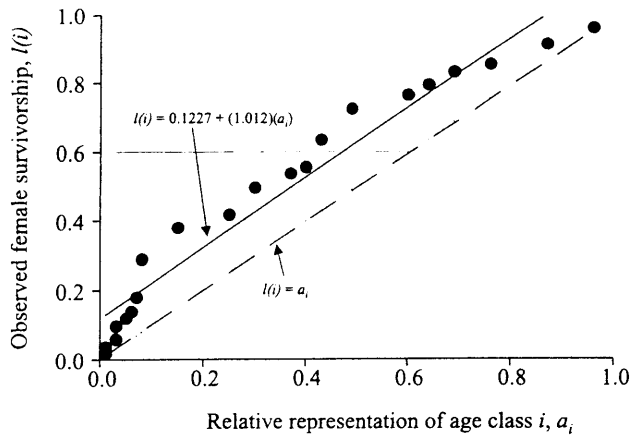


FIG. 4.6. Relationship between survivorship, $l(i)$, and age distribution, a_i, for wild-foraging female baboons in Amboseli. The x-axis represents the relative age distribution, normalized to 1.0 for age class 1. In the ideal case of an equilibrium population with $\lambda = 1$, $l(i) = a_i$ (dashed line). In Amboseli, the observed relationship between $l(i)$ and a_i (represented by the solid circles) is described by the solid line $l(i) = 0.1227 + (1.012)(a_i)$.

sample sizes and survival in those age classes were low for both males and females; thus, this detailed correction was unlikely to improve those estimates very much.

This procedure for estimating survival may be employed for either age-based or stage-based models as long as animals progress from one class to the next sequentially (e.g., the method would not work for red-cockaded woodpeckers, where animals in a given class may move to or come from a number of other classes). In either case, accurate assignment to age or stage classes is critical. In the case of Amboseli males, our sample included 218 natal males with known birth dates. Of 114 immigrant males, 78 were assigned ages based on an estimation process developed for the Amboseli population (see Alberts and Altmann 1995 for details); 36 males with unassigned ages were excluded from the analysis.

Male birth rates. For males, some approximation to birth rate must be identified. Among Amboseli males, behavioral observations of mate guarding (consortships) correspond well to genetic paternity assignments (Altmann et al. 1996). Therefore, we used observational measures of mating success to approximate birth rates. We measured the proportion of available female consort hours obtained by males of each age class, then distributed live

births of male newborns (n = 194) across those age classes accordingly. Birth rates, m_i, were then calculated as the number of live male births per age class divided by the total number of male-years per age class (table 4.3). Fertility, F_i, was calculated from P_i and m_i as a birth-flow estimate, in the manner described for females.

Model Output

Here we focus on a subset of four results yielded by matrix models (see Caswell 2001 for a complete discussion). These results were all obtained from fairly straightforward manipulations of the matrix, which can be accomplished using computational programs such as Mathematica (Shuchat and Shultz 2000), Maple (Kamerich 1999), or Matlab (Pratap 1998). In appendix 4.2 we present a Matlab program that calculates these parameters.

Population Growth Rate

Population growth rate, λ, is the dominant eigenvalue of the demographic matrix (see Caswell 2001, appendix A, for a clear description of eigenvalues and eigenvectors). It is a direct measure of the rate at which the population is growing or shrinking, given the set of vital rates used in the model. Hence it is important for assessing any population deemed in need of management, and it is a key result for estimating the viability of threatened or endangered populations. λ also represents the mean fitness of a population (Lande 1982a; McDonald and Caswell 1993; Caswell 2001), and as such is the means by which alternative phenotypes (alternative sets of vital rates) are judged vis-à-vis the likelihood that they will spread in the population once introduced (for an excellent comparison of various measures of population increase and fitness, including λ, see Stearns 1992, chap. 2).

