CHAPTER 3

MATRIX METHODS FOR AVIAN DEMOGRAPHY

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1. INTRODUCTION

Demography is a tool for understanding population-level dynamics in terms of events (birth, death, maturation, etc.) at the level of the individual. Demographic models are a critical component of theory in population genetics, life history evolution, mating systems, and population biology. Demography is of fundamental concern to conservation biology; the demographic rather than genetic consequences of rarity may be the imminent threat to species facing rapid habitat destruction in many parts of the world (Lande, 1988b).

Population studies of birds have a long history. Demographic methods for such studies were last reviewed by Ricklefs (1973). That review focused on methods derived from classical age-structured demography, using the life table as the framework for analysis. (We will refer to the combination of survivorship (l_x) and maternity (m_x) functions as an "$l_x m_x$ table"). Most avian demographic studies have used these methods, or simplifications that take advantage of particular aspects of avian life cycles (e.g., Mertz, 1971).

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In the nearly two decades since Ricklefs' review, matrix population models have been developed into a powerful general framework for demographic analysis. They subsume classical life table analysis as a special case but have capabilities that go far beyond that analysis:

1. They are not limited to classifying individuals by age. Instead, they can accommodate classifications by stages that describe social status, spatial location, developmental stage, habitat quality, or other variables of biological interest.

2. They lead easily to sensitivity analysis, which pinpoints the most ecologically and evolutionarily important portions of the life history. The core of ecology and evolutionary biology lies in understanding the growth rates of lineages and populations (demography) and building links to the genetic consequences and constraints (population genetics). Sensitivity analysis links these cornerstones by means of its direct correspondence to the selection gradients of quantitative genetics. Further, sensitivity analysis provides an objective basis upon which to allocate field effort. For example, if either adult survival or offspring production, but not both, could be measured with high accuracy and precision, sensitivity analysis could guide the balance of investment, ensuring the most accurate possible estimate of population parameters such as the growth rate.

3. They can be constructed using the life cycle graph, an intuitively appealing graphical description of the life cycle, which helps to assure correct parameterization of the model and provides a mechanism for evaluating alternative life histories.

4. They are easily extended to include stochastic variation and density-dependent nonlinearities, forming the basis of complex simulation models, if desired.

Matrix models were initially developed by Leslie (1945, 1948). They have been thoroughly reviewed in Caswell (1989b); this paper is based largely on, and intended as an introduction to, Caswell's book. Stochastic versions of the models are lucidly summarized by Tuljapurkar (1990). Harvesting strategies in nonlinear matrix models are analyzed by Getz and Haight (1989).

To nonmathematicians, much of the practice of demography may appear daunting. The field is littered with double integrals, strange notation, and seemingly impenetrable thickets of equations. As with much theory, confusion in demographic analysis has often resulted from differences in assumptions and from confusion over notation. As an aid and reference guide, therefore, a glossary is given as an appendix. Italic font

will highlight early occurrences in the text of terms listed in the glossary. We will compare and contrast our approach with other treatments that use very different techniques. Examples from well-known published studies will illustrate formal equivalences among difference equations, *projection matrices*, and *life cycle graphs* (Fig. 1). As we hope to show, the translation from field observations to sophisticated analysis is both easier and more intuitive with matrix methods and life cycle graphs than with previous techniques. In our final section we provide a case study.

a

$$n_1(t+1) = F_1 n_1(t) + F_2 n_2(t) + F_3 n_3(t) + 0$$

$$n_2(t+1) = P_1 n_1(t)$$

$$n_3(t+1) = P_2 n_2(t)$$

$$n_4(t+1) = P_3 n_3(t)$$

b

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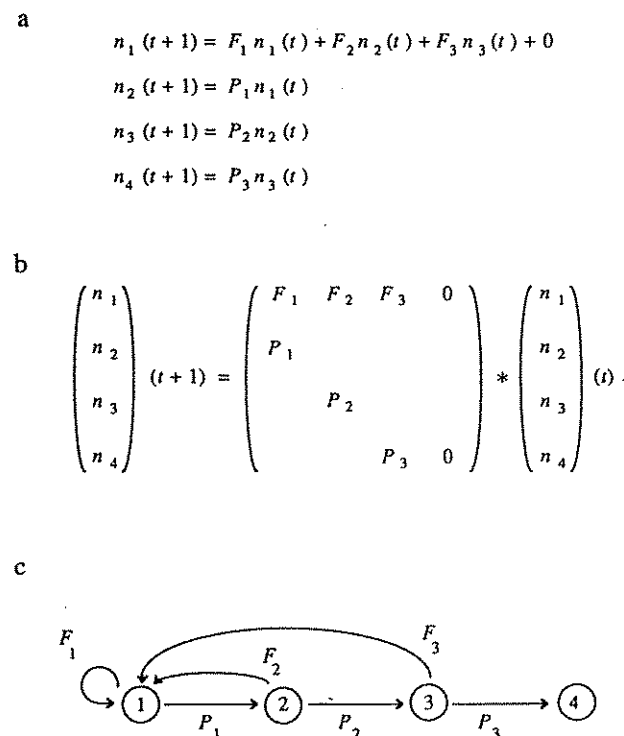
c

FIGURE 1. Equivalent formulations for a simple age-classified life cycle. (a) Difference equations (Section 2.1.1). (b) Leslie matrix and census vector (Section 2.1.2). The first element of the vector is equivalent to the n_1 of the equations. (c) Life cycle graph (Section 2.1.3). Node 1 represents first-year birds, the n_1 of the equations. Coefficients on the arcs represent survival, P_i, or fertility, F_i, and are equivalent to the elements, a_{ij}, in the ith row and j^{th} column of the matrix. All the arcs that point back to Node 1 represent fertility transitions, and comprise terms related both to number of offspring produced and to survival of either the parents or offspring.

2. SETTING UP MATRIX-BASED MODELS

In matrix-based models, individuals are classified into discrete stages or age classes. Although stages such as "breeder" or "floater" pose no intuitive problem, discrete age classes can prove confusing when one is used to dealing with age as a continuous variable. The subscript x in an $l_x m_x$ life table begins at 0, and represents continuous calendar age. In discrete, matrix-based approaches the subscript i begins at 1 and represents the stage (or age class). Figure 2 shows the relationship between continuous age and discrete age classes. Using discrete age classes will require taking special care with organisms that exhibit *birth-pulse* reproduction that peaks during a predictable breeding season. Birth-pulse reproduction on an annual interval is characteristic of most birds. It is distinguished from *birth-flow* reproduction, in which reproduction can occur at any time of the year, with no detectable peak, as in humans.

In this section, we begin by formulating difference equations that describe population growth (Section 2.1.1) for a simple age-classified life cycle. We then show how the equations can be arranged in matrix format (Section 2.1.2) and as a life cycle graph (Section 2.1.3). Next (Section 2.2), we discuss the *projection interval* and the effects of timing of census on the projection techniques before reviewing the assumptions (Section 2.3). We then (Section 2.4) demonstrate the calculation of the *fertility*, F_i, and survival, P_i, coefficients from the $l_x m_x$ table and provide a worked example of the dependence of the coefficients on the timing of the census. Finally (Section 2.4.4) we introduce stage-structured transitions.

2.1. Population Projection

2.1.1. The Difference Equation Formulation

One can generate a series of equations that will predict the population size at time $t + 1$ from that at time t. These equations will provide a projection from present to future populations sizes. We will treat the case in
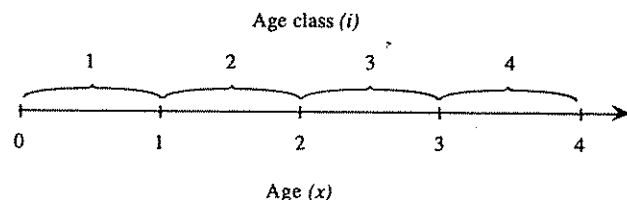

FIGURE 2. The relation between the continuous variable x, used in the life table functions m_x and l_x, and the discrete variable i, used in matrix-based parameters such as P_i and F_i.

which individuals can be classified in discrete age classes, where $n_i(t)$ denotes the abundance of age class i at time t. Individuals in the first age class are the offspring produced during the interval from t to $t + 1$. We can write

$$n_1(t + 1) = F_1 n_1(t) + F_2 n_2(t) + \ldots, \tag{1}$$

where the *fertility* coefficients F_i give the number of individuals in age class 1 at time $t + 1$ per individual in age class i at time t. We will use the term *fertility* to refer to realized production of offspring, in contrast to *fecundity*, which represents potential production. As we will see in Section 2.2.4, the F_i comprise terms not only for production of offspring, but also for the survival of adults to produce those offspring and the survival of the offspring to appear in the population at time $t + 1$. The abundance of individuals in the other age classes depends upon survival,

$$n_i(t + 1) = P_{i-1} n_{i-1}(t) \qquad \text{for } i = 2, 3, \ldots \omega, \tag{2}$$

where P_{i-1} is the survival probability of members of age class $i - 1$ and ω is the number of age classes. The full set of equations for a simple life cycle with four age classes is shown in Figure 1a, in which we make the simplifying assumption that all individuals die on their fourth birthday.

2.1.2. The Matrix Formulation

The projection equations of Figure 1a can be organized in matrix form as in Figure 1b, represented in concise form by

$$\mathbf{n}(t + 1) = \mathbf{A}\,\mathbf{n}(t). \tag{3}$$

A bold uppercase letter refers to a matrix, whereas a bold lowercase letter refers to a vector. (A matrix is a set of terms arranged in two or more rows and columns, and a vector is a matrix with a single row or column). The term a_{ij}, refers to the coefficient in the ith row and jth column of the matrix. For the special case of an age-classified life cycle, the resulting *projection matrix* is known as a *Leslie matrix* (Leslie, 1945).

2.1.3. The Life Cycle Graph Formulation

An intuitively pleasing method of portraying the life cycle is to use a *life cycle graph*. The graph is simply an alternative formulation of the difference equation or matrix projection methods. In Figure 1c the numbered circles are called *nodes* and the directed lines connecting nodes are *arcs*. A *path* is a sequence of arcs linking two nodes (that are not necessarily adjacent). A path from a node back to itself is called a *loop*. If a loop passes through no other nodes it is called a *self-loop*.

The nodes represent stages or age classes, while the arcs represent transitions between the stages in the form of survival, production of offspring, or transition probabilities (e.g., probability that a floater will become a breeder). Node 1 in Figure 1c has a self-loop, which denotes the number of first-year birds at time $t + 1$ per first-year bird at time t; that is, each of the arcs that points back to Node 1 (including the self-loop) represents a fertility transition. As we will see in Section 2.4.2, the coefficients, F_i, which describe these fertility transitions, include terms both for the number of offspring produced (m_i) and the survival rate of either the parents or the offspring $(P_i$ or $l_i)$. In Section 6.2.2, we will show how many analyses, such as calculating *reproductive values* and *sensitivities*, can be done directly from such a graph, because it is the direct graph theory equivalent of the demographic projection matrix. The nodes are numbered from 1 to ω, the number of stages or age classes in the classification. The ordering of the numbers does not matter, but it is usually convenient to assign the number 1 to the node that refers to "newborns" (first-year birds). The coefficients, a_{ij}, of the projection matrix, A, are simply the coefficients on the arcs from Node j to Node i in the life cycle graph.

2.2. Projection Interval and Timing of Census

Inherent in the projection of population growth is the choice of a projection interval, since the transition an individual makes between t and $t + 1$ obviously depends on whether t is measured in days, weeks, or years. Because most birds breed during a well-defined season each year, they are usually modelled with an annual projection interval. The major reference mark in the year will tend to be the breeding season. Most studies will usually census the population and project it from just before the breeding season (prebreeding census) or immediately afterwards (postbreeding census). The timing of the census will affect the parameterization of the life cycle graph or matrix but does not affect the assessment of underlying dynamics, such as population growth rates or sensitivities.

