Chapter 2
Matrix Models as Building Blocks for Population Dynamics

In this chapter, we develop a "building block" approach to defining population dynamics models, in which each building block corresponds to one biological process, and is represented by one matrix (Lebreton 1973; Lebreton and Isenmann 1976; Buckland et al. 2004, 2007). Matrix models are usually defined within a deterministic framework, but we will need stochastic models. Thus we will think of the matrix as a mathematical tool for telling us how many animals of each type we expect to have in our population once the process (e.g. survival, birth, movement) has occurred, given the numbers present beforehand. We separately specify the probability distribution associated with the process, which will determine the actual numbers of each type. We refer to the types of animal as *states*.

We will introduce each process using a simple example to aid understanding, then define it in more general terms. We will assume that the natural time unit is one year, although a shorter unit will often be appropriate. We will also assume that births are restricted to a short breeding season. The year is taken to run from one breeding season to the next. If the breeding season is not short, then the birth process operates alongside a death process, which would be better represented by continuous-time models. We can approximate such models in our framework by modelling births and deaths on say a daily basis through the breeding season.

Within a year, multiple biological processes typically occur, e.g. survival, birth and movement. At times these individual processes will be labelled sub-processes: the annual changes in numbers of animals are a reflection of an annual process, which in turn is the consequence of multiple sub-processes. Further, in the constructions that follow, sub-processes are treated as if they occur sequentially in discrete, non-overlapping time intervals; e.g. mortality takes place, then births occur, then movement, and so on. Temporal overlapping of sub-processes can in fact occur so long as the overlapping sub-processes are affecting different categories or sub-populations; otherwise, the following formulations are approximations.

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2.1 Using Matrices to Represent Processes Within a Single Population

Caswell (2001) gives a comprehensive account of matrix population models, and of properties of matrices relevant to modelling population dynamics. In this book, we need to know remarkably little about matrices. The basic property of matrix multiplication is needed to understand the expected effect on states of processes. Suppose A is a 2×2 matrix comprising four values a_{11}, a_{12}, a_{21} and a_{22}, and $\mathbf{b}$ is a column vector of length two (i.e. it is a 2×1 matrix) with elements b_1 and b_2. Then the product $A\mathbf{b}$ is given by

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} = \begin{bmatrix} a_{11}b_1 + a_{12}b_2 \\ a_{21}b_1 + a_{22}b_2 \end{bmatrix}.$$

For example

$$\begin{bmatrix} 1 & 2 \\ 3 & 8 \end{bmatrix} \begin{bmatrix} 3 \\ 5 \end{bmatrix} = \begin{bmatrix} 13 \\ 49 \end{bmatrix}.$$

Note that in any product of two matrices, the number of columns of the first matrix must equal the number of rows of the second matrix. The number of rows of the product is equal to the number of rows of the first matrix, and the number of columns of the product is equal to the number of columns of the second matrix. More generally, if $\mathbf{A}$ is a $k \times m$ matrix and $\mathbf{B}$ is an $m \times n$ matrix, then the $k \times n$ matrix $\mathbf{AB}$ is given by:

$$\begin{bmatrix} a_{11} & \dots & a_{1m} \\ \vdots & \ddots & \vdots \\ a_{k1} & \dots & a_{km} \end{bmatrix} \begin{bmatrix} b_{11} & \dots & b_{1n} \\ \vdots & \ddots & \vdots \\ b_{m1} & \dots & b_{mn} \end{bmatrix}$$

$$= \begin{bmatrix} a_{11}b_{11} + \dots + a_{1m}b_{m1} & \dots & a_{11}b_{1n} + \dots + a_{1m}b_{mn} \\ \vdots & \ddots & \vdots \\ a_{k1}b_{11} + \dots + a_{km}b_{m1} & \dots & a_{k1}b_{1n} + \dots + a_{km}b_{mn} \end{bmatrix}.$$

Throughout this book, we use matrices, called *process matrices*, to define the sub-processes operating on our population of interest, and vectors, called *state vectors*, to represent the various categories or *states* of animal in our population. The start of the annual cycle will be defined for convenience, often immediately before or after the breeding season. The numbers of animals in each state at the end of year $t - 1$ will be represented by a vector $\mathbf{n}_{t-1}$, comprising elements $n_{j,t-1}$, for $j = 1, \dots, m$, where m is the number of distinct states of interest. After each sub-process, these numbers (or some of them) will change. We use the following notation to indicate numbers of animals in each of the m states after sub-process k has occurred in year t:

Survival

$$\begin{tikzcd}
n_{1,t-1} \arrow[r, dashed, "\phi_1"] & u_{1(s),1,t} \\
n_{2,t-1} \arrow[r, dashed, "\phi_2"] & u_{1(s),2,t}
\end{tikzcd}$$

Fig. 2.1 Starting with $n_{1,t-1}$ young animals and $n_{2,t-1}$ adults at the end of year $t-1$, we expect $\mathrm{E}(u_{1(s),1,t}) = n_{1,t-1}\phi_1$ young and $\mathrm{E}(u_{1(s),2,t}) = n_{2,t-1}\phi_2$ adults to survive through year t. The arrows are dashed to indicate that the processes are stochastic, so that in general $\mathrm{E}(u_{1(s),j,t}) \neq u_{1(s),j,t}$ for $j = 1, 2$. The rates associated with the processes are shown above the arrows

$$\mathbf{u}_{k(x),t} = \begin{bmatrix} u_{k(x),1,t} \\ \vdots \\ u_{k(x),m,t} \end{bmatrix}$$

where x is a letter indicating the type of sub-process: s is used to indicate survival, b for birth, a for age incrementation, r for growth, c for sex assignment, g for genotype allocation, and v for movement.

We use the same letters, but capitalized, to label our models. For example a BAS model is one with three sub-processes in a year, starting with survival, then age incrementation, and finally birth. The reason for reversing the chronological order of the sub-processes in these labels will become apparent.

2.1.1 Survival

Suppose we wish to model a single population of animals, divided into two states representing age classes, with $n_{1,t-1}$ newly born animals and $n_{2,t-1}$ adults at the end of year $t-1$. Then the expected number of survivors through year t can be expressed as

$$\begin{bmatrix} \mathrm{E}(u_{1(s),1,t}) \\ \mathrm{E}(u_{1(s),2,t}) \end{bmatrix} = \begin{bmatrix} \phi_1 & 0 \\ 0 & \phi_2 \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \end{bmatrix}, \tag{2.1}$$

where $u_{1(s),j,t}$ signifies the number of animals in state j after the first sub-process (survival) of year t has occurred, $\mathrm{E}(u_{1(s),j,t})$ denotes the corresponding expectation conditional on $n_{1,t-1}$ and $n_{2,t-1}$, and ϕ_j is the survival probability of animals in state j. The structure of Eq. (2.1) is shown diagrammatically in Fig. 2.1. We write Eq. (2.1) equivalently as $E(\mathbf{u}_{1(s),t}|\mathbf{n}_{t-1}) = \mathbf{S}\mathbf{n}_{t-1}$, where $\mathbf{S} = \begin{bmatrix} \phi_1 & 0 \\ 0 & \phi_2 \end{bmatrix}$ is the survival matrix.

We will also need to specify a probability distribution associated with the process. For survival, an obvious choice is the binomial, so that

$$\begin{pmatrix} u_{1(s),1,t} \sim \text{binomial}(n_{1,t-1}, \phi_1) \\ u_{1(s),2,t} \sim \text{binomial}(n_{2,t-1}, \phi_2) \end{pmatrix}. \tag{2.2}$$

We will develop this example in subsequent sections, where it will be referred to as Example 1.

More generally, suppose we have m states (types of animal), with survival rates $\phi_1, \ldots, \phi_m$. Then the expected numbers of survivors may be expressed

$$\begin{bmatrix} \text{E}(u_{1(s),1,t}) \\ \text{E}(u_{1(s),2,t}) \\ \vdots \\ \text{E}(u_{1(s),m,t}) \end{bmatrix} = \begin{bmatrix} \phi_1 & 0 & \ldots & 0 \\ 0 & \phi_2 & \ldots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & \phi_m \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \\ \vdots \\ n_{m,t-1} \end{bmatrix}$$

with $u_{1(s),j,t} \sim \text{binomial}(n_{j,t-1}, \phi_j)$ for $j = 1, \ldots, m$.

Available data may not support m distinct survival parameters. A simple solution is to explore models in which some of the survival parameters are set equal; for example, a common adult survival rate is often assumed. We explore more flexible solutions, in which survival is modelled as a function of covariates or as a random effect, in Sect. 2.2.

In our matrix formulations, wherever we see $\text{E}(\cdot)$ on the left-hand side, indicating expectation of a random variable, we will need to specify a probability distribution for the corresponding stochastic process. If there is no expectation, then the corresponding process is deterministic. We now consider the deterministic process of age incrementation.

2.1.2 Age Incrementation

In Example 1, there are just two age classes. Assuming young animals become adults by the end of their first year, we can represent this as a deterministic matrix model: all survivors are deemed to be adults by the time of the next breeding season. The number of animals after age incrementation at the end of year t, given the number of survivors, is known without error:

$$\begin{bmatrix} u_{2(a),2,t} \end{bmatrix} = \begin{bmatrix} 1 & 1 \end{bmatrix} \begin{bmatrix} u_{1(s),1,t} \\ u_{1(s),2,t} \end{bmatrix}. \tag{2.3}$$

Note that this can equivalently be written

$$\begin{bmatrix} 0 \\ u_{2(a),2,t} \end{bmatrix} = \begin{bmatrix} 0 & 0 \\ 1 & 1 \end{bmatrix} \begin{bmatrix} u_{1(s),1,t} \\ u_{1(s),2,t} \end{bmatrix}.$$

Age incrementation

$$\begin{tikzcd}
u_{1(s),1,t} \arrow[dr, "1"] & \\
u_{1(s),2,t} \arrow[r, "1"] & u_{2(a),2,t}
\end{tikzcd}$$

Fig. 2.2 Before age incrementation, we have $u_{1(s),1,t}$ young animals and $u_{1(s),2,t}$ adults in year t. After age incrementation, we have $u_{2(a),2,t} = u_{1(s),1,t} + u_{1(s),2,t}$ adults. The arrows are solid to indicate that the processes are deterministic, with $\mathrm{E}(u_{2(a),2,t}) \equiv u_{2(a),2,t}$. The rates associated with the processes are both unity because all animals follow the routes indicated by the arrows, and no new animals are generated

We adopt the convention that the dimension of the state vector is reduced when one or more states necessarily have no animals; the vector is then expanded again when a subsequent sub-process potentially generates animals that belong to these deleted states.