Values of λ for the hypothetical population shown in table 4.1, as well as for the birth-flow and birth-pulse models for Amboseli, are shown in table 4.4. As noted earlier, separate models for males and females in a population should yield roughly equivalent values of λ unless one sex is increasing in frequency relative to the other. In the case of the wild-foraging Amboseli baboons, the female model yields λ = 1.039 and the male model yields λ = 1.036; therefore, the population is growing. The two models produce remarkably close estimates of λ given the challenges associated with estimating male fertility and survival.

Stable Age Distribution

A striking property of most populations is that if age- or stage-specific mortality and fertility schedules are constant from one generation to the next, each population will converge on its own characteristic and unchanging age

Table 4.4 Values of λ for the models presented in this chapter

Model[a]	λ
Hypothetical birth-pulse monkeys	0.914
Amboseli baboon females, birth-flow	1.039
Amboseli baboon females, birth-pulse	1.034
Amboseli baboon males, birth-flow	1.036

[a]Amboseli baboon models are for wild-foraging animals only.

(or stage) distribution (Stearns 1992, chap. 2; Charlesworth 1994, chap. 1). This stable age distribution is described by the right dominant eigenvector of the matrix (Caswell 2001, appendix A) and is a direct consequence of the population's vital rates. The population will converge on a stable age distribution regardless of its initial age distribution and regardless of its value of λ. The meaning of a stable age distribution is that the proportional representation of age classes remains the same as the population grows or shrinks. In most natural populations, both stochastic and deterministic processes result in vital rates changing over time, so that populations rarely if ever reach stable age distributions. Nonetheless, populations that experience relative stability will converge on a stable age distribution.

The Amboseli baboon population exhibits a sex difference in its stable age distributions (fig. 4.7), such that a larger proportion of males are in the younger age classes, and a smaller proportion in the older ones, than is the case for females. This difference reflects the generally higher mortality rates of males as compared with females, a typical pattern for many primates and, indeed, for many animals, including humans (Shapiro, Schlesinger, and Nesbitt 1968), red deer (Clutton-Brock, Albon, and Guinness 1988), lions (Packer et al. 1988), and Belding's ground squirrels (Sherman and Morton 1984; see also discussions in Clutton-Brock, Albon, and Guinness 1985; Trivers 1985, chap. 12).

The sex difference in age distributions for the Amboseli baboons has some potentially interesting behavioral implications. At any one time, juvenile and infant males will have fewer adult role models than will juvenile females (35% of males are adults, 53% of females are adults). However, because secondary dispersal results in frequent changes in the identities of the adult males in a group, young males may over time have a larger set of role models, as well as ones that come from more diverse backgrounds, than females do (see Pereira 1988b for a discussion of the importance of same-sex role models in the development of sex-typical behavior in nonhuman primates). Differences in age cohort sizes within each sex also have implica-

FIG. 4.7. Stable age distributions for wild-foraging female and male baboons in Amboseli.

tions for behavior. For instance, the fact that each cohort shrinks as it ages means that in species such as baboons, in which age cohorts are likely to be paternal sibships (Altmann 1979; Altmann et al. 1996; Smith 2000), older females will have fewer paternal relatives with which to interact than younger females. The consequences of this difference for decisions involving agonistic support, grooming, and patterns of social group fission are just beginning to be explored (Smith 2000).

Reproductive Value

At any given time, the individuals in a population differ in the extent to which they will contribute to future population growth. Their expected contribution depends on the age or stage class they currently occupy, their expected changes in fertility as they move between classes, and on the probability that they will survive to reproduce again. This class-dependent expected contribution to future generations is known as reproductive value, a concept first developed by R. A. Fisher (1930; see also Stearns 1992, chap. 2; Charlesworth 1994, chap. 1; Caswell 2001, chap. 4), and is defined by the left dominant eigenvector of the demographic matrix (see Caswell 2001, appendix A). Reproductive value is usually scaled to the value of the first class (so that the reproductive value of the first class is 1). With each successive interval that a young animal survives, its likelihood of reproducing increases; hence its reproductive value typically increases steadily from birth until near the age of first reproduction. Its reproductive value then drops because the expected number of future young declines as the animal ages. The rate at which reproductive value declines reflects the rates of adult mortality and reproductive senescence, a finding that helps to develop our intuition that selection events occurring late in life have relatively little effect on overall fitness (see fig. 4.8 for reproductive values for Amboseli baboons).