2.3. Assumptions and a Note on the Meanings of "Adult"

Before presenting the fertility, survival, and transition probability coefficients of the matrix and life cycle graph formulations, we review the assumptions that underlie the basic matrix model:

1. Individuals are classified into discrete age classes or stages.
2. The vital rates (survival and fertility transitions from any given stage) are time-invariant processes.

3. The vital rates are density independent.

If, as may often be the case, stochastic variation is a recurring feature of the environment, or density or frequency dependence are known or suspected to be important, then special extensions are needed to the methods presented here (e.g., Cohen, 1987; Caswell, 1989b). Often these will involve simulations. Nevertheless, as with any useful model, the time-invariant methods presented here can highlight important selective pressures, expose unsuspected features of populations, and point to areas in which key assumptions are not met.

The term *adult* has been variously applied to describe individuals (1) that are in the definitive plumage, (2) that are at or beyond the age of first reproduction, (3) that have attained an age-independent fertility rate, or (4) that have attained an age-independent survival rate. These processes of maturation may vary heterochronically and independently. In Long-tailed Manakins (*Chiroxiphia linearis*), for example, both the timing and order of these processes differ between males and females, as well as interspecifically (McDonald, 1993). For brevity, we will use the term to refer to any stage that meets one or more of criteria 2, 3, or 4, depending upon the nature of the problem addressed.

2.4. Deriving the Coefficients in the Graph or Matrix

For some age-classified cases, an $l_x m_x$ life table may already be available and we would like to be able to use it for a discrete matrix-based analysis. In the following two sections we will see that parameterization of the coefficients in the life cycle graph or matrix depends upon the timing of the census.

2.4.1. Deriving the Survival Coefficients, P_i, from an $l_x m_x$ Table

The coefficients P_i of an age-classified (Leslie) projection matrix refer to survival from age class i to age class $i + 1$ and occur only along the subdiagonal. For a prebreeding census, P_1 tracks the first age class from being "almost 1-year-olds" until they are "almost 2-year-olds." In terms of l_x, $P_1^{(pre)}$ is l_2/l_1. If, however, the census is postbreeding, $P_1^{(post)}$ represents survival from just after fledging (or hatching) to just after the first birthday, equivalent to the life table formulation l_1/l_0.

The formulae by which the P_i values relate to the l_x values are

$$P_i = \frac{l_{(i+1)}}{l_i} \qquad \text{(prebreeding census)} \qquad (4a)$$

or

$$P_i = \frac{l_i}{l_{(i-1)}} \quad \text{(postbreeding census)}. \quad (4b)$$

With either census type, P_1 is the survival rate from the first age class to the second. As noted above, the census time affects what one first sees in the field (almost 1-year-olds or fresh fledglings). Note also that a prebreeding census does not provide any information on first-year survival, l_1. In order to compute l_1, one must make a special effort to count first-year birds at fledging and to monitor their fate; they would otherwise first be counted at the census almost a year after they fledged.

Although certain species can be censused exhaustively, and missing individuals can safely be assumed dead, this is not true for the majority of species. In such species, one must estimate survival rates from recaptures or resightings of banded birds. A number of models and techniques are available for such estimates (Brownie et al., 1985; Pollock et al., 1990; Clobert and Lebreton, 1991). Karr et al. (1990) challenge the long-held assumption that temperate species of birds have generally lower survival rates than do tropical species. Important work remains to be done for estimating survival rates in species with long "juvenile" stages and incorporating complications such as emigration. Caughley (1977) discusses techniques for obtaining a life table from field data (see also Gani, 1973). In practice, calculation is often limited to females (female demographic dominance) because their fertility is easier to assess. In principle, however, demographic analysis can be applied to either sex or both (see Caswell and Weeks, 1986, for ensuing complications).

2.4.2. Deriving the Fertility Coefficients, F_i

In an age-classified Leslie matrix, the fertility elements occur along the top row. As we will see, they contain terms relating to survival as well as the fertility rates, m_i. Deriving the m_i from the age-specific fertility, m_x is straightforward for birth-pulse populations. Because m_i is defined as the production by an individual of age class i on its ith birthday,

$$m_i = m_x, \quad (5)$$

with either a prebreeding or postbreeding census. For birth-flow reproduction, deriving m_i from m_x is more complex (Caswell, 1989b). With a prebreeding census, F_i is

$$F_i = \frac{l_1}{l_0} m_i = l_1 m_i \quad \text{(prebreeding census)}. \quad (6a)$$

The first-year survival rate, l_1, remains a part of the F_i coefficient, whatever the age (Fig. 3). Remember that with a prebreeding census adult individuals are censused just as they are about to reproduce. The resulting offspring must survive for a year to appear in the population at time $t + 1$. Thus in calculating the F_i, reproduction is weighted by the first-year survival probability, l_1. With a postbreeding census, adults have just completed breeding. In order to reproduce they must survive to their next birthday (with probability P_i), but, if they do survive, their offspring will be counted in the population immediately. Thus in calculating F_i, reproduction is weighted by adult survival, which yields

$$F_i = P_i m_i \quad \text{(postbreeding census)} \quad (6b)$$

Retaining a firm grasp on the dependence of P_i and F_i on census time, the inclusion of a survival term in F_i, and the indexing difference between continuous x (age-specific) and discrete i (age class- or stage-specific) vital rates, will prevent potential confusion when using matrix methods. Improper setup of matrix approaches has led to considerable confusion in the literature (see Jenkins, 1988) and may be partly responsible for Caughley's (1977) pessimism about the fruitfulness of matrix approaches. Careful development of parameters for the model (Caswell, 1989b:8–15) is important.
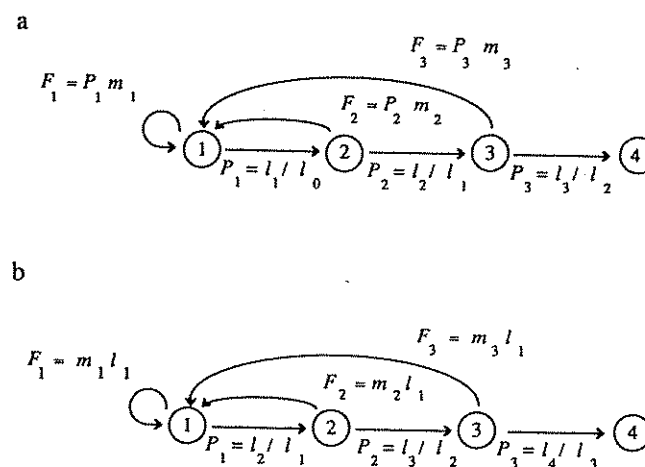

FIGURE 3. Parameterization of the graph for the life cycle of Figure 1. (a) Postbreeding census. Note the inclusion of the term P_i in formulating the F_i, to account for the survival of parents from census to the birth-pulse. (b) Prebreeding census. Note the inclusion of the term l_1 in the F_i to account for the survival of offspring from the birth-pulse to the census. Note also the difference in the formulation of the P_i.

2.4.3. Parameterization as a Function of Census Time—an Example

Figures 3a and 3b represent the simple life history of Figure 1, with different times of census (postbreeding vs. prebreeding). Both representations have the same dynamics; they differ only in the formulation of the transitions (arc coefficients). Note that three loops exist from Node 1 back to itself. The self-loop from Node 1 represents the production of offspring by first-year birds. With the postbreeding census of Figure 3a, we must account for the survival of the first-year birds from the time of the census (at fledging or hatch) to the time they become parents at the birth-pulse almost a year later; this survival is given by P_1. The term m_1 represents their production of offspring (which are immediately censused). With the prebreeding census of Figure 3b, individuals in the first age class are censused when almost 1 year of age. They immediately produce offspring (m_1), but we must then follow the offsprings' survival (l_1) for almost a year until they, in turn, can be censused. Likewise, in every subsequent year, production occurs immediately following the census. We therefore do not need to account for parental survival but must account for the survival of the offspring to the time of census. An interesting hidden assumption here is that all offspring are equivalent. In some cases, however, the demographic properties of the offspring may depend upon the age class or stage of the parent. Such complications are readily explored with life cycle graph analyses (van Groenendael *et al.*, 1988). See Caswell (1989b:11–15) for formulae that can accommodate censuses at any time during the cycle.

2.4.4. Stage-Classified Analyses and Transition Probabilities

Birds usually have been considered ideally suited to age-classified analysis. In many cases, however, social status, colony position, size, territory quality, or some other attribute may be of greater importance to population dynamics than is age. Matrix-based analyses easily accommodate such attributes and allow analysis of stage-structured transitions. We will demonstrate stage-classified analyses in Sections 6 and 7.

With a stage-classified model individuals might, for example, remain the same size or move back and forth from floater to breeder status. As a result, coefficients of the projection matrix other than those in the first row (the F_i in a Leslie matrix) or the subdiagonal (the P_i in a Leslie matrix) may be nonzero. Each cell in the matrix represents a transition to another cell (from the jth stage to the ith stage, or from the columns to the rows). In the top row, for example, we go to stage 1 (first-year birds) from the given column. Each arc or matrix coefficient can be viewed as a transition to an expected fate from a current state over the course of the projection interval.

The life cycle graph is particularly useful for setting up stage-

structured analyses because it forces explicit depiction of the transitions in the life cycle (Caswell, 1989b:48, 116) and makes it easier to check that all the transitions depicted are possible and that all transitions that do occur are represented in the graph and matrix.

3. CALCULATING DEMOGRAPHIC PARAMETERS

The classic use of a Leslie matrix is for projecting population size. Multiplying a Leslie matrix on the left by a census vector on the right yields a column vector of the expected number of individuals in each age class at the next census. Often, however, we would like to go on to assess parameters such as the growth rate, the proportion of individuals in the various stages or age classes at equilibrium, and their relative importance to population dynamics. The projection matrix allows one to calculate these and other parameters with ease. Caswell (1989b) provides a brief appendix that reviews the basics of matrix algebra, including matrix multiplication, which is the heart of the projection process.

3.1. The Stable Stage Distribution

Imagine that we start with an initial census vector $\mathbf{n}(t)$, and continue projecting by multiplying it by the matrix A. With the time-invariant assumption (Section 2.3), no matter what the initial distribution of stages, the eventual product vector will converge on what is called the *stable (st)age distribution*. (The convergence requires irreducibility and primitivity of the matrix, conditions that are very likely to be met by models for bird populations; see Caswell 1989b: chapter 4). The stable stage distribution, $\mathbf{w}$, is a column vector whose elements, w_i, give the proportion of the population in stage i once sufficient time has passed that fluctuations due to initial conditions have passed. Although the number of individuals in each stage may then change (depending upon whether the population is growing or shrinking), the proportions will not (assuming, of course, that only the forces spelled out by the matrix are in operation). Even for initial census vectors far from the stable stage distribution, the vector will usually stabilize within a few generations. The vector, $\mathbf{w}$, is the right *eigenvector* (associated with the dominant *eigenvalue*) of the matrix.

3.2. Reproductive Value

Likewise, if we continually left-multiply the projection matrix by *any* initial row vector (having at least one nonzero value and no negative values), we will eventually obtain a vector of *reproductive values*. Repro-

ductive value, v_i, can be defined as the importance, or relative contribution, of an individual of stage i to population growth (see Caswell, 1989b:67, 108, 136). The value of the first element, v_1, of the reproductive value vector, **v**, is usually set to 1.0 and all the other values are adjusted accordingly. This is equivalent to measuring the value of all stages relative to that of the first stage. Thus, for example, Crouse *et al.* (1987) found a mature loggerhead turtle to be "worth" 587 hatchlings. The vector, **v**, is the left *eigenvector* of the matrix.

3.3. λ, the Population Growth Rate

With either right or left multiplication of the projection matrix by a vector, we would also notice that, once it reaches the stable stage distribution, each element in the product vector grows by a factor λ over the course of the projection interval. λ is the dominant *eigenvalue* of the matrix. For a projection interval of a year, for example, λ is the annual population growth rate.

3.4. Calculating the Eigenvectors and Eigenvalues

For computing the demographic parameters presented in this treatment, we recommend a software package such as MATLAB, EISPACK or GAUSS. We will also show a method for reading the *characteristic equation* and eigenvectors directly from a life cycle graph in Section 6.2.2.