The effect of two ones in one row of a matrix is to combine two states; in this case, young and old animals. Equation (2.3) may be expressed diagrammatically as shown in Fig. 2.2. The model can equivalently be written $\mathbf{u}_{2(a),t} = \mathbf{A}\mathbf{u}_{1(s),t}$, where $\mathbf{A}$ is the age incrementation matrix. In fact, for this simple model and adopting the formulation of Eq. (2.3), $\mathbf{A}$ is a row vector, and $\mathbf{u}_{2(a),t}$ is a scalar.

If we have m states corresponding to ages 0, 1, 2, ..., then state m comprises all animals aged $m - 1$ or older. The following (deterministic) model ensures that each age class except the oldest moves up one year, and the two oldest age classes merge, at the year end. (The first entry of the state vector becomes $u_{2(a),2,t}$ because conceptually there are no animals in their first year until births occur.)

$$\begin{bmatrix} u_{2(a),2,t} \\ u_{2(a),3,t} \\ \vdots \\ u_{2(a),m-1,t} \\ u_{2(a),m,t} \end{bmatrix} = \begin{bmatrix} 1 & 0 & \ldots & 0 & 0 & 0 \\ 0 & 1 & \ldots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & \ldots & 1 & 0 & 0 \\ 0 & 0 & \ldots & 0 & 1 & 1 \end{bmatrix} \begin{bmatrix} u_{1(s),1,t} \\ u_{1(s),2,t} \\ \vdots \\ u_{1(s),m-2,t} \\ u_{1(s),m-1,t} \\ u_{1(s),m,t} \end{bmatrix}.$$

2.1.3 Growth

Suppose in Example 1, the two states are size classes rather than age classes, and suppose that at the year end, animals in the smaller size class move to the larger class with probability π. Animals in the larger class remain there. (The same model applies if the two classes correspond to immature and mature animals.) The expected numbers of animals in each state, conditional on the numbers before reallocation of animals according to their size, are then

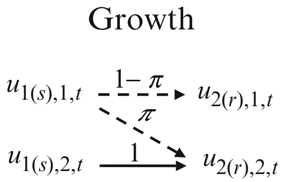

Fig. 2.3 Before growth, we have $u_{1(s),1,t}$ small animals and $u_{1(s),2,t}$ large animals in year t. After growth, we expect to have $\mathrm{E}(u_{2(r),1,t}) = (1-\pi)u_{1(s),1,t}$ small animals and $E(u_{2(r),2,t}) = \pi u_{1(s),1,t} + u_{1(s),2,t}$ large animals. The solid arrow with an associated rate of unity indicates that large animals remain large, while the dashed arrows indicate that the growth process for small animals is stochastic

$$\begin{bmatrix} \mathrm{E}(u_{2(r),1,t}) \\ \mathrm{E}(u_{2(r),2,t}) \end{bmatrix} = \begin{bmatrix} 1-\pi & 0 \\ \pi & 1 \end{bmatrix} \begin{bmatrix} u_{1(s),1,t} \\ u_{1(s),2,t} \end{bmatrix}, \tag{2.4}$$

which may also be expressed as $E(\mathbf{u}_{2(r),t}|\mathbf{u}_{1(s),t}) = \mathbf{R}\mathbf{u}_{1(s),t}$, where $\mathbf{R} = \begin{bmatrix} 1-\pi & 0 \\ \pi & 1 \end{bmatrix}$ is the growth matrix. This process is shown diagrammatically in Fig. 2.3.

As with survival, the binomial distribution is an appropriate model for stochasticity in the growth process:

$$\begin{pmatrix} u_{2(r),1,t} \sim \text{binomial}(u_{1(s),1,t}, 1-\pi) \\ u_{2(r),2,t} = u_{1(s),2,t} + (u_{1(s),1,t} - u_{2(r),1,t}) \end{pmatrix}. \tag{2.5}$$

If there are m size classes, and we allow animals in state j to remain the same with probability $1-\pi_j$ or move up one size class with probability π_j for states $1, 2, \ldots, m-1$, then

$$\begin{bmatrix} \mathrm{E}(u_{2(r),1,t}) \\ \mathrm{E}(u_{2(r),2,t}) \\ \mathrm{E}(u_{2(r),3,t}) \\ \vdots \\ \mathrm{E}(u_{2(r),m-1,t}) \\ \mathrm{E}(u_{2(r),m,t}) \end{bmatrix} = \begin{bmatrix} 1-\pi_1 & 0 & \ldots & 0 & 0 & 0 \\ \pi_1 & 1-\pi_2 & \ldots & 0 & 0 & 0 \\ 0 & \pi_2 & \ldots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & \ldots & \pi_{m-2} & 1-\pi_{m-1} & 0 \\ 0 & 0 & \ldots & 0 & \pi_{m-1} & 1 \end{bmatrix} \begin{bmatrix} u_{1(s),1,t} \\ u_{1(s),2,t} \\ u_{1(s),3,t} \\ \vdots \\ u_{1(s),m-1,t} \\ u_{1(s),m,t} \end{bmatrix}.$$

Note that, if we allow the possibility that an animal in the smallest size class remains there ($\pi_1 < 1$), then we do not lose state 1 at this stage, in contrast with the aging model.

2.1.4 *Birth*

For Example 1, suppose births take place after age incrementation. Thus last year's young have been combined with adults, and births create the new cohort of young animals. If the birth rate is denoted by ρ, then

Births

$$\begin{tikzcd}
 & u_{3(b),1,t} \\
u_{2(a),2,t} \arrow[ur, dashed, "\rho"] \arrow[r, "1"] & u_{3(b),2,t}
\end{tikzcd}$$

Fig. 2.4 Before births but after age incrementation, we have no young animals and $u_{2(a),2,t}$ adults in year t. After births, we expect to have $\mathrm{E}(u_{3(b),1,t}) = \rho u_{2(a),1,t}$ young animals, shown by the dashed arrow with associated rate ρ. The number of adults remains at $u_{3(b),2,t} = u_{2(a),2,t}$, indicated by a solid arrow with an associated rate of unity. The rates emanating from $u_{2(a),2,t}$ sum to $1 + \rho > 1$, indicating that new animals have been created

$$\begin{bmatrix} \mathrm{E}(u_{3(b),1,t}) \\ u_{3(b),2,t} \end{bmatrix} = \begin{bmatrix} \rho \\ 1 \end{bmatrix} \begin{bmatrix} u_{2(a),2,t} \end{bmatrix},$$

or equivalently, $E(\mathbf{u}_{3(b),t}|\mathbf{u}_{2(a),t}) = \mathbf{B}\mathbf{u}_{2(a),t}$ where $\mathbf{B} = \begin{bmatrix} \rho \\ 1 \end{bmatrix}$ is the birth matrix. (In this simple example, it is a column vector.) We illustrate this process in Fig. 2.4.

If each animal gives birth to at most one young per year, we might again invoke the binomial distribution:

$$\begin{pmatrix} u_{3(b),1,t} \sim \text{binomial}(u_{2(a),2,t}, \rho) \\ u_{3(b),2,t} = u_{2(a),2,t} \end{pmatrix}. \tag{2.6}$$

Thus the newly-born animals are placed in the recreated state for young animals, and the number of adults remains unchanged after the birth sub-process.

With m states, we have

$$\begin{bmatrix} \mathrm{E}(u_{3(b),1,t}) \\ u_{3(b),2,t} \\ u_{3(b),3,t} \\ \vdots \\ u_{3(b),m,t} \end{bmatrix} = \begin{bmatrix} \rho_2 & \rho_3 & \dots & \rho_m \\ 1 & 0 & \dots & 0 \\ 0 & 1 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 1 \end{bmatrix} \begin{bmatrix} u_{2(a),2,t} \\ u_{2(a),3,t} \\ \vdots \\ u_{2(a),m,t} \end{bmatrix}$$

where ρ_i is set to zero for states i that correspond to immatures or males.

To generalize the birth model, we need distributions that allow multiple births to a single mother. Possible distributions include the Poisson and negative binomial, but a more flexible choice is the multinomial distribution, where the number of trials is equal to the number of breeding females, and the probability that a female gives birth to i young is p_i for $i = 0, 1, \ldots$, with $\sum_i p_i = 1$ and $\rho = \sum_i i p_i$.

If the birth process completes the modelling of the annual cycle, then we have $u_{3(b),j,t} \equiv n_{j,t}$ for $j = 1, \ldots, m$.

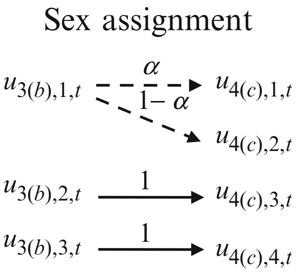

Fig. 2.5 Before sex assignment but after births, there are $u_{3(b),1,t}$ young animals in year t. We expect $\mathrm{E}(u_{4(c),1,t}) = \alpha u_{3(b),1,t}$ of these to be female, and the remainder male. For adult females, we have $u_{4(c),3,t} = u_{3(b),2,t}$, while for adult males, $u_{4(c),4,t} = u_{3(b),3,t}$

2.1.5 Sex Assignment

Commonly, only the female component of a population is modelled. Suppose we wish to add males to Example 1, and handle them as additional states. Thus we now have four states, corresponding to adult and young of each sex. We specify our sex assignment model conditional on number of births $u_{3(b),1,t}$. If $u_{3(b),2,t}$ is number of adult females, $u_{3(b),3,t}$ is number of adult males, and the probability that a young animal is female is α, then

$$\begin{bmatrix} \mathrm{E}(u_{4(c),1,t}) \\ \mathrm{E}(u_{4(c),2,t}) \\ u_{4(c),3,t} \\ u_{4(c),4,t} \end{bmatrix} = \begin{bmatrix} \alpha & 0\;0 \\ 1-\alpha & 0\;0 \\ 0 & 1\;0 \\ 0 & 0\;1 \end{bmatrix} \begin{bmatrix} u_{3(b),1,t} \\ u_{3(b),2,t} \\ u_{3(b),3,t} \end{bmatrix} \tag{2.7}$$

where $u_{4(c),1,t}$, $u_{4(c),2,t}$, $u_{4(c),3,t}$ and $u_{4(c),4,t}$ are numbers of newborn females, newborn males, adult females and adult males respectively. If this is the last process of the year, then $u_{4(c),j,t} \equiv n_{j,t}$ for $j = 1, 2, 3, 4$.