In primate studies, reproductive value has figured prominently in mod-

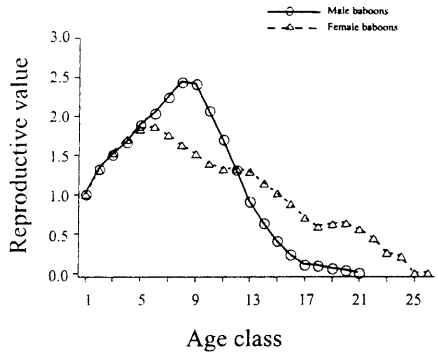


FIG. 4.8. Reproductive values for wild-foraging female and male baboons in Amboseli.

els of, and debates about, the evolution of dominance patterns within matrilines (e.g., Hrdy and Hrdy 1976; Chapais and Schulman 1980; Schulman and Chapais 1980; Horrocks and Hunte 1983). The general argument has been that the reproductive value of each female in the family will have consequences for the relative rank that her kin "allow" her to occupy, because of her effects of their inclusive fitness. Thus, for instance, Schulman and Chapais (1980) propose that when rank is contested between sisters, mothers will support the daughter with the highest reproductive value (see also the critique of this model by Horrocks and Hunte 1983). Recent work with the Amboseli baboons (Combes and Altmann 2001) supports a reproductive value model for the pattern of rank reversal between mothers and daughters. Reproductive value has other potential implications for the evolution of behavior (see, e.g., discussion and cautions in Charlesworth 1994, chap. 5, pp. 237–239).

Perturbation Analysis: Sensitivities, Elasticities, and Other Simulated Life History Changes

One of the most powerful and useful applications of the matrix model is perturbation analysis. Each vital rate in a matrix model has a characteristic sensitivity, which is an estimate of the extent to which λ changes as that vital rate undergoes small changes (and while other vital rates are held constant) (fig. 4.9).

The sensitivity of a matrix element, s_{ij}, is defined as

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}}.$$

Thus, a vital rate with a high fitness sensitivity is one for which changes result in a relatively large change in λ. The changes are measured from an initial starting value for that vital rate, which is the specific mean value a_{ij} in the

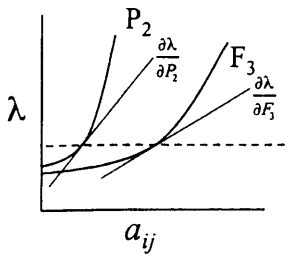


FIG. 4.9. Two vital rates from Figure 4.1 and their hypothetical effect on λ. λ_0 (denoted by the dotted line) is the observed λ in the population. Sensitivities are defined by the slope of the lines tangent to the curves at λ_0. Note that in neither case is the relationship between a and λ linear; in general, there is no reason to expect it to be so.

matrix; a different mean value, derived from a different population or from different time periods for the same population, could have a different sensitivity if the effects on λ of one or more vital rates are not constant throughout the range of that vital rate.

Sensitivity can be calculated as

$$s_{ij} = \frac{v_i w_j}{\sum_{i=1}^{\infty} v_i w_i},$$

where v_i is the reproductive value of class i and w_i is the proportional representation of class i in the population. Note that the calculation of sensitivity is based on changes in fitness in response to infinitesimally small, absolute changes in a_{ij} that are unspecified in magnitude. Sensitivities answer the question, if we perturb each matrix element by some small amount, what is the consequent change in λ? In other words, what is the slope of each relationship between λ and a_{ij}? We cannot extrapolate from the sensitivity analysis to predict the effect of large changes in a_{ij} unless we assume that the relationship between λ and a_{ij} is (at least locally) linear.