To calculate the eigenvectors and eigenvalue oneself, one can raise the matrix to a high power. Raising even quite a large matrix to a power is straightforward on a microcomputer using Pascal (see Crandall and Colgrove, 1986), BASIC, or any other programming language. If one raises the matrix to a high enough power, it reaches a point at which the proportions do not change, moving either across rows or down columns. In practice, seven squarings is often sufficient ($2^7 = 128$ projections, yielding A^{128}). To avoid underflow or overflow (extremely small values when $\lambda \ll 1$, or large when $\lambda \gg 1$), one can divide each cell in the product matrix by the value of the largest cell on each round. In the matrix A^{128}, the coefficients of each of the columns come to be in the proportions of **w**. The rows (after dividing each coefficient by the value of the first coefficient) represent **v**. One can then compute λ by first multiplying A^{128} by A and then dividing any cell in A^{129} by the corresponding cell in A^{128}. The precision of this estimate can be checked by comparing the value derived from A^{128} with that for A^{64} or A^{256}.

The parameters **w**, **v**, and λ are in some ways demographic analogs of the Hardy–Weinberg equilibrium in population genetics. They describe properties in the absence of other forces. No matter how many individuals are in the different stages initially, the final stable stage distribution, reproductive values, and growth rate depend only upon the matrix values, not the initial conditions.

3.5. The Characteristic Equation

The calculation of the intrinsic rate of increase, r, for age-classified populations is familiar from life table analysis in the form of Lotka's equation:

$$1 = \int_{x=0}^{\omega} e^{-rx} l_x m_x \, dx. \tag{7}$$

We want to calculate the population growth rate, λ (equivalent to e^r), for populations classified by stage as well as age. The equation generalizing (7) is called the *characteristic equation* of the matrix **A**. It is given by

$$det(A - \lambda I) = 0, \tag{8}$$

where **I** is the identity matrix and *det*( ) denotes the determinant. The determinant is a scalar function of a matrix that plays an important role in the solution of linear equations. (A scalar is a single value.) Unless the matrix is very small, it requires a computer for evaluation. What is important for our purposes is that the result of applying the determinant in Eq. (8) is a polynomial, of the same order as the size of the matrix **A**, in the unknown quantity λ. The solutions of this polynomial are the eigenvalues of A; the largest of these, λ_1, is the eventual population growth rate. The other eigenvalues provide potentially useful information about the transient dynamics of the population (Caswell, 1989b), but we will treat only λ_1 here and therefore use no subscript. λ tells us whether the population is *stationary* ($\lambda = 1$), shrinking ($\lambda < 1$), or growing ($\lambda > 1$). A stationary population is one that is not growing. The term *stable* is best reserved for a population that has achieved a *stable stage distribution* (see Section 3.2).

For an age-classified Leslie matrix model, the characteristic equation can be written down explicitly (because of the special structure of the Leslie matrix). It is

$$1 = F_1\lambda^{-1} + P_1F_2\lambda^{-2} + P_1P_2F_3\lambda^{-3} + \ldots \tag{9a}$$

$$= \sum_{i=1}^{\omega} \lambda^{-i} F_i \prod_{j=1}^{i-1} P_j. \tag{9b}$$

It is not difficult to see Eq. (9b) as a direct counterpart of Eq. (7) with summation replacing integration, λ^{-i} replacing e^{-rx}, F_i replacing m_x, and ΠP_j replacing l_x. This is as it should be.

It is sometimes useful to be able to write down the characteristic equation for more complex life cycles. This is possible using a simple algorithm applied to the life cycle graph (Hubbell and Werner, 1979). We discuss this briefly in Section 6.2.2; see Caswell (1989b) for more details.

Another occasionally useful measure of population growth is the *net reproductive rate* $R_\emptyset$, defined as the expected number of offspring produced during an individual's lifetime. In terms of the life table, it is given by

$$R_\emptyset = \int_{x=0}^{\omega} l_x m_x \, dx. \tag{10a}$$

The corresponding formula for age-classified matrix models is

$$R_\emptyset = \sum_{i=1}^{\omega} F_i \prod_{j=1}^{i-1} P_j. \tag{10b}$$

3.6. Generation Times

It is also possible to calculate the generation time from the information included in the population projection matrix. Three measures of generation time are in common use. The first is the cohort generation time, T_c, (denoted μ_1 in Caswell, 1989b). Imagine following a cohort of individuals through their lives, collecting their offspring, and then calculating the mean age of parents of these offspring; this mean is T_c. The second measure, denoted by $\overline{A}$ (denoted T by Caughley, 1977), would be obtained by collecting the offspring of the population at a point and calculating the mean age of their parents. This measure obviously depends upon the age distribution of the population at the time of the measurement, and the standard is to use the stable age distribution. The third index, T, measures the time required for the population to grow by a factor $R_\emptyset$, the net reproductive rate, given by Eq. (10b). Once one can calculate λ, it is possible to calculate measures of generation time.

The formulae for these quantities are

$$T_c = \frac{\displaystyle\sum_{i=1}^{\omega} i F_i \prod_{j=1}^{i-1} P_j}{\displaystyle\sum_{i=1}^{\omega} F_i \prod_{j=1}^{i-1} P_j}, \tag{11}$$

$$\overline{A} = \frac{\displaystyle\sum_{i=1}^{\omega} i \lambda^{-i} F_i \prod_{j=1}^{i-1} P_j}{\displaystyle\sum_{i=1}^{\omega} \lambda^{-i} F_i \prod_{j=1}^{i-1} P_j}, \quad \text{and} \tag{12}$$

$$T = \frac{\ln(R_\emptyset)}{\ln(\lambda)} \qquad [\lambda^T = R_\emptyset]. \tag{13}$$

Note that in the formulae for T_c and $\overline{A}$, P_0 is defined equal to 1 [see Eq. (4a,b)]. Also, the denominator in the formula for $\overline{A}$ is the characteristic equation, Eq. (9b), and hence equals 1. Eq. (11) is the discrete analog of the mean of the $l_x m_x$ schedule.

All three of these measures were originally defined, and are given here, for age-classified models. Caswell (1989b) presents a method for calculating them from stage-classified models, although it becomes awkward if the life cycle graph is not very simple. Cochran and Ellner (1992) present a much simpler and more generally applicable method; their method also allows calculation of such intriguing parameters as the average age of individuals in the stable stage distribution.

4. FITNESS, SENSITIVITIES, AND ELASTICITIES

Although it seems that many populations are neither growing nor shrinking appreciably, there are several good reasons to calculate the population growth rate, λ. First, λ integrates the diverse and often contradictory effects of the environment on the rates of survival, reproduction, growth, etc. into a single index. This index quantifies the suitability of the environment (at the time and place it is measured) for the population in an intuitively meaningful manner. An environment that produces a higher value of λ is, all other things being equal, better for the population than one that produces a smaller value of λ. An environment that produces a value of $\lambda < 1$ cannot, all else being equal, support the population at all. Second, in a genetic context, λ is an appropriate measure of fitness (Charlesworth, 1980; Lande, 1982a,b; Caswell, 1989b:161–177), given certain genetic assumptions (weak selection, stable population structure, no frequency dependence).

Often, one may be interested only in a few potential tradeoffs within a life history schedule or the relative importance of a particular life history transition. For example, one field worker might be interested in ensuring that the greatest effort to obtain accurate and precise data went to the most evolutionarily or ecologically important transitions in the life cycle. Another might be interested in assessing the impact of floater to breeder transition probabilities that have changed as the result of natural or experimental habitat modifications. In such cases, one would like to know the relative contribution to overall fitness (λ) of individual life history traits (the a_{ij} of the projection matrix) without having to resort to extensive

simulations. Sensitivity and elasticity analysis allow one to assess just those sorts of effects directly from the projection matrix or life cycle graph.

4.1. Sensitivity Analysis—Absolute Changes

The elements, a_{ij}, of the projection matrix represent stage-specific life history traits. Using the eigenvectors $\mathbf{v}$ and $\mathbf{w}$, calculated earlier, one can calculate a matrix of the *sensitivities* of λ to changes in those life history traits. The sensitivity coefficients are

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \tag{14a}$$

$$= \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \tag{14b}$$

The sensitivity, s_{ij}, is the partial derivative of λ with respect to the element a_{ij} of the projection matrix, holding all other entries constant. The term $\langle \mathbf{w}, \mathbf{v} \rangle$ in the denominator of Eq. (14b) is the scalar product of the vectors $\mathbf{v}$ and $\mathbf{w}$. It is calculated by summing the element-by-element product of the two vectors.

$$\langle \mathbf{w}, \mathbf{v} \rangle = \sum_{i=1}^{\omega} v_i w_i. \tag{15}$$

Perhaps one of the most intriguing aspects of the sensitivity matrix is its direct link to theory in quantitative genetics. The coefficients of a sensitivity matrix are directly equivalent to selection gradients (see Lande, 1982b) because each is the partial regression of relative fitness (λ) on a character (e.g., age-specific fertility, probability of becoming a breeder), holding all other characters constant (see Arnold, 1983:98). This is the direct force of selection on characters. Selection differentials (shifts in the mean of characters before vs. after selection) are the covariances between relative fitness and characters, and measure both direct and indirect selection. The selection differentials are given by the product of the additive genetic covariance matrix and a vector of selection gradients.

4.2. Elasticity Analysis—Proportional Changes

What if one wishes to assess the effect of a proportional change in a life history trait (e.g., a 10% increase in production of offspring at age 1)? In that case, one can compute the *elasticity* matrix (Kroon et al., 1986). Elasticity is defined verbally as the effect on λ of a proportional change in a life history trait. The equation is

$$e_{ij} = \frac{\partial \ln (\lambda)}{\partial \ln (a_{ij})} \tag{16a}$$

$$= \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \tag{16b}$$

$$= \frac{a_{ij} s_{ij}}{\lambda}. \tag{16c}$$

The coefficients of the projection matrix (or the graph), the sensitivities, given by Eq. (14), and λ are the terms necessary for calculating the elasticity matrix. The coefficients of an elasticity matrix sum to unity. An advantage of the elasticity matrix is that, since it addresses proportional changes, it is easier to compare survival and fertility changes (e.g., a 10% increase in 3-year-old fertility vs. a 10% increase in fledgling survival rate). Further, because the sensitivities are obtained by multiplying each element in the stable stage distribution by each element in the reproductive value vector, every cell in the sensitivity matrix is nonzero, even though corresponding cells in the original projection matrix had zero values. This is less perplexing if we remember that selective value can exist in the absence of a trait, as shown, for example, by recent work on "preexisting" mating preferences of female frogs for calls that do not exist in their population (Ryan et al., 1990). The elasticity matrix, on the other hand, has nonzero values only where the corresponding projection matrix cells are nonzero.

5. VARIANCES AND CONFIDENCE LIMITS

Thus far we have dealt with population averages. The matrix and its associated growth rate, reproductive values, and other parameters yield a single average value. For many questions of interest to students of life history strategies, reproductive effort or alternative reproductive strategies, however, the crux of the argument lies in variability among individuals. For brevity, we introduce only a simple binomial estimate of the variance of demographic parameters. Caswell (1989b) and Meyer et al. (1986) discuss resampling methods (bootstrap and jackknife) for generating estimates of the variance.

5.1. An Approximation to the Variance

No general formula exists for the variance of λ as a function of the variances and covariances of the matrix elements. There is, however, a useful approximate formula, valid for small amounts of variability (how small "small" must be is not completely clear).

$$V(\lambda) \approx \sum_{i,j} \sum_{k,l} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}} Cov (a_{ij}, a_{kl}) \qquad (17a)$$

$$= \sum_{i,j} \sum_{k,l} (s_{ij})(s_{kl}) Cov (a_{ij}, a_{kl}) \qquad (17b)$$

where $Cov (a_{ij}, a_{kl})$ is the covariance of a_{ij} and a_{kl}, and the partial derivatives are given by the sensitivity formula, Eq. (14). If the matrix elements are assumed to vary independently, only the variances appear in Eq. (17a).