Equation (2.7) may be expressed as $E(\mathbf{u}_{4(c),t}|\mathbf{u}_{3(b),t}) = \mathbf{C}\mathbf{u}_{3(b),t}$, where $\mathbf{C}$ is the sex assignment matrix, and is represented by Fig. 2.5.

The binomial is the natural model for sex assignment:

$$\begin{pmatrix} u_{4(c),1,t} \sim \text{binomial}(u_{3(b),1,t}, \alpha) \\ u_{4(c),2,t} = u_{3(b),1,t} - u_{4(c),1,t} \\ u_{4(c),3,t} = u_{3(b),2,t} \\ u_{4(c),4,t} = u_{3(b),3,t} \end{pmatrix}.$$

If there are m age classes for each sex, then this generalizes straightforwardly:

$$\begin{bmatrix} \mathrm{E}(u_{4(c),1,t}) \\ \mathrm{E}(u_{4(c),2,t}) \\ u_{4(c),3,t} \\ u_{4(c),4,t} \\ \vdots \\ u_{4(c),2m,t} \end{bmatrix} = \begin{bmatrix} \alpha & 0\,0 \ldots 0 \\ 1-\alpha & 0\,0 \ldots 0 \\ 0 & 1\,0 \ldots 0 \\ 0 & 0\,1 \ldots 0 \\ \vdots & \vdots\ \vdots \ddots \vdots \\ 0 & 0\,0 \ldots 1 \end{bmatrix} \begin{bmatrix} u_{3(b),1,t} \\ u_{3(b),2,t} \\ u_{3(b),3,t} \\ u_{3(b),4,t} \\ \vdots \\ u_{3(b),2m-1,t} \end{bmatrix}.$$

2.2 Models Within Models

In the previous section, models were presented for which all animals in a given state were subject to the same processes with the same parameter values, and those values were treated as fixed over time. We require flexible models with more parameters, yet we are unlikely to have adequate data to fit large numbers of parameters. We consider two solutions to this dilemma, each of which appreciably enhances the capabilities and realism of our models.

2.2.1 Modelling Processes Through Covariates

The first process model we considered was survival. We specified that animals in state j all had the same survival rate ϕ_j. However, even for animals in the same state, the survival rate may vary according to many different factors. Suppose we wish to model first-year survival ϕ_1 as a function of winter rainfall r_t and total abundance $N_{t-1} = \sum_{j=1}^{m} n_{j,t-1}$ at the end of year $t-1$. We would like our model to respect the constraint that ϕ_1 must lie between zero and one. A logistic model is a natural choice:

$$\phi_{1,t-1} = \frac{1}{1+\exp\{\beta_0 + \beta_1 r_t + \beta_2 N_{t-1}\}}. \tag{2.8}$$

where $\phi_{1,t-1}$ is the probability that animals recruited into the population at the end of year $t-1$ survive to the end of year t. This incorporates an environmental effect, with $\beta_1 > 0$ if high winter rainfall increases first-year mortality, and density dependence, with $\beta_2 > 0$ if high abundance increases mortality. The above formulation corresponds to using a logit link function. Other link functions for binary data could also be used: the probit and the complementary log–log links (McCullagh and Nelder 1989:31).

This model allows ϕ_1 to be time-varying. We could also include covariates that vary by space (e.g. habitat) or by individual animal (e.g. weight). Thus individual-based models are feasible, without the necessity of more parameters than the data can support.

The rate parameters associated with other processes could be modelled similarly. For example the growth model parameter π of Sect. 2.1.3 might be modelled as a function of time spent in that size class and of resources available, or the birth rate ρ of Sect. 2.1.4 might be modelled as a function of the mother's weight, or a measure of her position in the social hierarchy, or of the habitat she occupies—or all three.

We note that some classic nonlinear, density-dependent population dynamic models such as the Beverton-Holt and Ricker models, which typically simultaneously incorporate survival and reproduction, can be extended to include covariates (Maunder and Deriso, 2011).

2.2.2 Processes as Random Effects

Often, we expect rates to vary but we do not have relevant covariates to model that variation. In this case, an option is to specify the rate as a random effect. For example, instead of specifying that the survival rate ϕ_j is the same for all animals in state j, we can assign a random distribution to ϕ_j, allowing it to vary in time, or by location, or by individual animal. A good candidate distribution is the beta distribution, which is constrained to lie between zero and one. Thus if we wish ϕ_j to vary by individual animal, instead of having to fit a different parameter for each animal (impossible in practice), we simply have to fit the two parameters of the beta distribution. For example, in the case of time-varying survival, for animals in state j at time t, the survival rate is $\phi_{j,t} \sim \text{beta}(\alpha_j, \beta_j)$. More commonly, random effects are assumed to be normal on some scale; in the case of modelling survival, the natural scale would be logit, ensuring that survival is constrained between zero and one. Such models as these where the parameters themselves are random variables are sometimes called hierarchical or multi-level models; random observations are at the lowest level and random parameters at higher levels. The parameters of the distributions at the higher levels are called hyperparameters.

Random effects and covariates can be combined in various ways to yield even more flexible models. For example, first-year survival in year t could be a function of a covariate, such as rainfall, and a random effect. Instead of Eq. (2.8), we might have

$$\phi_{1,t-1} = \frac{1}{1 + \exp(\beta_{0,t} + \beta_1 r_t)}$$

where

$$\beta_{0,t} \sim \text{normal}\left(\mu_0, \sigma^2\right).$$

This is an example of a nonlinear mixed effects model, where the effect of rainfall is a fixed effect and the intercept $\beta_{0,t}$ is a random effect.

Alternatively, the hyperparameters of a hierarchical model can be modelled as functions of covariates. Again referring to the example of first-year survival, one of the hyperparameters of the beta distribution could be a function of rainfall:

$$\phi_{1,t} \sim \text{beta}\left(\alpha(r_t), \beta_1\right)$$

where

$$\alpha(r_t) = \exp\left(\gamma_0 + \gamma_1 r_t\right).$$

2.3 Leslie Matrices and Lefkovitch Matrices

We now return to Example 1 with just two states, corresponding to the two age classes. We start the year just after the breeding season, so that the first process is survival, followed by age incrementation, and then births. Taking these in order, we have:

$$\begin{bmatrix} \mathrm{E}(u_{1(s),1,t}) \\ \mathrm{E}(u_{1(s),2,t}) \end{bmatrix} = \begin{bmatrix} \phi_1 & 0 \\ 0 & \phi_2 \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \end{bmatrix}$$

$$\begin{bmatrix} u_{2(a),2,t} \end{bmatrix} = \begin{bmatrix} 1 & 1 \end{bmatrix} \begin{bmatrix} u_{1(s),1,t} \\ u_{1(s),2,t} \end{bmatrix}$$

$$\begin{bmatrix} \mathrm{E}(n_{1,t}) \\ n_{2,t} \end{bmatrix} = \begin{bmatrix} \mathrm{E}(u_{3(b),1,t}) \\ u_{3(b),2,t} \end{bmatrix} = \begin{bmatrix} \rho \\ 1 \end{bmatrix} \begin{bmatrix} u_{2(a),2,t} \end{bmatrix}.$$

We may combine these into a single model simply by expressing the process matrices as a product in reverse chronological order:

$$\begin{bmatrix} \mathrm{E}(n_{1,t}) \\ \mathrm{E}(n_{2,t}) \end{bmatrix} = \begin{bmatrix} \rho \\ 1 \end{bmatrix} \begin{bmatrix} 1 & 1 \end{bmatrix} \begin{bmatrix} \phi_1 & 0 \\ 0 & \phi_2 \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \end{bmatrix}, \tag{2.9}$$

or alternatively, $E(\mathbf{n}_t | \mathbf{n}_{t-1}) = \mathbf{BASn}_{t-1}$. Evaluating the product, we obtain

$$\begin{bmatrix} \mathrm{E}(n_{1,t}) \\ \mathrm{E}(n_{2,t}) \end{bmatrix} = \begin{bmatrix} \rho\phi_1 & \rho\phi_2 \\ \phi_1 & \phi_2 \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \end{bmatrix}. \tag{2.10}$$

Provided that none of ϕ_1, ϕ_2 and ρ depend on numbers of animals present in year t, the expectations in the above expression are exact. For example Eq. (2.10) implies that $\mathrm{E}(n_{1,t}) = \rho\left(\phi_1 n_{1,t-1} + \phi_2 n_{2,t-1}\right)$. As the expectations are conditional

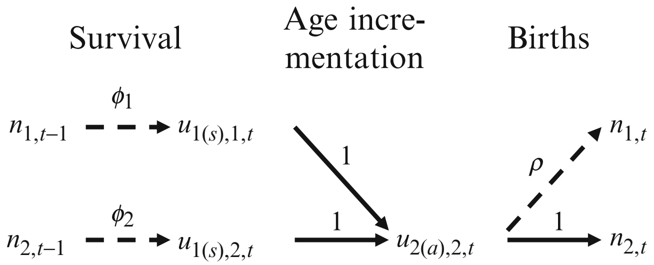

Fig. 2.6 In the BAS model, the sub-processes of Figs. 2.1, 2.2 and 2.4 are combined to create a model for which the annual processes, in chronological order, are survival (S), age incrementation (A) and births (B). Note that $n_{j,t} = u_{3(b),j,t}$ for $j = 1, 2$

on $n_{1,t-1}$ and $n_{2,t-1}$, then they hold if ϕ_1, ϕ_2 and ρ are either independent of numbers of animals in each state or dependent only on the states at time $t - 1$ (or earlier). However, density-dependent effects in the birth rate might be more plausibly modelled by expressing ρ as a function of $n_{2,t}$, as this is the number of breeding adults present at the end of year t when births occur. In this case, the above expectation no longer holds.

The above matrix representations are useful for defining and understanding models. As will be seen in Chap. 4, we can fit these models without having to assume that expectations of the type shown in Eq. (2.10) hold. When such methods are used, the approximation is of no consequence.