A related, alternative measure of the effect on λ of matrix perturbations is elasticity. Elasticities are standardized sensitivities that measure the effects of proportional changes in vital rates. That is, elasticities report the effect of perturbations that are all of the same relative (and not absolute) magnitude. Elasticities answer the question, if we perturb each matrix element by the same relative amount (e.g., 0.05%), what are the consequent changes in λ? Elasticities, e_{ij}, are defined and calculated as

$$e_{ij} = \frac{\partial \ln(\lambda)}{\partial \ln(a_{ij})} = \frac{a_{ij} s_{ij}}{\lambda}.$$

The elasticities of a projection matrix sum to 1 over the entire matrix and can be thought of as the relative contributions of each element a_{ij} to λ. An important difference between sensitivities and elasticities is that matrix elements for which $a_{ij} = 0$ (such as the fertility of the newborn age class) can

have nonzero sensitivities, but all matrix elements for which $a_{ij} = 0$ will have $e_{ij} = 0$.

Perturbation analyses for wild-foraging female and male baboons in Amboseli indicated that λ is much more sensitive to changes in survival than to changes in fertility; fertility represents just 9% of the total elasticity in the life history for both males and females (fig. 4.10). Prereproductive survival, in contrast, represents 37% of the total elasticity in the female matrix and 62% of the total elasticity in the male matrix. This difference between males and females results entirely from the difference in age at first reproduction; elasticity values for survival in each of the first four age classes are nearly identical for the two sexes. In comparing a range of social vertebrates, McDonald (1993) showed that survival commonly shows higher elasticity than does fertility, particularly in long-lived species. McDonald also discussed the significance of sex differences in elasticity patterns, noting that such differences may be the consequence of sexual selection and thus may amount to sexually selected characteristics.

Perturbation analysis may also involve direct manipulation of matrix entries. The advantage of direct manipulation is that one is not confined to the infinitesimal changes described by the partial derivatives. For instance,

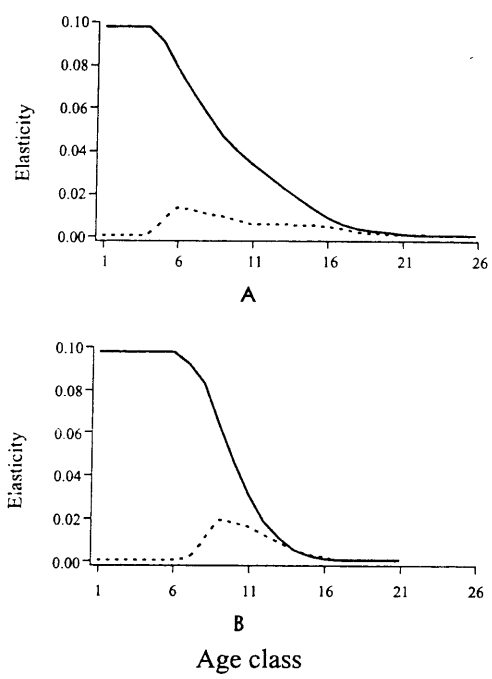


FIG. 4.10. Elasticity in survival (solid line) and in fertility (dashed line) as a function of age class for *(A)* female baboons and *(B)* male baboons in Amboseli.

if a species such as the savanna baboon experiences infant survival values in natural habitats that range from 0.5 to 0.9, elasticity analysis alone will not capture the consequences of this range of values. Instead, matrix entries for the infant age class can be directly manipulated so that the effect of the whole natural range of infant survival on λ can be examined. Mills, Doak, and Wisdom (1999) used this method of manual changes in matrix entries in a very useful discussion of the assumptions and limitations of elasticity analysis.

Perturbation analysis is increasingly being used to assess management strategies for threatened populations. Heppell, Crowder, and Crouse (1996) evaluated the practice of "head-starting" young turtles, in which hatchlings are reared in captivity and then released after the age of high mortality in the wild. The authors concluded that survival elasticity is much lower for hatchlings than for adults, so that headstarting is of little or no value without efforts to increase adult survival as well. Crooks, Sanjayan, and Doak (1998) reached a similar conclusion for cheetahs, in which high cub mortality has been cited as a major factor limiting wild populations. In contrast to the analyses for these threatened populations, our elasticity analyses of the Amboseli baboon models indicated that throughout the range of survival values seen in natural populations, juvenile survival has a much greater effect on λ than either adult survival or fertility (fig. 4.10) (S. C. Alberts and J. Altmann, unpub.). Moreover, this is the case whether we consider starting rates that would result in a declining ($\lambda < 1.00$), stationary ($\lambda = 1.00$), or increasing ($\lambda > 1.00$) population.