The variance and covariance information needed for calculation of Eq. (7) can, at least in principle, be obtained from many sources. Lande's (1988a) analysis of Spotted Owls used this approach. He used the literature-based approximation that in owl populations the individual variance in clutch size is 1.3 times the mean. He estimated the variance in survival probabilities from the binomial distribution, which gives the variance in P as

$$V(P) = \frac{P(1 - P)}{N}, \qquad (18)$$

where N is the number of individuals sampled to obtain the estimate of the survival rate. This approach could be used with a stage-classified population as well, except that transitions may occur for which more than two outcomes are possible. For example, survival is binomial, with outcomes alive or dead; stage-classified transitions might allow several outcomes (floater, breeder, or helper). In such cases, the distribution will be multinomial and the transitions, a_{ij}, cannot be assumed to vary independently.

6. APPLICATIONS TO FIELD STUDIES AND EXISTING MODELS

In this section we examine the application of the techniques presented here to a variety of avian studies that raise interesting demographic problems. After reviewing conceptual links to earlier models that used other techniques (Section 6.1), we address useful transformations of the life cycle graph and show how various important parameters can be read directly from the graph (Section 6.2). We then discuss the relationship between difference equation approaches and matrix-based approaches (Section 6.3), with an example from a study of the Wandering Albatross (Diomedea exulans) (Section 6.4) and a simplification of that analysis that applies also to the California Condor (Gymnogyps californianus) (Section 6.4.2). Finally, we discuss two complications that arise in demographic analyses—assessing the possible effects of senescence with a truncated life span

(Section 6.5) and the consequences of making an assumption of stationarity (mean population growth rate of zero, Section 6.6).

6.1. Conceptual Links to Some Previous Models

Perhaps because they have a tradition of demographic analysis based on the life table and because bird life histories are often well described in terms of age, ornithologists have been slow to adopt matrix population models. Nevertheless, a number of studies have approached avian demography in ways that can be clearly linked to those presented here.

Capildeo and Haldane (1954) introduced an approach to population modelling based on a difference equation model for breeding adults. They derived the characteristic equation for the rate of increase and tabulated solutions for some values of survival and fertility. Croxall et al. (1990) applied this method to a complex model for the Wandering Albatross (see Section 6.4). Leslie (1966) used an approach based more directly on the population projection matrix to analyze population dynamics of the Common Murres (Uria aalge), finding their intrinsic rate of increase and measuring generation time. Mertz (1971) subsequently used a similar difference equation approach to study the demography of the California Condor, focusing on the sensitivity of population growth rate to potential changes in the life history. Recently, Lande (1988a) used the same approach in a study of the Northern Spotted Owl (Strix occidentalis caurina).

Kosinski and Podolsky (1979) derived age-specific life tables for the Black-legged Kittiwake (Rissa tridactyla), distinguishing males and females, individuals nesting at the center and on the edges of the colony, and the growth and stable phases of colony development. They constructed Leslie matrices from these life tables and used simulation to measure the intrinsic rate of increase r. By manipulating the mortality and fertility schedules, they concluded that the difference in r between the grown and stable phases of the colony was due mainly to mortality effects, and that the differences between center and edge-nesting birds were due to differences in mortality during the growth phase and to differences in breeding success during the stable phase. This is a good example of the use of r (or λ) as an integrated measure of the quality of an environment. For a more powerful, matrix-based approach to such analyses see Caswell (1989a or 1989b:139–151).

Nichols et al. (1980) and Simons (1984) used matrix models to evaluate management strategies for endangered species—the Everglades Snail Kite (Rostrhamus sociabilis plumbeus) and the Hawaiian Dark-rumped Petrel (Pterodroma phaeopygia sandwichensis), respectively. Nichols et al.

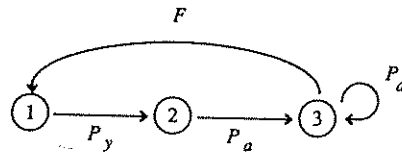FIGURE 4. Life cycle graph for the Everglades Snail Kite study of Nichols *et al.* (1980). P_y and P_a denote survival probabilities for young and adults, respectively.

(1980) used a model equivalent to the life cycle graph in Figure 4, where P_y and P_a are survival probabilities for young (Node 1) and adults (Node 2), and F denotes adult fertility. They had some data on fertility, but no data on juvenile or adult survival. Thus they varied P_y and P_a to examine the effects on λ. They found numerically that λ was most sensitive to changes in adult survival. Simons (1984) used a similar approach, but with an age at maturity of 6 years. He used a matrix with 36 age classes, reasoning that although individuals might live longer than this, they would be so rare as to make no significant contribution to population growth. We return to the question of truncating the matrix in Sections 6.5 and 7.

North (1985) used a simple two-stage model (juveniles and adults) to study Eastern Screech Owl (*Otus asio*) population dynamics. He used the characteristic equation to estimate the reproductive rate required to produce a stationary population. He then varied mortality in various ways and calculated the changes in other parameters required to return the population to stationarity. He also studied population subdivision by modelling dispersal among two subpopulations.

Pennycuick (1969) used a matrix approach as the basis for a simulation with density dependence for the Great Tit (*Parus major*). She inserted density dependence into different parts of the life cycle and compared the resulting population patterns with those observed in the field. Cooke and Leon (1976) analyzed a greatly simplified, two-stage version of Pennycuick's model.

These studies have in common the need to conduct demographic analyses based on fragmentary data (e.g., missing survival data, no age-specific adult mortality data) and the desire to use the analyses to evaluate the effects of changes—hypothetical, natural, or anthropogenic—in the vital rates. Some authors want to go beyond the basic analysis to add density-dependent coefficients or stochastic variation to the model. The combination of life cycle graphs with population projection matrices and their associated sensitivity analyses provides a simple and straightforward way to approach these goals. Developments in theory and software now make it possible to go far beyond the analyses in any of these papers.

6.2. Graphs for Incomplete Data and Other Uses of the z-Transform

In many cases, complete lifetime data for any but a few individuals will be lacking. One may, however, have a reasonably good idea of the following: (1) age of first reproduction, (2) survival rate of first-year birds to the age of reproduction, (3) fertility of adults, and (4) annual survival rate of adults. With these data (or estimates of them), one can still gain considerable insight into the demography using the simple two-stage or three-stage models illustrated in Figure 5. In Figure 5a, P_y and P_a are survival probabilities for young (Node 1) and adults (Node 2), and F denotes adult fertility. The use of the term *adult* denotes the assumption that fertility and survival rates are age independent beyond the age of first reproduction. The incorporation of terms involving λ is the result of a z-transform. The z-transform of a discrete function has a host of useful properties (Caswell, 1989b:95–97). It takes into account the time needed for transitions between stages and the growth rate, λ. To obtain the z-transform one simply multiplies each arc in the original graph by λ^{-t}, where t is the time required for the transition. In prior graphs we have been using $t = 1$, but the z-transform makes it possible to consider graphs with transitions that require more than a single projection interval. The utility of the z-transformed graph is that from it one can calculate directly the characteristic equation and other

FIGURE 5. z-transformed, reduced life cycle graphs for modelling a life cycle with incomplete data. (a) Maximal reduction, appropriate with a prebreeding census but only under special circumstances with a postbreeding census. Nodes: 1, young; 2, adults. P_y, survival of young to the adult stage; P_a, survival rate of adults; F, fertility of adults. (b) Reduced graph required with a postbreeding census formulation, when the survival rate in the year leading up to first breeding, P_f, differs from the adult rate, P_a. Nodes: 1, young; 2, first-time breeders; 3, adults. Neither of these reduced graphs can be converted directly into a matrix if any of the transitions require more than a single projection interval.
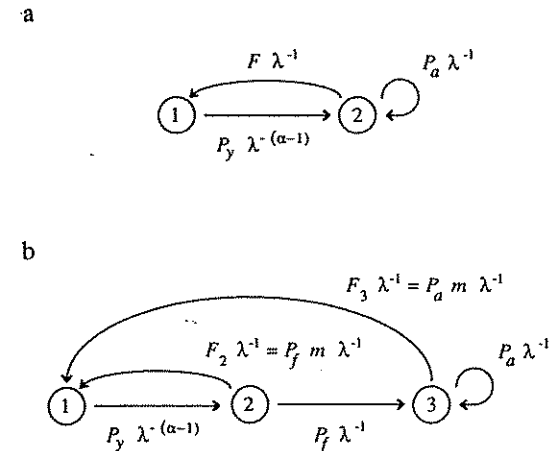
demographic parameters and that it allows one to reduce (simplify) the graph.

Note that the first arc in Figure 5a is multiplied by $\lambda^{-(\alpha-1)}$. The age at first reproduction is α; hence the first arc (the path from Node 1 to Node 2) is the probability of surviving to reproduce, Py, multiplied by a term for the time (and growth rate of the population) taken to get there, given by $\lambda^{-(\alpha-1)}$. A z-transformed graph can be reduced (collapsing arcs and nodes; Caswell, 1989b:97–99) to accommodate transitions that take more than one projection interval. Thus, Figure 5a is a reduced graph if $\alpha > 2$ (age-specific prereproductive arc coefficients would collapse into the single "juvenile" arc coefficient, Py). One cannot, however, use a z-transformed, reduced graph directly to construct a matrix; one must first expand the graph so that no transition requires more than one projection interval.

With a postbreeding census, the two-node simplification of Figure 5a is possible only under special circumstances. To understand why this is so, remember that with a postbreeding census the fertility coefficients, F_i, contain a P_i term for survival of the parents from the census to the birth-pulse (see Fig. 3a). At the age of first reproduction, therefore, F_i will require a P_i term for the final phase of juvenile survival, rather than the age-independent adult survival rate P_a. Thus the graph requires an extra node for first-time breeders, as shown in Figure 5b, where P_f is the survival rate of first-time breeders to their first birth-pulse, from the prior census. Only if juvenile and adult survival are the same (i.e., in the unlikely event that survival is age independent from fledging on), or if individuals enjoy a year or more of the "adult" survival rate before beginning to reproduce, is it appropriate to collapse the graph of Figure 5b further. Because F with a prebreeding census requires only the inclusion of first-year survival of offspring (l_1), the two-node graph applies, no matter what the timing of maturation rates. Despite the difference in the graphs required by the dependence of the coefficients on census time, the characteristic equation is the same when read from either graph by the method we will introduce in Section 6.2.2. The accounting differs, but the picture of population dynamics should be, and is, the same.

This example of the interaction between the timing of the census and the modelling of maturation transitions with birth-pulse reproduction highlights the importance of considering explicitly what is meant by "adult" and how the transitions to adulthood should be modelled. Perhaps the greatest pitfall in any demographic analysis lies in failing to account properly for the projection intervals and for completeness of the coefficients (do they account for all possible transitions and correctly account for the time intervals and the nature of transitions between stages?). Sketching out the transitions with life cycle graphs is of considerable assistance in avoiding these pitfalls, which can be very difficult to discern

in equation-based analyses. We return to the correspondence between reduced and unreduced models in Sections 6.3 and 6.4.

6.2.1. Absorbing the Self-Loops

Besides allowing the simplification of collapsing arcs and nodes to form a reduced graph, the z-transform allows direct reading of the stable stage distribution, reproductive values, and characteristic equation from the graph. First, however, one must absorb any self-loops. One does so by dividing all incoming arcs (i.e., those that point to the node with the self-loop) by $1 - s$, where s is the self-loop coefficient. The result for the life cycle of Figure 1 is shown in Figure 6a ($s = F\lambda^{-1}$). To calculate the reproductive values, one must first transpose the graph by changing the direction of its arcs (the graphical equivalent of transposing the corresponding matrix) and then divide the incoming arcs by $1 - s$. The z-transformed, transposed graph for the life cycle of Figure 1 is shown in Figure 6b. Note that its arcs point in the opposite direction and that the absorption occurred along the survival arc from Node 1 to Node 2 rather than on the fertility arcs between Nodes 2, 3 and Node 1.