The significance of Eq. (2.10) is that the product of the process matrices is an example of a Leslie matrix (Leslie 1945, 1948; Caswell 2001:8–11). (Note that the standard Leslie matrix would have ρ where we have $\rho\phi_j$; in our formulation, animals must survive to the year end to breed.) We call the above model a BAS model, because the Leslie matrix is obtained by taking the product of the matrices corresponding to the processes birth (B), age incrementation (A) and survival (S), in that order. The model is shown diagrammatically in Fig. 2.6.

If we replace the deterministic age incrementation model of Eq. (2.3) by the growth model of Eq. (2.4), and assume that only animals in the larger class breed, then we obtain the following Lefkovitch matrix (Lefkovitch 1965; Caswell 2001:59):

$$\begin{bmatrix} \mathrm{E}(n_{1,t}) \\ \mathrm{E}(n_{2,t}) \end{bmatrix} = \begin{bmatrix} 1 & \rho \\ 0 & 1 \end{bmatrix} \begin{bmatrix} 1-\pi & 0 \\ \pi & 1 \end{bmatrix} \begin{bmatrix} \phi_1 & 0 \\ 0 & \phi_2 \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \end{bmatrix}$$
$$= \begin{bmatrix} (1-\pi+\rho\pi)\phi_1 & \rho\phi_2 \\ \pi\phi_1 & \phi_2 \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \end{bmatrix}. \qquad (2.11)$$

Taking the three matrices in the first line of Eq. (2.11) in reverse order, the first gives us the expected numbers of animals that survive the year, given the numbers alive at the start of the year; the second gives the expected numbers of survivors

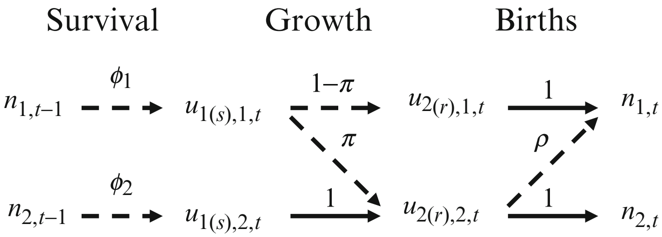

Fig. 2.7 In the BRS model, the sub-processes of Figs. 2.1, 2.3 and 2.4 are combined to create a model for which the annual processes, in chronological order, are survival (S), growth (R) and births (B). As in Fig. 2.6, $n_{j,t} = u_{3(b),j,t}$ for $j = 1, 2$

in the smaller size class that either remain in that size class or grow into the larger size class; and the third gives the expected number of newly-born animals that join the smaller size class. This is therefore a BRS model: the annual cycle starts with survival (S), then growth (R), and finally births (B) (Fig. 2.7). The Lefkovitch matrix of Eq. (2.11) is obtained as the matrix product **BRS**.

In general, if we take the product of the process matrices arranged in reverse chronological order, we obtain the *population projection matrix*[1]. Our modular approach allows for easy definition of more complex models. For example, if we retain the same processes as for the Leslie matrix of Eq. (2.10), i.e. survival, aging and births, but expand to include m states, then we obtain

$$\begin{bmatrix} \mathrm{E}(n_{1,t}) \\ \mathrm{E}(n_{2,t}) \\ \vdots \\ \mathrm{E}(n_{m,t}) \end{bmatrix} = \begin{bmatrix} \rho_2 & \rho_3 & \dots & \rho_m \\ 1 & 0 & \dots & 0 \\ 0 & 1 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & \dots & 0 & 0 & 0 \\ 0 & 1 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & 1 & 0 & 0 \\ 0 & 0 & \dots & 0 & 1 & 1 \end{bmatrix} \begin{bmatrix} \phi_1 & 0 & \dots & 0 \\ 0 & \phi_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \phi_m \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \\ \vdots \\ n_{m,t-1} \end{bmatrix}$$

$$= \begin{bmatrix} \rho_2\phi_1 & \rho_3\phi_2 & \dots & \rho_m\phi_{m-1} & \rho_m\phi_m \\ \phi_1 & 0 & \dots & 0 & 0 \\ 0 & \phi_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \\ 0 & 0 & \dots & \phi_{m-1} & \phi_m \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \\ \vdots \\ n_{m,t-1} \end{bmatrix}.$$

This model is shown diagrammatically in Fig. 2.8.

The sex assignment model of Sect. 2.1.5, with different survival rates for males and females as well as for adults and young, yields

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[1] Note that this matrix does not satisfy the definition of a projection matrix from linear algebra—the term "projection" is used here to indicate projection of the population from one time point to the next.

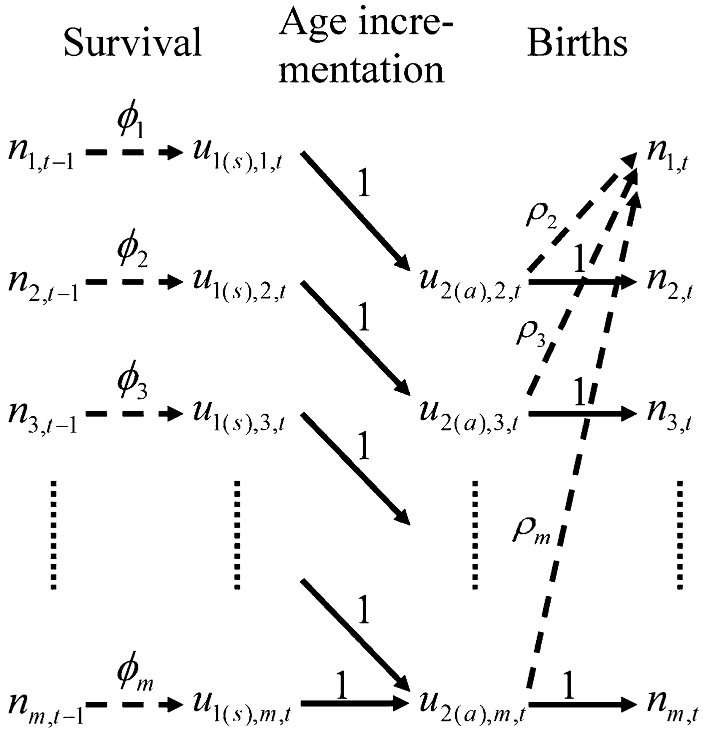

Fig. 2.8 The BAS model with *m* age classes. Compare this with Fig. 2.6

$$\begin{bmatrix} \mathrm{E}(n_{1,t}) \\ \mathrm{E}(n_{2,t}) \\ \mathrm{E}(n_{3,t}) \\ \mathrm{E}(n_{4,t}) \end{bmatrix} = \begin{bmatrix} \alpha & 0\,0 \\ 1-\alpha & 0\,0 \\ 0 & 1\,0 \\ 0 & 0\,1 \end{bmatrix} \begin{bmatrix} \rho & 0 \\ 1 & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} 1\,0\,1\,0 \\ 0\,1\,0\,1 \end{bmatrix} \begin{bmatrix} \phi_1 & 0 & 0 & 0 \\ 0 & \phi_2 & 0 & 0 \\ 0 & 0 & \phi_3 & 0 \\ 0 & 0 & 0 & \phi_4 \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \end{bmatrix}$$

$$= \begin{bmatrix} \alpha\rho\phi_1 & 0 & \alpha\rho\phi_3 & 0 \\ (1-\alpha)\rho\phi_1 & 0 & (1-\alpha)\rho\phi_3 & 0 \\ \phi_1 & 0 & \phi_3 & 0 \\ 0 & \phi_2 & 0 & \phi_4 \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \end{bmatrix}. \qquad (2.12)$$

The four matrices that combine to form the generalized Leslie matrix of Eq. (2.12) correspond to the following sub-processes. First chronologically but last of the four matrices in the first line of Eq. (2.12) is the matrix that handles the survival process (S) of young and adult males and females. Next comes age incrementation (A), where young females merge with the adults, and similarly for males, temporarily resulting in just two states: adult females and adult males. The matrix for the birth process (B) comes next, generating a single state for newly-born animals.

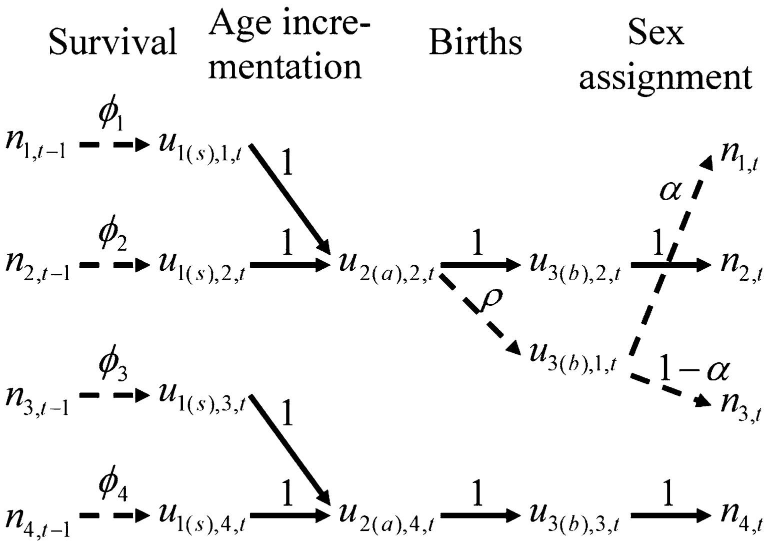

Fig. 2.9 The CBAS model: Example 1 with the addition of male animals. The *top row* corresponds to young females, then adult females, followed by young males and finally adult males. The *extra row* in the middle in the column for the birth sub-process corresponds to young before assignment of sex

Finally comes sex assignment (C), where this state is separated out into males and females. The matrix product **CBAS** therefore yields the generalized Leslie matrix. This CBAS model is illustrated in Fig. 2.9.

Even for such a simplistic model for population dynamics, it is starting to become apparent how much easier it is to formulate the model using this modular approach rather than direct specification of the population projection matrix. Caswell (2001:60) provides an example of how easily an error can occur in model formulation with the latter approach.

2.4 Using Matrices to Represent Processes of Multiple Populations

Here we consider situations where there are either subpopulations within a given species which are distinguished by criteria other than age or sex, or multiple populations of different species. In the former case we give two examples: one where the subpopulations are different genotypes of the same species and another where the subpopulations occupy different distinct locations, with some degree of movement between locations, and thus form a metapopulation. We could have included two-sex models in this section, but we chose to cover sex assignment within Sect. 2.1 because we consider that the state corresponding to the sex of an animal is one of the fundamental states in any population dynamics model, even if for many purposes, it is sufficient to model the female component of the population only.