Whether a vital rate changes in response to an ecological change, or in response to selection, will depend on the potential plasticity of that vital rate for a given species. From an evolutionary point of view, the great utility and appeal of elasticity is that it provides a measure of the relative strength of selection on vital rates (McDonald and Caswell 1993; Benton and Grant 1999). Whether a given vital rate responds to selection will depend, of course, on the presence of additive genetic variance for the vital rate and on genetic covariance between rates. Elasticities alone will not predict the response to selection, but will estimate the strength of selection on various rates.

Limitations of the Model

In spite of their power and utility, matrix models contain several important assumptions and limitations. Two key assumptions are density independence and time invariance of vital rates. Many populations violate these assumptions. However, methods are available for modifying the models to

relax these assumptions or to test the robustness of population projections when these assumptions are violated (e.g., van Groenendael, de Kroon, and Caswell 1988; Benton, Grant, and Clutton-Brock 1995; Benton and Grant 1996, 1999; Grant and Benton 2000; Wisdom, Mills, and Doak 2000). For instance, Benton and Grant (1996, 1999) report that while elasticity analysis is fairly robust to the assumption of time invariance in some circumstances, this is not usually true for short-lived organisms or when variance in vital rates is very high. Wisdom, Mills, and Doak (2000) have developed a probability-based resampling method that addresses this problem by incorporating variance in vital rates into estimates of elasticities (Benton and Grant 1999; Wisdom, Mills, and Doak 2000).

An increasingly common method of exploring the effect of variance in vital rates is the use of stochastic models, which investigate the effects of environmental variance, demographic variance, or both (Armbruster and Lande 1993; Gross et al. 1998; Kendall 1998). Stochastic models may reveal rather different population dynamics than deterministic models of the sort explored here. They are important tools where variable environments result in widely varying vital rates or where populations are small, so that demographic stochasticity becomes an issue in population dynamics (Caswell 2001).

Another important limitation of matrix models is that they do not generally incorporate covariance among vital rates; sensitivities and elasticities are explicitly calculated as partial derivatives of single matrix elements, holding all other elements constant. Empirical data have shown, however, that covariance among life history traits exists (e.g., Stearns 1989b; Benton, Grant, and Clutton-Brock 1995). In primates, for example, infant survival sometimes affects the mother's future reproduction (e.g., Altmann, Altmann, and Hausfater 1978 for baboons; Tanaka, Tokuda, and Kotera 1970 for macaques), and reproduction may increase maternal mortality (e.g., Altmann 1980 for baboons; Westendorp and Kirkwood 1998 for humans). Van Tienderen (1995) provides an excellent introduction to the use of integrated sensitivities, which incorporate covariance among vital rates in the calculation of sensitivities. They are calculated as the ordinary (not partial) derivatives of λ on a matrix entry, as follows:

$$\frac{d\lambda}{da_i} = \frac{\partial\lambda}{\partial a_i} + \sum_{j \neq i} \frac{\partial\lambda}{\partial a_j} \frac{\partial a_j}{\partial a_i}$$

Van Tienderen discusses the problems of estimating covariances among matrix entries and provides examples of such covariances and of integrated sensitivities using both animal and plant taxa.

An additional caution in interpreting elasticities is that, because they are measures of how λ changes with infinitesimal changes in a vital rate, they may not accurately predict the consequences of large perturbations in vital rates (Benton and Grant 1999; Mills, Doak, and Wisdom 1999), such as might occur with a major environmental change or the introduction of human-associated food enhancement. This issue is of particular importance when environments are highly variable, so that vital rates change greatly from one generation to the next, or when management techniques for threatened populations are likely to result in large changes in vital rates. Mills, Doak, and Wisdom (1999) show that large perturbations may actually cause changes in λ that are of the opposite sign from those predicted by elasticities, particularly when several rates are simultaneously changed by different amounts. They caution that manual perturbations of the matrix (in which matrix elements are modified directly and λ sensitivities are recalculated) are an important supplement to standard sensitivity analysis.