6.2.2. Reading Directly from the Graph

With the manipulations of the previous section, the stable stage distribution, reproductive values, and characteristic equation can be read directly from the graph. To illustrate, we will calculate these parameters for the life cycle graphs of Figure 6. To calculate the stable stage distribution, one uses the z-transformed graph (Fig. 6a). By definition, the value of w_1 is 1.0. The value of w_i ($i > 1$) is the sum of the path transmissions from Node 1 to Node i. A path transmission is defined as the product of all arc coefficients along the path. The formulae for reading from Figure 6a are

$$w_1 = 1. \tag{19}$$
$$w_2 = P_1\lambda^{-1}.$$
$$w_3 = P_1P_2\lambda^{-2}.$$
$$w_4 = P_1P_2P_3\lambda^{-3}.$$

Normalizing the distribution (dividing each value by the sum of the w_i) yields the usual format for a stable stage distribution. The age-classified graph of Figure 6 does not contain more than one path transmission from Node 1 to any other node. A more complex, stage-classified graph might, however, require summation of two or more path transmissions per stage (e.g., individuals might reach a breeder stage by passing through either a floater or a helper stage).
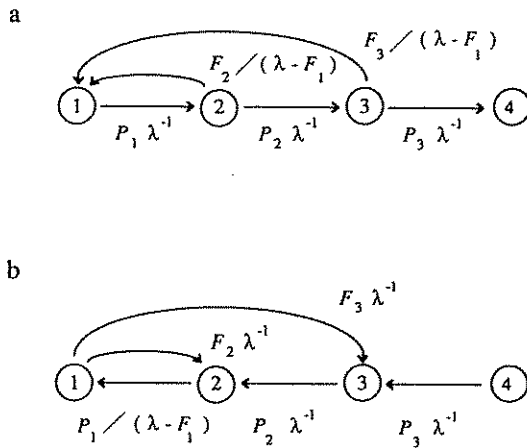
a

b

FIGURE 6. Transformations of the graph of Figure 1c to allow direct reading of demographic parameters. (a) The z-transformed graph from which the stable age distribution can be read as the path transmissions from Node 1 to Node i. (b) The z-transformed, transposed graph, from which the reproductive values can be read as the summed path transmissions from Node 1 back to Node i. Note the reversed direction of the arcs. The reversal is used only for calculation (tracing back reproductive values) and should not be interpreted to mean that, for example, individuals in the third age class produce or become individuals in the second age class.

To calculate the reproductive values, one sums the z-transformed, transposed transmission paths from Node 1 to Node i (Fig. 6b). v_1, the reproductive value of stage 1, is 1.0 by definition. The reproductive value of stage i ($i > 1$) is the sum of all the paths leading back (i.e., using the trick of following the direction of the now reversed arcs) from Node 1 to Node i. The formulae for reading from Figure 6b are

$$v_1 = 1,$$
$$v_2 = F_2\lambda^{-1} + F_3\lambda^{-1}P_2\ P_2\lambda^{-1}, \text{ and} \tag{20}$$
$$v_3 = F_3\lambda^{-1}.$$

With the method illustrated here, one can visualize the partitioning (Williams, 1966) of reproductive value, say v_2, into a portion due to "current reproduction" ($F_2\lambda^{-1}$) and a portion due to future reproduction ($F_3\lambda^{-1}P_2\lambda^{-1}$), weighted by transition probabilities (P_2 for the v_2 of this example, more generally a_{ij}) and the time required (λ^{-1}). Note that in Figure 6b with the reversed arcs the coefficients that constitute v_2 do not contain the absorbed first-year self-loop ($1/1 - F_1$). This is as it should be, because we are interested only in contributions from second-year and older stages. Heuristically, one can think of the matrix and graph inversion as a way of tracing back from offspring produced (the individuals in the first stage) to all the stages that contribute offspring.

One can also read the characteristic equation directly from the z-transformed graph. Define the loop transmission, $L^{(i)}$, as the product of the coefficients on the ith loop of the z-transformed graph. The characteristic

equation can be written by setting the sum of these loop transmissions equal to 1, unless the graph contains disjoint loops. A disjoint loop is one that does not share any nodes with another loop; in most cases all loops will share at least the first (newborn) node. To deal with disjoint loops, see Caswell (1989b:100). Applying this method to the life cycle graph of Figure 5 (with either census time version) yields a characteristic equation equivalent to that used by Lande (1988a) for Spotted Owls, with our P_y equivalent to his compound juvenile survival probability s_0s_1. Lande used implicit differentiation of the characteristic equation to assess the sensitivities.

6.3. Difference Equations and the Life Cycle Graph

Capildeo and Haldane (1954) constructed a difference equation in terms of the number of breeding adults $n(t)$. The order of this type of difference equation depends on the length of the life cycle. Suppose, for example, that juveniles become adult at age α and that both adults and juveniles are subject to the same survival rate P. Let F denote the age-independent adult fertility. Then

$$n(t) = P\,n(t-1) + P^{\alpha-1}F\,n(t-\alpha); \tag{21}$$

that is, the adults at time t are made up of adults from time $t - 1$ that survive and offspring produced at time $t - \alpha$ that survived through the intervening α years.

Difference equation models of this sort are equivalent to matrix population models (Keyfitz, 1967; Goodman, 1967). The trick in moving from one representation to the other is to replace the single difference equation of order α with a system of α first-order difference equations; i.e., with a matrix population model. In terms of the life cycle graph, this corresponds to expanding a reduced graph (e.g., that of Figure 5) so that no arc has a transition requiring more than one projection interval. This replacement is not, of course, unique. The terms in the difference equation represent products of survival probabilities and reproductive outputs around loops in the life cycle graph. Obviously, many combinations of survival and reproduction exist that will yield the same product.

Consider Eq. (21), for example. The characteristic equation of this model is

$$1 = P\lambda^{-1} + FP^{\alpha}\lambda^{-\alpha}. \tag{22}$$

This corresponds to a life cycle graph with two loops, one of length 1 and one of length α, as seen in the reduced z-transformed life graph in Figure 7a. That graph is equivalent to the unreduced graph in Figure 7b, which
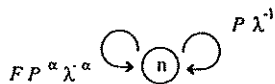
a

FIGURE 7. (a) z-transformed life cycle graph corresponding directly to the characteristic equation of Capildeo and Haldane's (1954) model. Transitions in this reduced graph may require longer than a single projection interval. (b) One possible unreduced graph (suitable for matrix construction) corresponding to the reduced graph of (a). In the unreduced graph, each transition requires only a single projection interval.
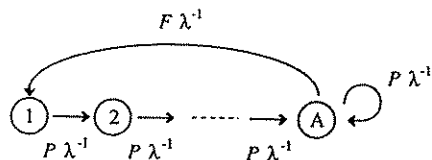
clearly reveals the assumptions of the model (maturity at age α, constant survival rate, and fertility of adults).

In general it is easier to work from the life cycle graph to the matrix and to use the matrix to derive demographic parameters (rate of increase, damping ratio, stable age distribution, reproductive value, sensitivity, elasticity) than it is to derive a difference equation and solve its characteristic equation. The characteristic equation is useful for deriving the sensitivity of the rate of increase to certain kinds of demographic changes, but since it can be derived directly from the life cycle graph, this only adds to the advantages of the matrix approach.

6.4. Nonbreeder Loops for Albatrosses and Condors

Croxall et al. (1990) report on a long-term study of the Wandering Albatross. In this population, juvenile birds begin to recruit to the adult population 8 years after hatch, and some recruit as late as 15 years after hatch. Adults that reproduce successfully skip at least 1 year, and perhaps as many as 3 years, before reproducing again. Adults that fail to reproduce may reproduce the following year, or wait one or more years.

6.4.1. Conversion of Difference Equations to a Graph

Croxall et al. present their model as follows (for clarity, we have eliminated the notation for possible time dependence of parameters used by Croxall et al.):

$$n(t+1) = f_1(1-b)n(t) + f_2(1-b)n(t-1) + f_3(1-f_2)n(t-2) +$$
$$s_2 b\, n(t-1) + s_3 b\, n(t-2) + s_4 b\, n(t-3) + \tfrac{1}{2}\sum_{k=8}^{15} r_k\, b\, n(t-k), \quad (23)$$

A life cycle graph corresponding to Eq. (23) is shown in Figure 8. Note that the structure of the life cycle—a long juvenile period, an age-independent breeding adult class, and the alternation of breeding and nonbreeding periods—is clearly revealed. Also note that the parameters used in Eq. (23) are insufficient completely to specify the life cycle graph. For instance, the recruitment probabilities r_i include the juvenile survival up to age i and the probability of recruiting to the adult population at age i, conditional on survival up to that age. Thus, in Figure 8 we have used the coefficient 1 in place of some of the unknown component probabilities of the r_i. Nevertheless, it is also apparent that Croxall's parameters permit calculation of the rate of increase, because the characteristic equation is defined in terms of the transmission around loops in the graph (see Section 6.2.2), and the parameters suffice to define those loop transmissions. Finally, it is clear that classical demographic methods for life table analysis are not applicable to this life history, because its structure does not follow the basic life table format.
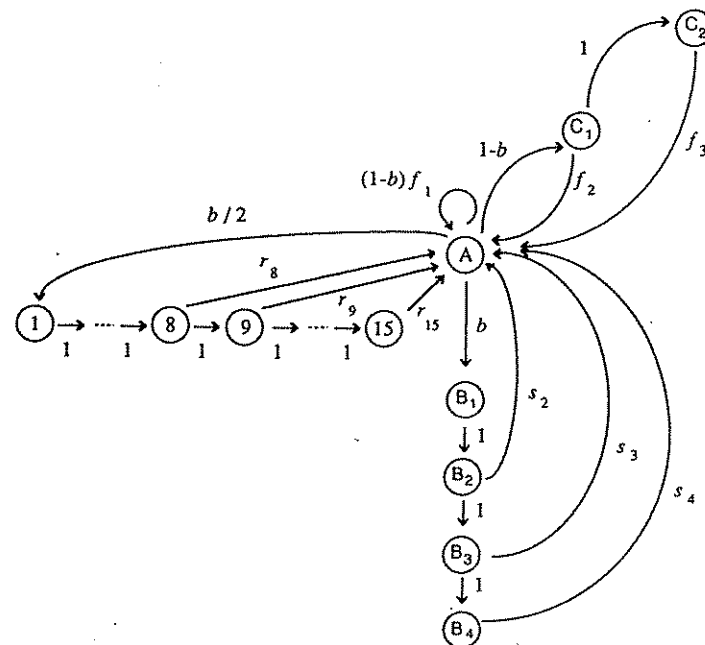

FIGURE 8. A life cycle graph for the Wandering Albatross, corresponding to the model of Croxall et al. (1990). A, breeding adults; 1–15, juveniles; B_1–B_4, adults that have bred successfully; C_1–C_2, adults that have failed to breed.
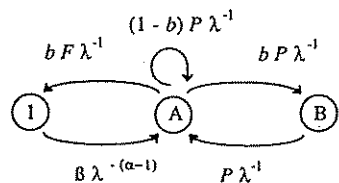
FIGURE 9. A z-transformed, reduced life cycle graph for the Wandering Albatross of Figure 8, also applicable to the analysis of the California Condor by Mertz (1971). A major feature of the life cycle is that successful breeders wait 2 years before breeding again, while failed breeders try again the next year. Nodes: 1, first-year birds; A, adults; B, adults that bred successfully.

6.4.2. A Simplified Graph for Condors and Albatrosses

It is instructive to consider simplifications of the graph in Figure 8, because few studies have accumulated such detailed data. If we know only an average age at maturity α, a survival probability β up to that age, an age-independent adult reproductive output F, and survival probability P, and if we assume that adults that breed successfully skip a single year of reproduction and that adults that fail try again the next year, we obtain the graph in Figure 9. The corresponding characteristic equation is

$$1 = b\beta F\lambda^{-\alpha} + bP^2\lambda^{-2} + (1 - b)P\lambda^{-1}, \qquad (24)$$

where b is the probability of breeding successfully and β is the probability that first-year birds recruit to breeding status. Such a simplified model can be used to explore qualitative properties of the life cycle, or in cases where only limited data are available. An example of both motivations is provided by Mertz's (1971) model of the California Condor, which is equivalent to Figure 9, with $\alpha = 5$ and $F = 0.05$. Very few demographic data were available for this species, and Mertz was interested in exploring the consequences of various life history modifications (repeated nesting, decreased development time, etc.). Mertz's analysis differs from that presented here in that he neglects the time required for offspring to appear in the first age class. This is a common problem with analyses based on discrete life tables; the solution is to work directly with the graph and matrix, where the projection interval is explicitly specified (Caswell, 1989b).