We first consider how offspring may be assigned to genotype, so that the population is split into genotypes. We then show how to model movement between the components of a metapopulation. Next we develop multiple-species models, first to show how inter-species competition might be addressed, then to illustrate how predator-prey systems may be modelled using our framework.

2.4.1 Modelling Genotypes

Suppose animals are classified as to whether they are first-year or older (adult), whether they are male or female, and whether they have two dominant genes at a particular locus (DD), a dominant and recessive gene (Dd), or two recessive genes (dd). Suppose further that age incrementation is sub-process k in the annual cycle, so that just after age incrementation in year t, we have $u_{k(a),1,t}$ adult females of type DD, $u_{k(a),2,t}$ adult males of type DD, $u_{k(a),3,t}$ adult females of type Dd, $u_{k(a),4,t}$ adult males of type Dd, $u_{k(a),5,t}$ adult females of type dd, and $u_{k(a),6,t}$ adult males of type dd. We first consider the expected number of young born to each female genotype. For simplicity, we assume that all genotypes have the same birth rate. Denoting number of births to females of type DD by $u_{k+1(b),1,t}$, number of births to females of type Dd by $u_{k+1(b),2,t}$, and number of births to females of type dd by $u_{k+1(b),3,t}$, we have

$$\begin{bmatrix} \mathrm{E}(u_{k+1(b),1,t}) \\ \mathrm{E}(u_{k+1(b),2,t}) \\ \mathrm{E}(u_{k+1(b),3,t}) \\ u_{k+1(b),4,t} \\ u_{k+1(b),5,t} \\ \vdots \\ u_{k+1(b),9,t} \end{bmatrix} = \begin{bmatrix} \rho\,0\,0\,0\,0\,0 \\ 0\,0\,\rho\,0\,0\,0 \\ 0\,0\,0\,0\,\rho\,0 \\ 1\,0\,0\,0\,0\,0 \\ 0\,1\,0\,0\,0\,0 \\ \vdots\;\vdots\;\vdots\;\vdots\;\vdots\;\vdots \\ 0\,0\,0\,0\,0\,1 \end{bmatrix} \begin{bmatrix} u_{k(a),1,t} \\ u_{k(a),2,t} \\ u_{k(a),3,t} \\ u_{k(a),4,t} \\ u_{k(a),5,t} \\ u_{k(a),6,t} \end{bmatrix}.$$

We now need to reallocate the births, not according to the genotype of the mother, but according to the genotype of the young. Denote the probability that the father of a young animal has genotype DD, given that the mother is of type DD, by $\psi_{DD|DD}$, the probability that the father has genotype Dd, given that the mother has genotype DD, by $\psi_{Dd|DD}$, and so on. Then we can express the probability that a young animal is of a given genotype, given the genotype of the mother, as follows: $\eta_{DD|DD} = \psi_{DD|DD} + \frac{1}{2}\psi_{Dd|DD}$; $\eta_{DD|Dd} = \frac{1}{2}\psi_{DD|Dd} + \frac{1}{4}\psi_{Dd|Dd}$; $\eta_{Dd|DD} = \frac{1}{2}\psi_{Dd|DD} + \psi_{dd|DD}$; $\eta_{Dd|Dd} = \frac{1}{2}(\psi_{DD|Dd} + \psi_{Dd|Dd} + \psi_{dd|Dd})$; $\eta_{Dd|dd} = \frac{1}{2}\psi_{Dd|dd} + \psi_{DD|dd}$; $\eta_{dd|Dd} = \frac{1}{4}\psi_{Dd|Dd} + \frac{1}{2}\psi_{dd|Dd}$; $\eta_{dd|dd} = \frac{1}{2}\psi_{Dd|dd} + \psi_{dd|dd}$. Let $u_{k+2(g),1,t}$ be the number of young of genotype DD, $u_{k+2(g),2,t}$ the number of young of genotype

Dd, $u_{k+2(g),3,t}$ the number of young of genotype dd, $u_{k+2(g),4,t}$ the number of adult females of genotype DD, and so on. Then conditional on the numbers of young born to each female genotype, expected numbers are:

$$\begin{bmatrix} \mathrm{E}(u_{k+2(g),1,t}) \\ \mathrm{E}(u_{k+2(g),2,t}) \\ \mathrm{E}(u_{k+2(g),3,t}) \\ u_{k+2(g),4,t} \\ u_{k+2(g),5,t} \\ \vdots \\ u_{k+2(g),9,t} \end{bmatrix} = \begin{bmatrix} \eta_{DD|DD} & \eta_{DD|Dd} & 0 & 0\;0 \ldots 0 \\ \eta_{Dd|DD} & \eta_{Dd|Dd} & \eta_{Dd|dd} & 0\;0 \ldots 0 \\ 0 & \eta_{dd|Dd} & \eta_{dd|dd} & 0\;0 \ldots 0 \\ 0 & 0 & 0 & 1\;0 \ldots 0 \\ 0 & 0 & 0 & 0\;1 \ldots 0 \\ \vdots & \vdots & \vdots & \vdots\;\vdots \ddots \vdots \\ 0 & 0 & 0 & 0\;0 \ldots 1 \end{bmatrix} \begin{bmatrix} u_{k+1(b),1,t} \\ u_{k+1(b),2,t} \\ u_{k+1(b),3,t} \\ u_{k+1(b),4,t} \\ u_{k+1(b),5,t} \\ \vdots \\ u_{k+1(b),9,t} \end{bmatrix}.$$

Assuming sex is independent of genotype, we can now assign sex to the young by extending the method of Sect. 2.1.5 appropriately.

Conditional on the $u_{k+1(b),j,t}$, we can specify the distributions of the $u_{k+2(g),j,t}$ as:

$$\begin{pmatrix} u_{k+2(g),1,t} &= r_{DD,DD} + r_{DD,Dd} \\ u_{k+2(g),2,t} &= r_{Dd,DD} + r_{Dd,Dd} + r_{Dd,dd} \\ u_{k+2(g),3,t} &= r_{Dd,dd} + r_{dd,dd} \\ u_{k+2(g),4,t} &= u_{k+1(b),4,t} \\ & \vdots \\ u_{k+2(g),9,t} &= u_{k+1(b),9,t} \end{pmatrix}$$

with

$$\begin{pmatrix} r_{DD,DD} &\sim \text{binomial}(u_{k+1(b),1,t}, \eta_{DD|DD}) \\ r_{Dd,DD} &= u_{k+1(b),1,t} - r_{DD,DD} \\ (r_{DD,Dd}, r_{Dd,Dd}, r_{dd,Dd}) &\sim \text{multinomial}(u_{k+1(b),2,t}, \eta_{DD|Dd}, \eta_{Dd|Dd}, \eta_{dd|Dd}) \\ r_{Dd,dd} &\sim \text{binomial}(u_{k+1(b),3,t}, \eta_{Dd|dd}) \\ r_{dd,dd} &= u_{k+1(b),3,t} - r_{Dd,dd} \end{pmatrix}.$$

Note that $r_{Dd,DD}$ for example denotes the number of offspring from genotype DD females that are of genotype Dd.

Under a random mating model, we have $\psi_{DD|DD} = \psi_{DD|Dd} = \psi_{DD|dd} = u_{k(a),2,t}/(u_{k(a),2,t} + u_{k(a),4,t} + u_{k(a),6,t})$ and similarly for other probabilities. More strictly, these proportions should relate to when the animals mate. For example if they mate a year before births occur, then $\psi_{DD|DD}$ in year t should be $u_{k(a),2,t-1}/(u_{k(a),2,t-1} + u_{k(a),4,t-1} + u_{k(a),6,t-1})$.

This approach is readily extendible to more complex genetics models. However, it would be advisable to develop computer algorithms for the tedious task of model formulation! Even this simple model is too complex to illustrate diagrammatically, due to the large number of arrows that would be required—especially if matings were represented in the diagram.

2.4.2 Modelling Metapopulations

Returning to Example 1 with just two age classes (see Sect. 2.1.1), suppose our population occupies two distinct sites. Suppose further that movement occurs after winter survival, but before the breeding season. Let $u_{1(s),1,t}$ be the number of surviving young and $u_{1(s),2,t}$ number of surviving adults in site 1 in year t, and let $u_{1(s),3,t}$ and $u_{1(s),4,t}$ be the young and adult survivors in site 2. Let $\mu_{1\to 2}$ be the probability that an animal in site 1 moves to site 2, assumed for simplicity to be the same for young and adults, and similarly $\mu_{2\to 1}$ is the probability of movement from site 2 to site 1. If $u_{2(m),1,t}$ represents number of young in site 1 after movement, with corresponding definitions for adults in site 1 ($u_{2(m),2,t}$), and young ($u_{2(m),3,t}$) and adults ($u_{2(m),4,t}$) in site 2, then expected numbers after movement, given numbers before movement, are

$$\begin{bmatrix} \mathrm{E}(u_{2(m),1,t}) \\ \mathrm{E}(u_{2(m),2,t}) \\ \mathrm{E}(u_{2(m),3,t}) \\ \mathrm{E}(u_{2(m),4,t}) \end{bmatrix} = \begin{bmatrix} 1-\mu_{1\to 2} & 0 & \mu_{2\to 1} & 0 \\ 0 & 1-\mu_{1\to 2} & 0 & \mu_{2\to 1} \\ \mu_{1\to 2} & 0 & 1-\mu_{2\to 1} & 0 \\ 0 & \mu_{1\to 2} & 0 & 1-\mu_{2\to 1} \end{bmatrix} \begin{bmatrix} u_{1(s),1,t} \\ u_{1(s),2,t} \\ u_{1(s),3,t} \\ u_{1(s),4,t} \end{bmatrix}. \quad (2.13)$$

Assuming binomial distributions, we have

$$\begin{pmatrix} u_{2(m),1,t} = w_{3,t} + (u_{1(s),1,t} - w_{1,t}) \\ u_{2(m),2,t} = w_{4,t} + (u_{1(s),2,t} - w_{2,t}) \\ u_{2(m),3,t} = w_{1,t} + (u_{1(s),3,t} - w_{3,t}) \\ u_{2(m),4,t} = w_{2,t} + (u_{1(s),4,t} - w_{4,t}) \end{pmatrix}$$

where

$$\begin{pmatrix} w_{1,t} \sim \mathrm{binomial}(u_{1(s),1,t}, \mu_{1\to 2}) \\ w_{2,t} \sim \mathrm{binomial}(u_{1(s),2,t}, \mu_{1\to 2}) \\ w_{3,t} \sim \mathrm{binomial}(u_{1(s),3,t}, \mu_{2\to 1}) \\ w_{4,t} \sim \mathrm{binomial}(u_{1(s),4,t}, \mu_{2\to 1}) \end{pmatrix}$$