Summary and Conclusions: Why Employ a Matrix Model?

There is wide general consensus that matrix models are the best approach to understanding population dynamics, and this makes them the method of choice for researchers working on endangered, threatened, or rare species or species that require management of any sort. However, other methods are available for examining selection on life history components (Arnold and Wade 1984a,b; Brown 1988). Matrix models have some advantages over these methods, as well as some limitations. (The methods of Arnold and Wade and Brown also have advantages and disadvantages relative to each other that will not be discussed here; the reader is referred to Brown 1988 for this discussion.)

First, for researchers working on primates or any other long-lived species, the multivariate methods of Arnold and Wade and Brown for estimating fitness and the strength of selection require extensive longitudinal data on individuals. Matrix methods can certainly utilize such detailed long-term data, but they require at a minimum careful, repeated yearly census data over some period of time, with individuals in the census accurately assigned to age classes. Indeed, in some circumstances, matrix methods do not require identification and tracking of individuals from year to year. If individuals can be accurately assigned to age classes so that age structure and age-specific fertility can be estimated, then cross-sectional data without individual identification is sufficient to construct a matrix model. The difficulty here is that without some information on known individuals, mortality can be estimated only by examining the age distribution, which may over- or

underestimate survival and thus inflate or deflate λ respectively. Moreover, one will not generally be able to analyze covariance among traits in the absence of information on individuals.

Second, the formal structure of matrix models makes it difficult to overlook any parameters; the survival and fertility of each recognized age or stage must be included. This is not true of the multivariate methods, in which the researcher chooses a set of fitness components presumed to encompass total fitness. For instance, in the male bullfrog example developed by Arnold and Wade (1984b), total fitness is calculated as the product of number of mates, zygotes per mate, and hatchlings per zygote. Survival from hatchling to adult and adult survival are missing as components of fitness. Thus, the structure of the model is determined by the researcher's a priori beliefs about which phases of the life cycle are important. Such assumptions will limit the capacity of the model to capture important life history variance and may result in misestimations of the strength of selection. For instance, in their male bullfrog example, Arnold and Wade demonstrate strong selection for large body size, but this finding is difficult to interpret without knowing whether large size also affects adult survival, which is excluded from the model.

Age-specific changes in fertility and survival are also largely ignored by the multivariate methods. Brown's approach, in particular, designed to overcome the limitations of the Arnold and Wade approach (Brown 1988), explicitly averages fitness components over the entire life span and disregards changes with age. The Arnold and Wade approach can incorporate age-specific changes by separating the fertility component of fitness into several age-specific fertilities, but this is not built into the approach, and again depends on whether the researcher decides a priori that such changes may be important. Matrix models, by forcing us to examine the entire life cycle and to explicate age-specific changes in survival and fertility, draw our attention to age-specific changes in fitness, which theory indicates are of great importance in the evolution of life histories (Roff 1992; Stearns 1992; Charlesworth 1994).

Matrix models also make it relatively easy to examine the effect of variation that is not directly observed in the study population. The multivariate methods are confined to the variation directly observed in the study population, while matrix methods allow researchers to explore the entire range of variation in life history parameters seen in the species through perturbation analysis. Thus, while both methods identify selection pressures, matrix methods allow more explicit analysis of the effect on fitness of varying life history parameters.

Matrix models also have significant limitations, some of which are described above. An important limitation not yet mentioned is that matrix models in themselves provide no clues about which phenotypic traits influence vital rates. Thus, a matrix model that paralleled the analysis of male bullfrogs developed by Arnold and Wade (1984b) would identify the phases of the life cycle under the strongest selection pressure (for example, adult fertility or zygote survival), but would not estimate the effects of male body size on these critical life cycle phases, or even identify male body size as an important trait. Similarly, perturbation analysis of the baboon matrix model indicates that infant and juvenile survival are under strong selection, but does not identify factors that contribute to variance in infant and juvenile survival.