6.5. Truncated Life Cycle Analysis

The trick of describing adult survival by a self-loop with some probability P assumes that adult survival is age independent. Such a life cycle has an "infinite tail"; at any future time a probability exists (however small) that some individuals will still be alive. Senescence, defined as a decrease in survival probability with age, is obviously incompatible with this assumption. How can we assess the effects of the age-independence as-

sumption? As a first approximation for true senescence data, one can truncate the life span at an estimated maximum age. If one has no basis for estimating such a maximum, the annual survival rate provides a reasonable, conservative measure for calculating the point at which the proportion surviving will be negligibly small (we, therefore, predispose the calculations to have relatively little effect on λ). Of those individuals surviving to reproductive maturity at age α, a proportion y will remain alive μ years later. One can calculate a truncation age, $\tau + \alpha$, with the equation.

$$\tau = \frac{\ln(y)}{\ln(P_a)}, \qquad (25)$$

where y is the final proportion, or rather the tolerance for ignoring any further survivors (e.g., for $y = 0.01$, we are ignoring individuals beyond the point where we expect 1% of those reaching maturity to remain alive). P_a is the annual survival rate of adults. For example, if annual adult survival were 0.85 and we decided on a tolerance, y, of 0.01, τ would be 28 years. If it takes a year or two to reach adulthood ($\alpha = 1$ or 2), the matrix will have a dimensionality of approximately 30. Such a matrix is easily handled on a personal computer with available programs. Having assessed various demographic parameters and compared them to those from models with untruncated life spans (i.e., those having self-loops for adult survival), one could then ask what truncation age would significantly affect the parameter of interest (e.g., λ).

Although the above method will not have a large effect on λ, truncation can have marked effects on other parameters. For example, Lande (1988a) calculated the stable age generation time, $\overline{A}$ (he denotes it as T), for the Northern Spotted Owl, using the simplified life cycle of Figure 5. He obtained $\overline{A} = 55$ years. Truncating the matrix at age 83 ($y = .01$) yields $\overline{A} = 35$ years, a 36% reduction, compared with a 1% reduction in λ (from .961 to .955). The long generation time resulting from the self-loop trick used by Lande reflects the shift toward older individuals in the stable age distribution when $\lambda < 1$; if λ is increased to 1.01, $\overline{A}$ for the untruncated life cycle is only 18 years and is reduced only 2% by truncation. The cohort generation time, T_c, is unaffected by the stable age distribution [cf. Eqs. (11) and (12)]. Its value for the untruncated life cycle (with $\lambda = 0.961$) is 20 years, and it is reduced by only approximately 4% by the truncation.

Of course, calculating the age at truncation to yield some proportion y of surviving adults may have no connection with the actual senescence process in the population under study. In the Florida Scrub Jay *Aphelocoma c. coerulescens*, for example, mortality seems to increase sharply by age 12 (Fitzpatrick and Woolfenden, 1989, and personal communication), whereas its truncation age (for $y = .01$) is approximately 30. The true value of $\overline{A}$ will depend upon the extent to which the actual patterns of

mortality represent significant truncation of the life span as compared to the "infinite tail" model; as we have seen $\overline{A}$ is also magnified when $\lambda < 1$ (which cannot, of course, be an equilibrium situation). Studies that are continued long enough to estimate the actual extent of senescent mortality are needed to determine its effects on demographic parameters.

6.6. Estimating Parameters by Assuming Zero Growth

Henny et al. (1970) introduced another use of the characteristic equation, which we can generalize using the life cycle graph. If we assume that the population is stationary and substitute $\lambda = 1$ into the characteristic equation, we can then solve for the value of any single parameter in the life cycle. This has two potential uses. The first is for estimating values that are necessary to maintain the population. The second is for estimating the value of an unmeasurable parameter in a case where the assumption of stationarity seems reasonable. In the latter case, calculation of λ from the resulting matrix would obviously be circular. However, the matrix can be used to calculate other quantities, particularly sensitivities, and to the extent that the sensitivities are not heavily dependent on the value of the parameter estimated (which can be checked by simulation), the method has real value. For applications in fisheries, see DeAngelis et al. (1980). McDonald (1993) used the stationarity assumption to convert age-specific relative copulatory success of male Long-tailed Manakins into estimates of the fertility coefficients, F_i. Because the characteristic equation was lengthy (many stages), McDonald used successive trial-and-error matrix computations rapidly to adjust the absolute values of the F_i distribution, while maintaining the relative distribution of mating success. The stationarity assumption is usually justified by arguing that a population that is neither extinct nor increasing to infinity must have a mean rate of increase of zero. While this is true, the population can spend different amounts of time increasing and decreasing, with important implications for demography and sensitivity (Caswell, 1982).

7. A CASE STUDY—FLORIDA SCRUB JAYS

In this section, we present a complete demographic analysis of a life table from the landmark study of Florida Scrub Jays by Woolfenden and Fitzpatrick (1984). Florida Scrub jays are cooperative breeders. Individuals only rarely begin breeding at age 1; usually they remain in their natal territory as helpers for one or a few years before becoming breeders. Annual survival of helpers increases to age 3 but is lower than that of experienced

breeders of the same age. Birds breeding for the first time (novice breeders) have lower fertility and survival than do experienced breeders.

7.1. Constructing a Stage-Classified Life Cycle Graph

Although Woolfenden and Fitzpatrick presented an $l_x m_x$ table in age-specific format (Table I from Table 9.10 of Woolfenden and Fitzpatrick, 1984), notice that many of the coefficients of Table I vary with social status rather than age. The m_x values, for example, are simply the fertilities of two categories—novice (0.786) or experienced (1.0) breeders—weighted by their frequencies (from the "proportion breeding" column). Likewise the l_x values are derived from death rates, d_x, for four categories (experienced breeders, first-year birds, second-year helpers, and older helpers), weighted by the proportion of breeders and helpers found at various ages. Note that the value for d_x of experienced breeders is shown as age independent. The age independence was data based for values to age 10 and then extrapolated to the presumed maximum age of 20 (Woolfenden and Fitzpatrick, personal communication; subsequent data show evidence of senescence at approximately age 12).

What would the analysis look like if we were to base it not solely on age (which lumps together individuals of very different status) but also on behaviorally important categories? The life cycle can be modelled as including six stages: first-year birds (F-y), second-year helpers (H 2), older helpers (H 3; third-year and older), novice second-year breeders (N 2), older novice breeders (N 3), and experienced breeders (E). The parameters necessary for construction of a stage-classified life cycle graph are listed in Table II. The transition probabilities B_i from helper to novice breeder status are given by

$$B_i = \frac{Nov_x}{1 - Exp_x}, \tag{26}$$

where Nov_x is the proportion of novice breeders at age x from Table I and Exp_x is the proportion of experienced breeders at age x. The survival probabilities are

$$P_i = 1 - d_x \text{ of first- and second-year birds } [i = (x + 1) = 1,2], \tag{27a}$$

$$P_3 = 1 - d_3 = 0.74 \text{ (third-year and older birds), and} \tag{27b}$$

$$P_E = 1 - d_x \text{ of experienced breeders} = 0.82. \tag{27c}$$

The fertility rates m_N and m_E are those of novice and experienced breeders, respectively. The resulting life cycle graph is shown in Figure 10. A few (proportion B_1) first-year birds breed, as shown by the self-loop on Node F-y. If they do not $(1 - B_1)$ they help and then either become novice

TABLE I
Life Table of the Florida Scrub Jay[a]

Age (x)	l_x	Death rate, d_x Breeder	Death rate, d_x Helper	Proportion breeding Novice, Nov_x	Proportion breeding Experienced, Exp_x	Fertility Novice, m_N	Fertility Experienced, m_E	m_x
0	1.000	—	0.66	0.000	—	0.000	—	0.000
1	0.339	0.18	0.36	0.040	0.000	0.786	—	0.031
2	0.210	"	0.26	0.500	0.040	"	1.000	0.433
3	0.172	"	0.26	0.366	0.540	"	"	0.828
4	0.140	"	0.26	0.084	0.906	"	"	0.972
5	0.115	"		0.010	0.990		"	0.998
6	0.094	"		0.000	1.000		"	1.000
7	0.077	"		"	"		"	"
8	0.063	"		"	"		"	"
9	0.052	"		"	"		"	"
10	0.043	"		"	"		"	"
11	0.035	"		"	"		"	"
12	0.029	"		"	"		"	"
13	0.023	"		"	"		"	"
14	0.019	"		"	"		"	"
15	0.016	"		"	"		"	"
16	0.013	"		"	"		"	"
17	0.011	"		"	"		"	"
18	0.009	"		"	"		"	"
19	0.007	"		"	"		"	"
20	0.006	"		"	"		"	"

[a]From Woolfenden and Fitzpatrick (1984), Table 9.10, with permission.

TABLE II
Parameters used in Constructing Stage-Classified Model of the Florida Scrub Jay

Parameter	Description	Notes
B_1	Probability of first breeding at age 1 (0.04)	Eq. (26)
B_2	Probability of first breeding at age 2 (0.521)	"
B_3	Probability of first breeding at age 3 (0.796)	"
B_4	Annual probability of first breeding at age $\geq$ 4 (0.894)	"
P_1	First-year survival (0.339)	Eq. (27a)
P_2	Second-year survival (0.64)	"
P_3	Annual survival of older novice breeders and helpers (0.74)	Eq. (27b)
P_E	Annual survival of experienced breeders (0.82)	Eq. (27c)
m_N	Fertility of novice breeders (0.582)	Table I
m_E	Fertility of experienced breeders (1.0)	Table I

breeders or continue helping as second-year birds. Stages $H3$, $N3$, and E contain individuals of various ages. The other stages are age graded. The nodes of the graph are numbered to facilitate construction of the corresponding matrix (the ordering scheme for the numbers makes no difference to the results). The numerical values of the coefficients are shown in Table III, which is the projection matrix corresponding to the life cycle graph of Figure 10.

Four of the six stages contribute offspring (denoted by arcs directed to Node F-y in the graph of Figure 10; these fertility coefficients are equivalent to the coefficients in the top row of the matrix of Table III). The productive stages include first-year birds that become breeders at age 1 (denoted by the self-loop on Node F-y), second-year novice breeders (an arc from $N2$), novice breeders third-year or older (an arc from Node $N3$), and experienced breeders (an arc from Node E). Remember that every fertility coefficient contains a survival term (cf., Figure 3 to see that the formulation here is based upon a postbreeding census). Further, the self-loop on Node F-y contains the further term B_1 for the conditional probability of breeding at age 1. Note also that the coefficient P_3 is age independent—individuals in the older helper stage return to that stage (via a self-loop) with a probability that depends upon their survival, P_3, and the probability of not becoming a novice breeder, given by $1 - B_4$. Thus, transition rates may contain component terms related to fertility, survival, and probabilities of change in status, such as the B_i.