Putting all the sub-processes together, namely survival (S), movement (M), age incrementation (A) and birth (B), we have a BAMS model:

$$\begin{bmatrix} \mathrm{E}(n_{1,t}) \\ \mathrm{E}(n_{2,t}) \\ \mathrm{E}(n_{3,t}) \\ \mathrm{E}(n_{4,t}) \end{bmatrix} = \begin{bmatrix} \rho & 0 \\ 1 & 0 \\ 0 & \rho \\ 0 & 1 \end{bmatrix} \begin{bmatrix} 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix} \begin{bmatrix} 1-\mu_{1\to 2} & 0 & \mu_{2\to 1} & 0 \\ 0 & 1-\mu_{1\to 2} & 0 & \mu_{2\to 1} \\ \mu_{1\to 2} & 0 & 1-\mu_{2\to 1} & 0 \\ 0 & \mu_{1\to 2} & 0 & 1-\mu_{2\to 1} \end{bmatrix}$$

$$\times \begin{bmatrix} \phi_1 & 0 & 0 & 0 \\ 0 & \phi_2 & 0 & 0 \\ 0 & 0 & \phi_3 & 0 \\ 0 & 0 & 0 & \phi_4 \end{bmatrix} \begin{bmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \end{bmatrix}. \quad (2.14)$$

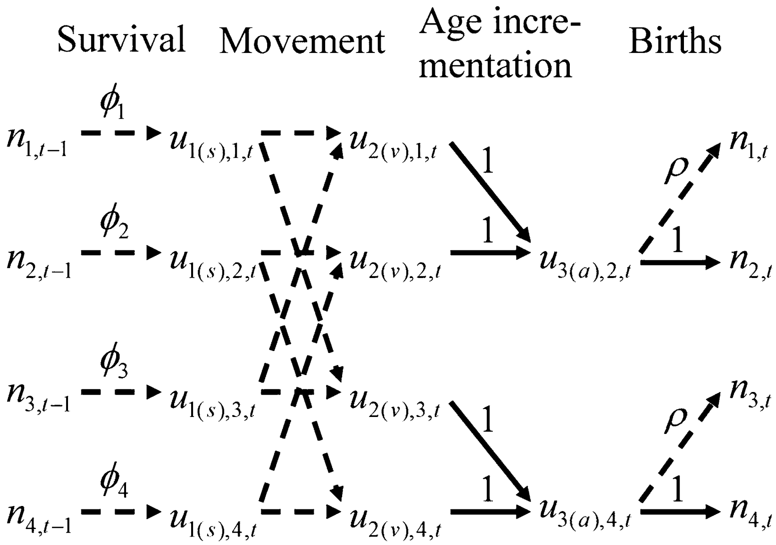

Fig. 2.10 The BAMS model: Example 1 but with two sites, and movement between them. The top row corresponds to young in site 1, then adults in site 1, followed by young in site 2 and finally adults in site 2. In this formulation, a different survival rate is assumed for each of the four states, but the birth rate ρ is assumed to be the same in each site. Within a site, young and adults have the same movement rate, but this is allowed to differ between sites. Rates associated with movement arrows are not plotted for clarity. The top two horizontal arrows have rate $1 - \mu_{1\to 2}$, the bottom two horizontal arrows have rate $1 - \mu_{2\to 1}$, the arrows from site 1 (top) to site 2 have rate $\mu_{1\to 2}$, and the arrows from site 2 to site 1 have rate $\mu_{2\to 1}$

Starting with the last of the projection matrices in Eq. (2.14), survival of the adults and young in each site is the first process of the year. The next matrix handles movement; diagonal terms correspond to animals that stay in their current site, while off-diagonal terms correspond to those that move. Age incrementation follows, in which the young animals at each site are merged with the adults, leaving just two states. The birth matrix then recreates four states, by generating newly-born animals in each site. The processes of this BAMS model are illustrated in Fig. 2.10.

Note that the movement sub-process matrix in Eq. (2.13) can be split into submatrices:

$$\begin{bmatrix} 1-\mu_{1\to 2} & 0 & \mu_{2\to 1} & 0 \\ 0 & 1-\mu_{1\to 2} & 0 & \mu_{2\to 1} \\ \mu_{1\to 2} & 0 & 1-\mu_{2\to 1} & 0 \\ 0 & \mu_{1\to 2} & 0 & 1-\mu_{2\to 1} \end{bmatrix} = \begin{bmatrix} M_{1\to 1} & M_{2\to 1} \\ M_{1\to 2} & M_{2\to 2} \end{bmatrix}$$

where $M_{1\to 1} = \begin{bmatrix} 1-\mu_{1\to 2} & 0 \\ 0 & 1-\mu_{1\to 2} \end{bmatrix}$ corresponds to animals that stay in site 1, $M_{2\to 1} = \begin{bmatrix} \mu_{2\to 1} & 0 \\ 0 & \mu_{2\to 1} \end{bmatrix}$ corresponds to animals that move from site 2 to site 1, and so on. Thus a general movement model is given by

$$\mathrm{E}(\mathbf{u}_{2(m),t}) = \begin{bmatrix} M_{1\to 1} & M_{2\to 1} & \ldots & M_{l\to 1} \\ M_{1\to 2} & M_{2\to 2} & \ldots & M_{l\to 2} \\ \vdots & \vdots & \ddots & \vdots \\ M_{1\to l} & M_{2\to l} & \ldots & M_{l\to l} \end{bmatrix} \mathbf{u}_{1(s),t}$$

where the vector $\mathbf{u}_{1(s),t}$ has elements equal to numbers of animals in each state before movement, and $\mathbf{u}_{2(m),t}$ represents numbers of animals by state after movement. For the case of just two states (age classes) per site, submatrix $M_{i\to j}$ is given by

$$M_{i\to j} = \begin{bmatrix} \mu_{i\to j} & 0 \\ 0 & \mu_{i\to j} \end{bmatrix}$$

for $i, j = 1, \ldots, l$, where $\mu_{i\to i} = 1 - \sum_{j\neq i} \mu_{i\to j}$ is the probability that an animal in site i remains there. For more states per site, these submatrices expand in the obvious way.

Given l sites, the numbers of animals at site i at time t that remain there or move to one of the other sites can be modelled by a multinomial

$$(u_{i\to 1}, \ldots, u_{i\to l}) \sim \text{multinomial}\,(\mu_{i\to 1}, \ldots, \mu_{i\to l})$$

where $\sum_{j=1}^{l} \mu_{i\to j}=1$. With the constraint on the sum of probabilities, there are $l-1$ movement parameters. Thus with l sites there are $l \times (l-1)$ parameters in total. Unless large-scale mark and release studies are carried out across all sites, empirical model-free estimates of $\mu_{i\to j}$ will generally not be available.

In the absence of individual site-to-site movement data, the use of covariates to model the movement parameters, as described in Sect. 2.2.1, is a pragmatic alternative. Site-specific information such as distances to other sites, animal densities at each site, and measures of site habitat quality are potential covariates. For example, Thomas et al. (2005) modelled the probability of movement between British grey seal colonies as a function of distance, animal density and site fidelity. Modelling must be constrained to ensure that the probabilities are non-negative and sum to one, but this can be easily handled by using exponential functions and then rescaling appropriately. Suppose one covariate x_1 is used. Then, for example,

$$\begin{aligned} p_{i\to j} &= \exp\left(\beta_0 + \beta_1 x_{1i} + \beta_2 x_{1j}\right) \\ \mu_{i\to j} &= \frac{p_{i\to j}}{\sum_l p_{i\to l}}. \end{aligned}$$

Hierarchical or random effects models can be used, in combination with any relevant covariates. Now (see Sect. 2.2.2) the movement parameters $\mu_{i \to j}$ are themselves random variables. A natural distribution for proportions that must sum to one is the Dirichlet distribution (a multivariate extension of the beta distribution). Similar to an example given in Buckland et al. (2004), suppose that there are three colonies in a metapopulation and that colony densities and distances between colonies affect the probability of movement. Consider movement from colony 2, for example:

$$(\mu_{2\to1}, \mu_{2\to2}, \mu_{2\to3}) \sim \text{Dirichlet}\,(\lambda_{2\to1}, \lambda_{2\to2}, \lambda_{2\to3})$$

with

$$\begin{aligned} \lambda_{2\to2} &= \exp(\beta_0) \\ \lambda_{2\to j} &= \exp\left(\beta_0 + \beta_1 N_{2t} + \beta_2 H_{2t} + \beta_3 N_{jt} + \beta_4 H_{jt} + \beta_5 d_{2j}\right), \quad j = 1, 3, \end{aligned}$$

where $\beta_1 > 0$, $\beta_2 < 0$, $\beta_3 < 0$, $\beta_4 > 0$ and $\beta_5 < 0$; N_{it} is the abundance at site i in year t, H_{it} is a measure of habitat quality with larger values indicating greater suitability, and d_{ij} is the distance between sites i and j. Given the parameters $\mu_{i\to j}$, movement is then modelled by a multinomial distribution.

2.4.3 *Multi-Species Models*

We can readily extend our models to multi-species systems by modelling rates for one species as functions of abundance of other species. For example, a competition model for a two-species system might make the survival or birth rate of one species a decreasing function of the abundance of the other. A predator-prey model might make the survival rate of the prey a decreasing function of the abundance of the predator, and the survival and birth rates of the predator an increasing function of the abundance of the prey. A host-parasite model might be similarly formulated. More complex interactions might be modelled for community models. For example, a model for marine fish stocks might allow adults of one species to prey on first-year fish of another, but to be prey for adults of the other species. It might also incorporate competition effects between species with similar diets, and movement rates might be modelled as functions of abundance of each species at different locations.

As an example of a multi-species model, we consider a system comprising one predator and two prey, with competition between the two prey species. Suppose we model the predator P in two age classes, first-year animals and adults. For simplicity, we model the two prey species A and B each as a single state. First-year survival of predators is assumed to depend on abundance of both prey species, whereas adult survival depends on abundance of species B alone. Species A is assumed to suffer a competition effect from species B, but not *vice versa*. All species show density dependence in their survival rates, but for the predators, this affects first-year survival alone. Then a simple model to describe this system is as follows.