However, matrix methods are excellent guides for subsequent analyses of sources of variance in fitness. Analyses of the sort exemplified in Pereira and Leigh (chap. 7), Godfrey et al. (chap. 8), and Ganzhorn et al. (chap. 6; all this volume), which describe detailed examinations of the causes and consequences of variation in particular life history stages, would be especially powerful if informed by a matrix analysis that identified critical stages of the life history. Another approach would be to follow a matrix analysis with a path analysis or multiple regression. Van Tienderen (2000) proposes a hierarchical method that incorporates matrix models and elasticity analysis with multivariate selection analysis of important phenotypic traits. He also provides an excellent discussion and comparison of the parameters used in multivariate models versus those used in matrix models (van Tienderen 2000). The two approaches are complementary and together offer a richness and completeness that is not possible with either alone.

Matrix models have multiple applications that make them flexible and useful tools for asking both evolutionary and ecological questions. They can provide insights into management strategies for threatened populations, identify life history parameters that are under selection within a given species, or even facilitate interspecific comparisons that may shed light on longstanding problems in life history theory. Their formal structure ensures that all life history stages of the animal are included in the analysis, so that they help to develop and correct our intuition about the biology of our study animals. The limitations of matrix models are increasingly being resolved, so that density dependence, variability over time, and covariance among life history parameters can be incorporated into the models. Especially in combination with other, more traditional techniques for identifying the importance of phenotypic variance, they provide an outstanding tool for primate life history analysis.

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Appendix 4.1

Reproductive Rate Terminology

The terms "fecundity" and "fertility" are used in a variety of ways in the literature. When developing a model and researching existing models, it is important to identify the meaning that each author attributes to these terms, rather than simply assuming a standard usage. For instance, the term "fecundity" is used to describe the top row matrix elements (F_i) by some authors (e.g., van Groenendael, de Kroon, and Caswell 1988; Heppell, Walters, and Crowder 1994; Pfister 1998), while others use the term "fertility" for F_i (e.g., McDonald 1993; Crooks, Sanjayan, and Doak 1998). Following Jenkins (1988), McDonald and Caswell (1993), and Caswell (2001), we have used the term "fertility" to indicate the values (F_i) in the top row of the projection matrix: the expected number of newborns that will have been produced by time ($t + 1$) per individual in age class i at time t. In this terminology, "fertility" refers to the realized reproductive rate (m_iP_i), while "fecundity" refers either to the unrealized maximum potential reproductive output (Caswell 2001, chap. 2) or to the uncorrected birth function, m_i (Jenkins 1988).

Similarly, various terms have been used to denote m_i. We have used the term "birth rate," but others may use the terms "natality" (e.g., Sade et al. 1976), "fertility rate" (e.g., McDonald and Caswell 1993), or "fecundity" (e.g., Jenkins 1988). Again, rather than assuming a standard usage, the meaning implied by the author must be identified.

Appendix 4.2

Matlab Program for Calculating Eigenvectors and Eigenvalues

This program employs a birth-pulse model to find the stable population growth rate (λ), stable age distribution, age-specific reproductive values, and various elasticity and sensitivity values for an age-structured population based on survival and fecundity values. This program was written in Matlab version 5.3.

STEP 1: Create a Leslie matrix with survival and fecundity values. First we create two vectors, ***P*** (which contains survival values) and ***F*** (which contains fecundity values). To do so, age-specific survival and birth rate values should be plugged into the vectors below, with values separated by commas.

Insert age-specific survival values, separated by commas, between brackets in command.

```
P=[ ];
```

Insert age-specific birth rates, separated by commas, between brackets in command.

```
B=[ ];
F=B.*P;
```

The survival and fecundity values are then plugged into the appropriate slots in an $(n*n)$ zero matrix to create the Leslie matrix, **M.** That is, the $n - 1$ entries in the survival vector are plugged into the subdiagonal, and the n entries in the fecundity vector are plugged into the first row.

```
dimensions=size(F);
n=dimensions(2);
M(n,n)=0;
for r=[2:n]
   M(r,r-1)=P(r-1);
end
for c=[1:n]
   M(1,c)=F(c);
end
```

The Leslie matrix is then displayed.

```
fprintf('Leslie Matrix:') M
```

STEP 2: Find the dominant and largest subdominant eigenvalues and calculate the damping ratio.