The model of Figure 10 is by no means the only way to describe this life cycle. For example, although we have distinguished between breeders and helpers in second-year and older birds, we have not done so for first-year birds, relying instead on the probability of first-year breeding (B_1) to sort
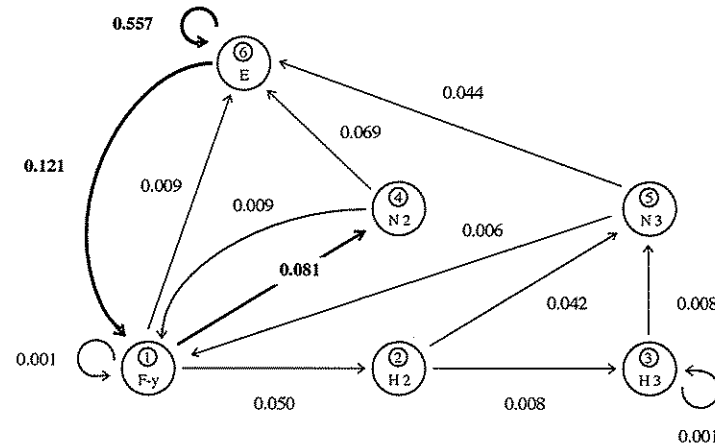
FIGURE 12. Elasticity graph for the stage-classified analysis of Florida Scrub Jays. The three transitions to which λ is most elastic are highlighted by bold lines. Note the small value of the elasticity coefficient for the transition from Node 1-F-y to Node 6-E. In the sensitivity analysis of Figure 11, λ was highly sensitive to this transition. Unlike the sensitivity graph, the elasticity graph can contain arcs only where arcs occurred in the original graph of Figure 10.

from second-year novice breeder to older novice). For this model, none of the nonexistent transitions is biologically plausible. With other models or life histories, however, nonexistent transitions might be plausible and the sensitivity might be of interest (e.g., fertility coefficients for third-year birds in a life history that presently begins reproduction in the fourth year).

Several points emerge from the analysis. In descending order, λ is most sensitive to (1) survival of experienced breeders, (2) the conditional probability that first-year birds will become experienced breeders, and (3) the conditional probability that first-year helpers will become second-year novice breeders. Any changes in these traits would have the greatest effect on λ (fitness). These highly sensitive transitions are highlighted by bolder lines on the arcs in Figure 11. The importance of transitions (2) and (3) would be masked in an analysis based solely on age. The elasticity analysis differs somewhat from the sensitivity analysis. The sensitive transition from first-year breeder to experienced breeder in Figure 11 has a small coefficient in the elasticity graph, shown in Figure 12. A proportional change in this trait has little impact, because it involves so few individuals (4% of first-year birds become novice breeders, the rest become helpers). Instead, in the elasticity analysis, experienced breeder survival is still most important, the production of offspring by experienced breeders becomes the second-ranking trait, and the transition from first-year helper to second-year novice breeder remains third ranked.

An advantage of the stage-structured formulation is that it highlights behaviorally important and notable features of the social biology of the jays. The sensitivity analysis weighs the importance of changes in reproductive status that are fundamental to the population dynamics. The stable stage distribution and reproductive values, shown in Table IV, refer not simply to age classes, but rather to behavioral categories readily apparent to a field worker (e.g., breeder vs. helper). Further, as shown in Table IV, one can generate means and variances for the ages of individuals in the various stages, when that is of interest (Cochran and Ellner, 1992). Thus, experienced breeders with a mean age of 6.2 years should constitute 42% of the population, if the model accurately describes the population dynamics. If a different population's proportion of breeders differed greatly, it would suggest that survival rates or breeding opportunities might be rather different from those of Woolfenden and Fitzpatrick's (1984) population. Even in the absence of long-term color banding, one could rapidly classify individuals into the categories shown here. The graph could also be collapsed into fewer, broader categories if data were scanty. One could then perform comparative analyses to explore differences among populations in one or more of those parameters that showed the greatest sensitivity. Analyses of such populations could constitute natural experiments of the sort described by Caswell (1989a; 1989b:139–151) as life table response experiments. Manipulative experiments, including habitat modification or the creation or elimination of breeding opportunities, would also be well suited to analysis by the techniques illustrated here and should be guided by consideration of the sensitivities.

7.3. Effect of Truncating the Life Span

Note that, as in Woolfenden and Fitzpatrick's original life table, the vital rates of Table I are truncated at age 20. The stage-classified model of Figure 10 does not truncate the life span. An "infinite tail" of possible survival exists (denoted by self-loops on Nodes H 3 and E in the life cycle graph). The results from an untruncated lifespan can be contrasted (Table V) with the results from analysis of a lifespan truncated at age 14; more recent data show 14 to be an approximate upper limit for Scrub Jay longevity (Fitzpatrick and Woolfenden, 1989 and personal communication). In order to model the truncated lifespan, Nodes H3 and E of Figure 10 must be expanded by age, and recruitment of individuals to novice and experienced status must be made age specific, so the resulting matrix is 28 × 28 (Nodes 2–7 are helpers, 8–14 are novice breeders, and 15–28 are experienced breeders). The difference between the model of Figure 10 and the age-expanded model with truncated life span is not that between a reduced vs. an unreduced version (cf., Section 6.2). Instead, the difference
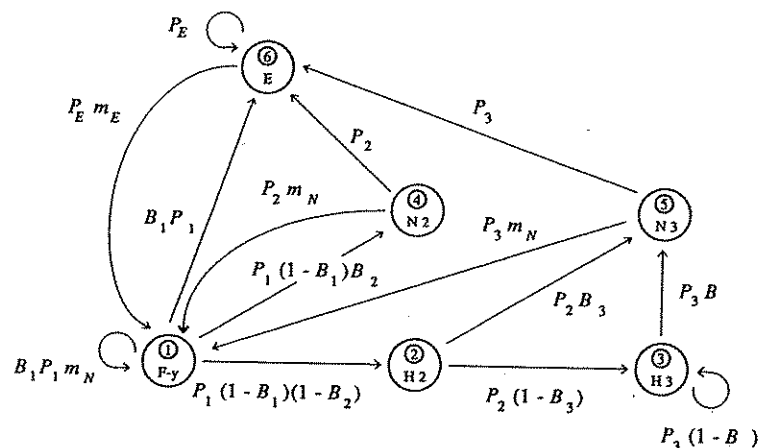
FIGURE 10. Life cycle graph for a stage-classified analysis of Florida Scrub Jays, based on the life table of Woolfenden and Fitzpatrick (1984). Nodes: 1-*F-y*, first-year birds; 2-*H* 2, second-year helpers; 3-*H*3, third-year and older helpers; 4-*N* 2, second-year novice breeders; 5-*N* 3, third-year and older novice breeders; 6-*E*, experienced breeders (second year or older).

out the contributions of the two categories. We could have created separate stages for first-year breeders and first-year helpers, at the expense of complicating the graph slightly. Recent evidence suggests that birds that breed for the first time in their third year or later experience lower survival and reproduction, compared to those that breed for the first time in their first or second year (J. Fitzpatrick and G. Woolfenden, personal communication). We could, therefore, have distinguished "fast" and "slow" categories among the experienced breeders, with only a slight additional complication of the graph. We could have added nodes to incorporate the effects of territory quality. If we had more detailed age-specific data we could expand

TABLE III
Stage-classified Projection Matrix for
the Florida Scrub Jay

Stage	1-F-y	2-H 2	3-H 3	4-N 2	5-N 3	6-E
1-F-y	0.08			0.372	0.431	0.820
2-H 2	0.156					
3-H 3		0.131	0.079			
4-N 2	0.170					
5-N 3		0.509	0.662			
6-E	0.014			0.640	0.740	0.820

the nodes for the helper–breeder transitions to reflect changing age-specific transition rates. (Even if each stage were age specific but we retained the distinction between helpers and novice breeders of the same age, we would still have a model that was not purely age classified and that would have been impossible with conventional life table analyses). In other studies, one might find variables other than age and social status to be crucial to the population dynamics, and these could then serve as the basis for designing stages and their accompanying transition rates. The possibilities are limited only by our ability to envision biologically relevant stages and to estimate the transition rates between them.

7.2. Results of the Analysis

The value of λ using the stage-classified model is 1.00, equal to the growth rate of the life table method of Woolfenden and Fitzpatrick (1984). The sensitivity and elasticity coefficients are shown in Figures 11 and 12. (The entire analysis of the matrix required less than 30 seconds on a personal computer.) Although we have shown the sensitivities on a life cycle graph to promote intuitive appeal, it is worth remembering that the computed sensitivity matrix contains other nonzero coefficients corresponding to nonexistent arcs (see Section 4.1; e.g., s_{54}, given by the dotted arc in Figure 11, represents the sensitivity of λ to the nonexistent transition
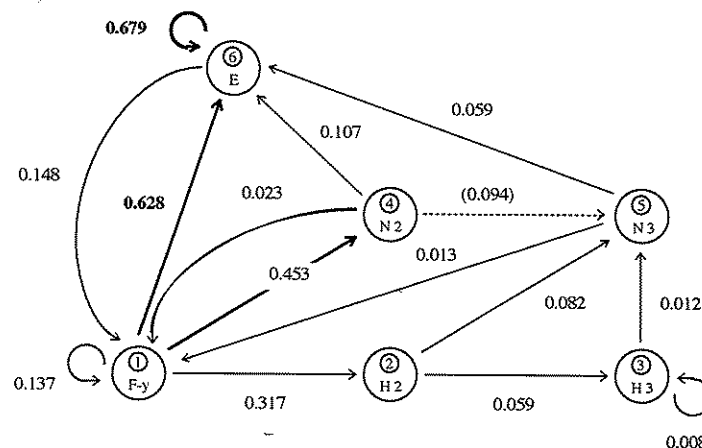

FIGURE 11. Sensitivity graph for the stage-classified analysis of Florida Scrub Jays. The three transitions to which λ is most sensitive are highlighted by bold lines. Only those sensitivities corresponding to existing (nonzero) transitions in the graph of Figure 10 are shown with solid arcs. The dotted arc is an example of a "nonexistent" (and in this case, impossible) transition for which a sensitivity can nonetheless be calculated.

TABLE IV

Reproductive Values, v, Stable
Stage Distribution, w, and Mean
Age at Start of Stage

Stage	v	w	Age ($\bar{x}$ ± s.d.)
1-F-y	1.00	0.403	0
2-H 2	2.33	0.063	1.0
3-H 3	2.77	0.009	2.08 ± 0.30
4-N 2	3.56	0.066	1.0
5-N 3	3.88	0.038	2.16 ± 0.40
6-E	4.47	0.420	6.19 ± 4.38

lies in whether the stages are age specific. Even in Figure 10 (before age expansion), no transition requires more than a year, which means that the graph was convertible directly into a matrix. As noted in Section 6.2, a reduced graph cannot be converted directly.

With the truncated life span analysis and its expanded age-specific nodes, sensitivities for experienced breeder survival at any given age are smaller than, for example, the sensitivity of first-year survival. In this more detailed model, the closest equivalent to the single experienced breeder survival sensitivity in the simple (untruncated life span) model is the sum of sensitivities to survival of all the experienced breeder age classes. Graphically, the single self-loop on Node E is expanded into 13 arcs denoting survival of experienced breeders from one age class to the next. It seems unlikely that either evolutionary or environmental factors would change survival from, say, age eight to age nine without also changing survival at all other adult ages. We therefore suggest presenting the summed adult sensitivities and elasticities when using an approach that incudes multiple stages or ages for adults. This is especially important when comparing a model with self-looped stages (e.g., Node E of Figure 10)

TABLE V

Parameters Obtained with Untruncated vs. Truncated Life Span Models for
the Florida Scrub Jay

	λ	$\bar{A}$	Sensitivities			Elasticities		
			F_s	P_s	G_s	F_e	P_e	G_e
Untruncated	1.00	6.5	0.15	0.66	1.38	0.12	0.54	0.26
Truncated	0.99	6.0	0.17	0.57	1.58	0.14	0.47	0.29

to an age-expanded model (e.g., our truncated life span example) or when comparing age-classified models for species with different life spans.

Table V compares various demographic parameters under the two variants of the model. The sensitivities of λ to fertility coefficients, F_s, and survival coefficients, P_s, for experienced breeders are compared, as well as the summed transitions toward becoming an experienced breeder (i.e., all upward transitions in Figure 10), which we will denote as G_s. The corresponding elasticities are given as F_e, P_e, and G_e. The truncated life span yields a slightly lower λ (0.99 vs. 1.0) and a slightly shorter generation time (5.5. vs. 6.0 years) than the simple model of Figure 10.