Denote number of first-year predators, adult predators, prey species A and prey species B at the end of year t by $n_{0,t}$, $n_{1,t}$, $n_{A,t}$ and $n_{B,t}$ respectively. Assuming that mortality (S) first occurs, followed by age incrementation (A), and then births (B), we have a multi-species BAS model:

$$\begin{bmatrix} \mathrm{E}(n_{0,t}) \\ \mathrm{E}(n_{1,t}) \\ \mathrm{E}(n_{A,t}) \\ \mathrm{E}(n_{B,t}) \end{bmatrix} = \begin{bmatrix} \rho_P & 0 & 0 \\ 1 & 0 & 0 \\ 0 & 1+\rho_A & 0 \\ 0 & 0 & 1+\rho_B \end{bmatrix} \begin{bmatrix} 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$
$$\times \begin{bmatrix} \phi_{0,t-1} & 0 & 0 & 0 \\ 0 & \phi_{1,t-1} & 0 & 0 \\ 0 & 0 & \phi_{A,t-1} & 0 \\ 0 & 0 & 0 & \phi_{B,t-1} \end{bmatrix} \begin{bmatrix} n_{0,t-1} \\ n_{1,t-1} \\ n_{A,t-1} \\ n_{B,t-1} \end{bmatrix}$$

where ρ_P, ρ_A and ρ_B are the birth rates of predators, prey species A and prey species B respectively, and the survival parameters ϕ are defined as

$$\phi_{0,t-1} = \frac{1}{1+\exp\{\alpha_1 - \beta_1 n_{A,t-1} - \beta_2 n_{B,t-1} + \beta_3(n_{0,t-1} + n_{1,t-1})\}}$$
$$\phi_{1,t-1} = \frac{1}{1+\exp(\alpha_2 - \beta_4 n_{B,t-1})}$$
$$\phi_{A,t-1} = \frac{1}{1+\exp\{\alpha_3 + \beta_5 n_{A,t-1} + \beta_6 n_{B,t-1} + \beta_7(n_{0,t-1} + n_{1,t-1})\}}$$
$$\phi_{B,t-1} = \frac{1}{1+\exp\{\alpha_4 + \beta_8 n_{B,t-1} + \beta_9(n_{0,t-1} + n_{1,t-1})\}}$$

where the α and β are parameters (which may be estimated using the methods of Chap. 4), with each $\beta > 0$, and where for example $\phi_{A,t-1}$ is the probability that an animal of species A that is alive at the end of year $t-1$ survives to the end of year t. Note that the birth rates may similarly be modelled, for example to allow lower birth rates at high densities of a given species.

2.5 Beyond Matrix Models

Matrices are linear operators. Consider the BAS model defined by Eq. (2.9). We may rewrite this equation

$$\mathbf{n}_t = \tilde{L}_{t-1}(\mathbf{n}_{t-1})$$

where the *process operator* $\tilde{L}_{t-1}(\cdot)$ is the composition $\tilde{L}_{t-1}(\cdot) = \tilde{L}_{b,t}(\tilde{L}_{a,t}(\tilde{L}_{s,t-1}(\cdot)))$, and $\tilde{L}_{s,t-1}(\cdot)$, $\tilde{L}_{a,t}(\cdot)$ and $\tilde{L}_{b,t}(\cdot)$ are the survival, aging and birth operators respectively (Buckland et al. 2007). Note that, for consistency with notation elsewhere in this book, we have adopted a different convention from Buckland et al. (2007) in that we give the operator $\tilde{L}_{t-1}$ the same suffix as the state vector $\mathbf{n}_{t-1}$ on the right-hand side of the above equation, as the operator acts on $\mathbf{n}_{t-1}$, whereas Buckland et al. (2007) defined $\mathbf{n}_t = \tilde{L}_t(\mathbf{n}_{t-1})$, giving the operator the suffix corresponding to the state vector on the left-hand side. Similarly, we give the survival operator $\tilde{L}_{s,t-1}$ suffix $t-1$, but the aging and birth operators act on animals that have survived to the end of year t, so have suffixes t.

If all sub-processes are deterministic, we obtain the classical matrix model

$$\mathbf{n}_t = \mathbf{L}_{t-1}\mathbf{n}_{t-1},$$

where $\mathbf{L}_{t-1} = \mathbf{BAS}$ is typically a generalized Leslie or Lefkovitch matrix. Note that elements of $\mathbf{L}_{t-1}$ can depend on $\mathbf{n}_{t-1}$, in which case the model is nonlinear in the states. Thus for example density dependence can be modelled in this framework.

The special case of most interest here occurs when one or more of the sub-processes is stochastic, but the expected values of the elements of $\mathbf{n}_t$ may be expressed as functions of the elements of $\mathbf{n}_{t-1}$. Then

$$E(\mathbf{n}_t|\mathbf{n}_{t-1}) = \mathbf{L}_{t-1}\mathbf{n}_{t-1}, \tag{2.15}$$

where $\mathbf{L}_{t-1}$ is a population projection matrix such that $E(\tilde{L}_{t-1}(\mathbf{n}_{t-1})|\mathbf{n}_{t-1}) = \mathbf{L}_{t-1}\mathbf{n}_{t-1}$. The BAS model of Eq. (2.9) is an example of this, in which $\mathbf{L}_{t-1}$ is the Leslie matrix of Eq. (2.10).

If we take the model of Sect. 2.4.3, but model the predator birth rate ρ_P as a function of prey and/or predator abundance immediately preceding the births, then this yields a more general example, for which $E(\tilde{L}_{t-1}(\mathbf{n}_{t-1})|\mathbf{n}_{t-1}) \neq \mathbf{L}_{t-1}\mathbf{n}_{t-1}$, although if the nonlinearity is not strong, we might expect the result to hold approximately. The model fitting algorithms of Chap. 4 do not need Eq. (2.15) to hold.

2.6 Observation Matrices

For practical wildlife management, the ability to fit a population matrix model to a time series of data is important. To use the model fitting algorithms of Chap. 4, we need to specify distributions for observations that respect their relationship with the (usually unobserved) states in $\mathbf{n}_t$.

As in Sect. 2.5 for the process operator, we can define a general random operator for the observation process:

$$\mathbf{y}_t = \tilde{\mathbf{O}}_t(\mathbf{n}_t)$$

where $\mathbf{y}_t$ is a vector of observations for year t (Buckland et al. 2007). If the operator is linear, then we obtain the following observation equation:

$$\mathbf{y}_t = \mathbf{O}_t \mathbf{n}_t + \boldsymbol{\epsilon}_t$$

for the appropriate matrix $\mathbf{O}_t$. Assuming $E(\boldsymbol{\epsilon}_t|\mathbf{n}_t) = \mathbf{0}$, then

$$E(\mathbf{y}_t|\mathbf{n}_t) = \mathbf{O}_t \mathbf{n}_t. \tag{2.16}$$

In this formulation, we assume that the observations are taken at the end of year t. If this is not the case, then the state vector $\mathbf{n}_t$ in the above equation would be replaced by the appropriate intermediate state vector. For example, if population size was estimated after winter mortality occurs but before breeding starts, then the intermediate state vector would correspond to the survivors from the previous year.

As an example of an observation matrix, consider the BAMS model of Sect. 2.4.2. Suppose we have estimates $y_{1,t}$ and $y_{2,t}$ of total population size in site 1 and site 2 respectively at the end of year t (just after breeding). Suppose further that we assume that these estimates are independently normally distributed with variances σ_1^2 and σ_2^2 respectively. Then

$$\begin{bmatrix} y_{1,t} \\ y_{2,t} \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix} \begin{bmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \end{bmatrix} + \boldsymbol{\epsilon}_t \tag{2.17}$$

with $\boldsymbol{\epsilon}_t = \begin{bmatrix} \epsilon_{1,t} \\ \epsilon_{2,t} \end{bmatrix} \sim \text{normal}\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_1^2 & 0 \\ 0 & \sigma_2^2 \end{bmatrix} \right)$.

If the estimates of abundance are of adults only, then the observation matrix becomes $\mathbf{O}_t = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$.

Usually, the observational study in year t would provide estimates of σ_1^2 and σ_2^2. Often those estimates are treated as known values when fitting a state-space model to data as simultaneously estimating variances for the state process and for the observation model is often difficult due to identifiability problems (Dennis et al. 2006). An alternative, when using the Bayesian methods of Chap. 4, is to use these estimates to inform the prior distributions for σ_1^2 and σ_2^2 (although such double usage of the data is not strictly Bayesian).

The observations in the above example are single point estimates of the individual states along with estimates of the variances. Multiple point estimates of the individual states are easily incorporated by inserting additional components in the observation vector and duplicating rows in the observation matrix.

A less trivial variation in the observation model is to work with the *raw* sample data, the measurements actually made in the field say, rather than summaries of the sample data. Typically point estimates of state vector components will be summaries of the actual measurements taken. For example, mark-recapture studies might be carried out over a sequence of years and estimates of population abundance constructed from the data. Rather than treat the point estimates as observations, the mark recoveries could be the observations. This is an intuitively attractive idea in that all estimation is done in a single step and complete within-sample variation is retained. A practical limitation, in some situations, is that the raw data may be unavailable or difficult to access. A technical limitation is that, to use the raw data in a matrix model, the observations must be written as linear functions of the states. The ease with which such a linear mapping can be done will depend upon how the data were collected, and may in some cases, e.g. distance sampling, be at best cumbersome and at worst infeasible.

2.7 Defining a Population Dynamics Model

We consider two examples to illustrate the steps involved in formulating a matrix model for population dynamics. In the first, we develop a model for coho salmon and in the second a metapopulation of deer, comprising just two populations with movement between them. We will describe the dynamics in deterministic or expected value terms and in the next chapter we will develop a fully stochastic formulation.

2.7.1 Coho Salmon

The following description of a matrix model for coho salmon *Oncorhynchus kisutch* (Fig. 2.11) is based on a model described in Newman (1998). That model fitted recoveries (in samples taken from ocean fishery catches) of marked coho salmon released from a hatchery located on a river on the west coast of the Olympic Peninsula in Washington State USA. The population sub-processes included survival, movement in the ocean, harvest, and migration back to the natal river.