First we create a matrix, **Right_Eigenvectors,** of the right eigenvectors of **M** and a diagonal matrix, **Values,** of the eigenvalues of **M.** From **Values** we then create a vector **Eigenvalues,** which lists the eigenvalues of **M.**

```
[Right_Eigenvectors,Values] = eig(M);
Eigenvalues=eig(M);
```

The dominant eigenvalue, lambda, is then found and printed by selecting the maximum value from **Eigenvalues.** Note that the dominant eigenvalue of a Leslie matrix will always be both positive and real.

```
fprintf('Dominant Eigenvalue:')
lambda=max(Eigenvalues)
```

Next, a vector **Magnitudes** is created that lists the absolute values of each of the eigenvalues. The entry occupied by the dominant eigenvalue is then set to zero.

```
Magnitudes = abs(Eigenvalues);
for j=[1:n]
   if Magnitudes(j)==lambda
      dominant=j;
      Magnitudes(j)=0;
   end
end
```

The magnitude of the largest subdominant eigenvalue, abs_lambda2, is then extracted from **Magnitudes.**

```
fprintf('Magnitude of Largest Subdominant Eigenvalue:')
abs_lambda2=max(Magnitudes)
```

STEP 3: Find the stable age distribution. First the right dominant eigenvector, **RDE,** is extracted from **Right_Eigenvectors,** and the sum of its entries, sadnormalizer, is calculated in order to normalize the stable age distribution.

```
for j=[1:n]
   RDE(j)=Right_Eigenvectors(j,dominant);
end
sadnormalizer=sum(RDE);
```

Then the normalized stable age distribution is calculated from **RDE** and sadnormalizer.

```
Stable_Age_Distribution=RDE/sadnormalizer
```

STEP 4: Find the age-specific reproductive values. First, we create a matrix, **Left_Eigenvectors,** of left eigenvectors. (For an explanation of the methodology used, see Caswell 2001, pp. 92–94.)

```
Left_Eigenvectors=conj(inv(Right_Eigenvectors))';
```

We then extract the left dominant eigenvector, **LDE,** from **Left_Eigenvectors.** We also extract the reproductive value of the first age class, rv1, from **LDE** in order to scale the reproductive values.

```
for j=[1:n]
   LDE(j)=Left_Eigenvectors(j,dominant);
end
rv1=LDE(1);
```

The reproductive values are then scaled to the reproductive value of the first age class, yielding the vector **Reproductive_Values,** which lists the relative reproductive values for each age class.

```
Reproductive_Values=real(LDE/rv1)
```

STEP 5: Calculate sensitivities for all entries of **M.** The sensitivity of a Leslie matrix entry a_{ij} is the partial derivative of the population growth rate, λ, with respect to a_{ij}. (For further details, see Caswell 2001, pp. 206–211.)

```
Sensitivities(n,n)=0;
for i=[1:n]
   for j=[1:n]
Sensitivities(i,j)=((Reproductive_Values(i)*Stable_Age_Distribution(j))/
sum(Stable_Age_Distribution.*Reproductive_Values));
   end
end
```

```
fprintf('Dominant Eigenvalue')
Sensitivities
```

STEP 6: Calculate elasticities for all entries of **M.** The elasticity of a Leslie matrix entry a_{ij} is a scaled sensitivity value, giving the proportional change in the population growth rate, λ, that results from a proportional change in a_{ij}. (For further details, see Caswell 2001, p. 132.)

```
Elasticities(n,n)=0;
for i=[1:n]
   for j=[1:n]
      Elasticities(i,j)=((M(i,j)*Sensitivities(i,j))/lambda);
   end
end
fprintf('Dominant Eigenvalue')
Elasticities
```