8. SUMMARY AND SYNTHESIS

8.1. The Uses of Matrix Population Models

Caswell (1989b) makes a distinction between projection and forecasting. The former tells us what would happen if present trends continued and thus enlightens us about the present, as well as about the underlying processes. The latter purports to tell what will happen, perhaps with little insight into either process or present patterns. Caswell uses the analogy of a speedometer. It does not tell us that we _will_ arrive in Santa Rosalia from Uppsala in 12 hours, but that we _would if we_ maintained our present pace. As with the Hardy–Weinberg equilibrium in population genetics, demographic techniques point us to areas where assumptions are not met and allow us to make clearer, more precise predictions about the genetic or life history consequences of empirically observed demographic schedules. Most of the assumptions of matrix-based methods hold reasonably well for birds. Where the assumptions are clearly violated (e.g., if density dependence is important), the methods are usually readily extended to encompass relaxing the assumptions, either by simulation or by a slight modification of the basic approach (e.g., functions that modify the vital rates according to variation with time, space, or density).

In his important and influential treatise, Caughley (1977) dismissed matrix methods due to the difficulty of computation and to alleged problems that seem to result largely from mistakes of parameterization in the literature (see Jenkins, 1988, for a review of problems). We suggest (1) that matrix calculations are actually considerably simpler than other techniques, especially given the advances in microcomputers, (2) that sensitivity analysis is a powerful tool that is difficult with many other techniques but easy with matrix methods, (3) that the ability to crosscheck rapidly and to sketch alternatives provided by life cycle graphs is a valuable ancillary benefit, and (4) that the opportunity to used stage-classified models greatly expands the scope of potential analyses. These

factors combine to make matrices the method of choice for many evolutionary and management analyses of demographic problems.

8.2. Suggestions for Field Workers

An important implication of the methods presented here is that field workers have a simple but powerful method for allocating research effort (Lande, 1988a,b). At every stage of conducting a study, one can assess the sensitivity of λ to age- or stage-specific vital rates. Ornithologists traditionally have devoted considerable attention to measuring clutch size and production of offspring. If λ is relatively insensitive to these elements of the vital rates, but highly sensitive to adult survival, as seen in the Scrub Jay analysis of Section 7, then any increase in field effort might better be devoted to gaining a more accurate and precise estimate of the sensitive parameters, either by increasing the number of birds monitored at key stages or by engaging in long-term studies that yield sample sizes sufficient to estimate the parameters with greater confidence.

Further, because the analyses are readily performed, they should be a stock in trade of any field study that deals with demographic aspects of populations. Even crude approximations based on preliminary data or on data for similar species from the literature may yield insights as to fruitful areas for further exploration or experimentation. No study or collection of data can be free of assumptions. The advantage of life cycle graph and matrix approaches is that they force one to be explicit about many of the assumptions. For example, examining ways to collapse life cycle graphs can point out crucial stages or transitions and highlight areas where lack of data prevents full enumeration of vital rates for each stage or age class. Stage-based classifications allow analysis in terms of behaviorally or ecologically important categories, even in the absence of long-term age-specific data. For example, in species for which habitat variation is the most important factor governing population dynamics, the stages used in developing the life cycle graph could incorporate transitions based on the distribution of food resources, vacancy rates as a function of territory quality, or the distribution of nest sites. Knowing the most sensitive transitions in the life cycle, a field worker would be prepared to search for behavioral or environmental changes that could affect the distribution of sensitivities.

8.3. Synthetic and Comparative Analyses

Just as fruitful links have arisen between behavioral ecology and molecular biology, so matrix and other demographic techniques provide links between studies in genetics, behavioral ecology, and population biology. Sensitivity analysis, for example, is important partly because of its equivalence to selection gradients in the quantitative genetics models of Lande (1982a,b) and Arnold and Wade (Arnold, 1983; Arnold and Wade, 1984a,b). As a result, another link exists between two major bodies of theory that relate to the evolution of life history traits. The potential topics addressed by matrix-based models range into chaotic sex ratios (Caswell and Weeks, 1986), chaotic population growth (Caswell, 1989b), bet hedging, optimal clutch size, brood reduction, and extinction probabilities.

As long-term studies become available that provide data on demography as well as morphological and genetic data, important comparative treatments will become possible (Ricklefs, 1983). Even when data are scarce, projections based upon estimates or upon the range of values considered likely may yield insights into the stages at which selection is most likely to act strongly or the potential effects of differing survival or recruitment regimens on different populations. Further, stage-classified analyses allow comparative approaches when few age-specific data are available and can focus on important biological similarities that might be obscured by major differences in age structure.

8.4. Application to Conservation Problems

Although traditional concern for threatened and endangered species has often focused on the genetic consequences of small population size, the demographic consequences of habitat loss may generally present a more immediate threat of extinction (Mertz, 1971; Lande, 1988b; Lande and Orzack, 1988). Even when extinction is not an imminent threat, many populations may face changing environmental conditions in which the demographic consequences are more serious than the genetic consequences. Widespread use of a consistent and accessible method for assessing the demographic implications of habitat destruction, management plans, or harvesting is therefore an important goal. The techniques developed by Caswell (1989b), Lande (1988a,b), and others and outlined in this treatment provide such a framework. They provide a bases for decisions about which stages of the life cycle most need protection in order to maintain healthy populations. Again, stage-classified models allow the assessment not only of the effects of age structure but also of habitat modification or other environmental forces that influence population dynamics. For many endangered species, we do not have the luxury of time to conduct long-term or exhaustive studies. Matrix calculations allow one to use whatever data are available, with a minimum of expensive materials, to answer rapidly questions about whether habitat loss or harvesting have, or would have, significant impacts on the probability of persistence.

APPENDIX: GLOSSARY OF TERMS

Greek alphabet:

α: age at sexual maturity.

λ: population growth rate; factor by which the population grows over the *projection interval*.

τ: truncation parameter for assessing possible effects of senescence [see Eq. (25)].

ω: the number of stages or age classes in the life cycle, used as a summation index.

Roman alphabet:

a_{ij}: the element in row i and column j of the projection matrix.

A: The projection matrix. Bold upper case letters denote matrices.

$\overline{A}$: The mean age of parents of offspring produced by a population that has achieved a *stable age distribution* [see Eq. (12); cf. T_c and T].

Arc: The directed line joining one *node* to another in the *life cycle graph*. An arc represents the contribution of individuals, by survival, transition probability, or reproduction, from one node (stage) to another.

Birth-flow reproduction: reproduction that occurs continuously rather than with a sharp peak.

Birth-pulse reproduction: reproduction that can be abstracted as occurring at a single point in time and modelled using discrete methods (see *birth-flow reproduction*).

Characteristic equation: an equation whose roots are the eigenvalues of a matrix.

Cohort generation time: see T_c.

e_{ij}: coefficients of the elasticity matrix, given by Eq. (16).

Eigenvalues: the roots of the characteristic equation [see Eqs. (9a,b)] for population growth. The dominant eigenvalue, λ_1, gives the population growth rate and can be used as a measure of fitness.

Eigenvector: a column vector, c, such that $\mathbf{Bc} = \lambda\mathbf{c}$ or a row vector, r, such that $\mathbf{rB} = \mathbf{r}\lambda$ are said to be eigenvectors of the matrix B; that is, a vector such that its multiplication by the matrix has the same

effect as its multiplication by a scalar (every coefficient grows or shrinks by the same factor). v and w are the eigenvectors of the projection matrix, A.

Elasticity: the effect on λ (fitness) of a <u>proportional</u> change in one of the a_{ij}, (st)age-specific vital rates (see *sensitivity*).

Fecundity: potential production, as opposed to *fertility*, which is actual production.

Fertility: actual, as opposed to potential, production, which is called *fecundity*.

F_i: the "fertility" entries in the demographic matrix [see Eqs. (6a,b)]. F_i will contain both production (m_i) and survival terms. Calculation from the $l_x m_x$ table depends upon the time of the census.

i: subscript for discrete age classes or stages, as opposed to subscript x for age, which is continuous (see Fig. 2).

l_x: "el ex" the survivorship, defined as the probability of survival from birth to age x. l_x is part of the $l_x m_x$ life table.

Leslie matrix: a demographic *projection matrix* for age-classified life histories. Only the top row and subdiagonal coefficients of the matrix have nonzero coefficients.

Life cycle graph: the graph theory equivalent of the demographic *projection matrix*. Nodes in the graph represent stages, while arcs represent transitions between stages.

Loop: *path* from a node back to itself in a *life cycle graph*. A *self-loop* is a loop of length 1, where length represents the number of *arcs*.

Loop transmission: the product of the coefficients of the arcs along a *loop*. The characteristic equation can be read as the summed loop transmissions.

m_i: the fertility (number of offspring) of an individual on its ith birthday. $m_i = m_x$ for birth-pulse reproduction, with either a prebreeding or postbreeding census.

m_x: "em ex" the number of offspring produced by an individual of age x.

Net reproductive rate: see R_o.

Node: represents an age class or stage in a *life cycle graph*.

P_i: survival from age class i to age class $i + 1$.

Path: sequence of *arcs* from one *node* to another, passing through no node more than once.

Projection interval: the time scale chosen for constructing a matrix population model; that is, the unit in which the difference between time t and time $t + 1$ is measured. For birds, the projection interval will usually be 1 year.

Projection matrix: a matrix of vital rates (fertilities, and survival rates or transition probabilities) from which one can assess demo-

graphic parameters (e.g., λ, reproductive value, sensitivities). Life cycle graphs and difference equations are equivalent, alternative formulations (Fig. 1).

Reproductive value: the contribution of an indivudal of stage i to future population growth (see Caswell, 1989b:67, 108, 136).

$R_\emptyset$: the expected number of offspring produced during an individual's lifetime [see Eqs. (10a,b)].

s_{ij}: coefficients of the sensitivity matrix, given by Eq. (14).

Scalar product: the sum of element by element multiplication of two vectors [see Eq. (15)].

Self-loop: a *loop* from a *node* directly back to itself (length of 1).

Sensitivity: a measure of the effect on λ (fitness) of an absolute change in a vital rate, holding all other rates constant [see Eq. (14); cf. *elasticity*].

Stable: a population that has achieved a *stable* (st)*age distribution* [cf. *stationary*].

Stable (st)age distribution, **w**: the proportion of individuals in each stage or age class once transient dynamics have passed. In the absence of forces other than those specified in the projection matrix (given irreducibility and primitivity), a population will eventually achieve a stable age distribution regardless of its initial distribution. **w** is the right eigenvector of the projection matrix.

Stationary: a population that is not growing ($R_\emptyset = 1.0$; $\lambda = 1.0$; $r = 0$) (cf. *stable*).

T: the time required for a population to grow by a factor $R_\emptyset$ [see Eq. (13); cf. $\overline{A}$ and T_c.] differs from T of Caughley (1977), which we call $\overline{A}$].

T_c: the cohort generation time, (μ_1 in Caswell, 1989b:110) [see Eq. (11); cf. $\overline{A}$ and T].

Transmission: product of the arc coefficients along a *loop* or *path*. Used in reading demographic parameters directly from z-transformed graphs (see Section 6.2.2).

Transpose: (1) make the rows of a matrix into columns and vice versa, or (2) reverse the direction of the arcs in a life cycle graph. (1) and (2) are mathematically equivalent operations.

v: vector (denoted by bold lower case letters) of *reproductive values*. The left eigenvector associated with λ. Usually adjusted so that v_1 is 1.0.

$\langle \mathbf{v},\mathbf{w} \rangle$: the *scalar product* of the vectors, **v** and **w**, element by element. Used in the calculation of sensitivities [see Eq. (14)].

w: vector of the *stable age distribution*. Usually normalized, so that it sums to 1.

x: subscript for age, which is continuous, in the $l_x m_x$ life table (cf. i).

z-transform: has the effect of multiplying each arc in the *life cycle graph* by λ^{-t}, where t is the time required for the transition (N.B. in a reduced graph t may be longer than the projection interval; a reduced graph cannot be converted to a matrix).

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