Juvenile coho salmon are bred and reared in a hatchery for approximately 18 months. They are then released from the hatchery in May to enter the river where they travel downstream to enter the Pacific Ocean. Shortly before release, the fish are marked (with a batch-specific mark). Upon entry to the ocean they disperse up and down the coast and experience natural mortality (from predators, disease, etc). About 14 months after entry (roughly July of the following year), they begin to be harvested by ocean fisheries in 12 different regions (management areas) along the coast. The ocean fishery operates for up to 16 weeks and then the surviving, and now mature adult fish, migrate back to the river where they are harvested in the river, return to the hatchery, or spawn in the river and die.

The data include the number of marked fish released from the hatchery (denoted R), the number of marked fish caught in the ocean fisheries, stratified

Fig. 2.11 Leaping coho salmon. Photo: courtesy of Northwest Indian Fisheries Commission

by management area and week ($y_{a,t}$ for area a, $a = 1, \ldots, 12$ and week t, $t = 1, \ldots, 16$), and the number of fish returning to the river as mature adults (y_T).

The matrix model is initialized by calculating a vector of abundances in the management areas prior to the fishing season, i.e. the initial state vector. First the expected total number of survivors (summed over all regions) from the R released fish to the beginning of the fishing season is determined, i.e. $R\phi_J$, where ϕ_J is the survival probability from time of release to beginning of fishing. The expected numbers per area are allocated using the probabilities for a beta(α_i, β_i) distribution, its domain being a line segment beginning at the southern boundary of the most southern fishing region to the northern boundary of the most northern fishing region, i.e. the values from the beta distribution are essentially latitudinal coordinates. The fishing regions are thus defined as a non-overlapping (and exhaustive) partitioning of the line segment into 12 individual segments. The expected initial abundance in area a is then $n_{a,0} = R\phi_J p_a$, where p_a is the probability of being present in area a.

The heart of the matrix model is the projection of the abundances by fishing management area on a week by week basis during the fishing season. The vector of abundances is denoted $\mathbf{n}_t' = [n_{1,t}, n_{2,t}, \ldots, n_{12,t}]$. At the beginning of each week, mortality occurs, a combination of natural and harvest mortality, and movement follows. The survival probability in a given area is $\phi_{a,t} = \exp(-N - F_{a,t})$, where N is the natural mortality rate parameter, assumed constant, and $F_{a,t}$ is the fishing mortality rate parameter (and is a function of the fishing effort in the area that week). Movement from one area to another is a function of location and time (details in

Newman 1998) and the probability of moving from area a to area b during week t is denoted $m_{a \to b,t}$. The expected abundances in week t are written as:

$$E[\mathbf{n}_t|\mathbf{n}_{t-1}] = \mathbf{M}_t\mathbf{S}_{t-1}\mathbf{n}_{t-1} \tag{2.18}$$

where

$$\mathbf{S}_{t-1} = \begin{bmatrix} \phi_{1,t-1} & 0 & \dots & 0 \\ 0 & \phi_{2,t-1} & \dots & 0 \\ \vdots & \vdots & \dots & \vdots \\ 0 & 0 & \dots & \phi_{12,t-1} \end{bmatrix} \tag{2.19}$$

and

$$\mathbf{M}_t = \begin{bmatrix} m_{1\to1,t} & m_{2\to1,t} & \dots & m_{12\to1,t} \\ m_{1\to2,t} & m_{2\to2,t} & \dots & m_{12\to2,t} \\ \vdots & \vdots & \dots & \vdots \\ m_{1\to12,t} & m_{2\to12,t} & \dots & m_{12\to12,t} \end{bmatrix}. \tag{2.20}$$

The catch data, $\mathbf{y}_t$, are linked to the state vector of abundances, $\mathbf{n}_t$, by a harvest matrix, $\mathbf{H}_t$. The elements $h_{a,t}$ of the harvest matrix are the fractions of mortality attributed to fishing:

$$h_{a,t} = \frac{F_{a,t}}{M + F_{a,t}}\left(1 - \exp(-M - F_{a,t})\right). \tag{2.21}$$

The expectation of the observations in matrix form is

$$E[\mathbf{y}_t|\mathbf{n}_t] = \mathbf{H}_t\mathbf{n}_t \tag{2.22}$$

where

$$\mathbf{H}_t = \begin{bmatrix} h_{1,t} & 0 & \dots & 0 \\ 0 & h_{2,t} & \dots & 0 \\ \vdots & \vdots & \dots & \vdots \\ 0 & 0 & \dots & h_{12,t} \end{bmatrix}. \tag{2.23}$$

Let P_I be a column vector of length 12 with elements representing probabilities of the initial locations at the beginning of the fishing season. Then the matrix models for the states and observations are summarized below.

$$E[\mathbf{n}_0] = R\phi_J P_I \tag{2.24}$$

$$E[\mathbf{n}_t|\mathbf{n}_{t-1}] = \mathbf{M}_t\mathbf{S}_{t-1}\mathbf{n}_{t-1}, \quad t = 1, \dots, 16 \tag{2.25}$$

$$E[\mathbf{y}_t|\mathbf{n}_t] = \mathbf{H}_t\mathbf{n}_t, \quad t = 1, \dots, 16. \tag{2.26}$$

Fig. 2.12 Red deer in Scotland provide an example of where state-space models have been used to help wildlife managers set cull levels (Trenkel et al. 2000). Photo: Steve Buckland

2.7.2 A Deer Metapopulation

The following example of two deer populations, labeled A and B, is hypothetical but it identifies some of the sub-processes, and their complexity, that underlie the dynamics of real metapopulations. It is based loosely on red deer *Cervus elaphus* dynamics (Fig. 2.12). As said previously, deterministic formulations are given here, with stochasticity added in the next chapter.

We arbitrarily take the year to start just after breeding, assumed to be early summer. Survival rate for calves is assumed to be density-dependent and a function of day-degrees frost in winter (a measure of winter severity equal to number of degrees of frost, summed over all days for which the daily low fell below zero), while adult survival (age one or more) is assumed to differ by sex, but to be constant otherwise. Movement between populations is assumed to occur just before breeding: conceptually, it is the population to which animals belong at breeding that we are primarily concerned with, rather than an accurate model of when animals switch between populations. Movement rate is assumed to be a function of animal density in the respective populations just before births occur. Age incrementation occurs after movement. One-year-old animals are assumed to have a separate, low birth rate, while older animals all have the same birth rate. Each female is assumed to give birth to at most one young. New-born animals can of course be male or female.

We now know all the processes which we need to model, but we have not fully specified the model for each process. To incorporate all the features of the conceptual model, we need just two age classes for males and three for females (to allow one-year-old females to have a lower birth rate), giving five states for each of two populations, and the state vector, $\mathbf{n}_t$, then has ten components. (If we wished to model survival or birth rates as more complex functions of age, we would need to retain more age classes.)

Consider first survival. We can express the expected number of survivors to year t from just after breeding at the end of year $t-1$ as $E(\mathbf{u}_{1(s),t}|\mathbf{n}_{t-1}) = \mathbf{S}_{t-1}\mathbf{n}_{t-1} = \begin{bmatrix} \mathbf{S}_{A,t-1} & \mathbf{0}_{5\times5} \\ \mathbf{0}_{5\times5} & \mathbf{S}_{B,t-1} \end{bmatrix} \mathbf{n}_{t-1}$, where $\mathbf{0}_{5\times5}$ is a 5×5 matrix of zeros, and the survival matrices for populations A and B are

$$\mathbf{S}_{A,t-1} = \begin{bmatrix} \phi_{1,A,t-1} & 0 & 0 & 0 & 0 \\ 0 & \phi_{1,A,t-1} & 0 & 0 & 0 \\ 0 & 0 & \phi_f & 0 & 0 \\ 0 & 0 & 0 & \phi_f & 0 \\ 0 & 0 & 0 & 0 & \phi_m \end{bmatrix} \tag{2.27}$$

and

$$\mathbf{S}_{B,t-1} = \begin{bmatrix} \phi_{1,B,t-1} & 0 & 0 & 0 & 0 \\ 0 & \phi_{1,B,t-1} & 0 & 0 & 0 \\ 0 & 0 & \phi_f & 0 & 0 \\ 0 & 0 & 0 & \phi_f & 0 \\ 0 & 0 & 0 & 0 & \phi_m \end{bmatrix} \tag{2.28}$$

respectively. We have ordered the state vector so that the first element corresponds to first-year females in population A, followed by first-year males, second-year females, older females, and finally males in their second year or older. This is then repeated for population B.

The probabilities of the survival matrix, $\mathbf{S}_{t-1}$, vary by age class and sex. Survival for first year animals is assumed to be affected by both the population abundance (hence density dependent) as well as winter temperatures. We assume a logistic form for this dependence:

$$\phi_{1,A,t-1} = \frac{1}{1 + \exp\{\beta_0 + \beta_1 f_{A,t} + \beta_2 N_{A,t-1}\}} \tag{2.29}$$

where $f_{A,t}$ is number of day-degrees frost experienced by population A in year t, and $N_{A,t-1} = \sum_i n_{i,t-1}$ where summation is over the five states corresponding to population A, and so represents size of population A just after breeding. A similar model may be specified for $\phi_{1,B,t-1}$. Adult survival differs between sexes, with ϕ_f and ϕ_m the survival probabilities for females and males, respectively, but they are the same for both populations and are assumed constant over time. Thus the components of the survival matrix $\mathbf{S}_{t-1}$ that are time-dependent relate to survival of male and female first-year animals only.

The next model component required relates to movement, which we wish to be density-dependent. Denote the probability that an animal moves from population A to population B in year t by $\mu_{A\to B,t}$, and the probability that an animal moves from population B to population A by $\mu_{B\to A,t}$. The expected state vector after movement has occurred is then given by $E(\mathbf{u}_{2(m),t}|\mathbf{u}_{1(s),t}) = \mathbf{M}_t\mathbf{u}_{1(s),t} = \begin{bmatrix} \mathbf{M}_{A,A,t} & \mathbf{M}_{B,A,t} \\ \mathbf{M}_{A,B,t} & \mathbf{M}_{B,B,t} \end{bmatrix} \mathbf{u}_{1(s),t}$, where $\mathbf{M}_{A,A,t}$ is a 5×5 diagonal matrix with diagonal elements all equal to $1 - \mu_{A\to B,t}$, $\mathbf{M}_{A,B,t}$ is a 5×5 diagonal matrix with diagonal elements all equal to $\mu_{A\to B,t}$, and similarly for $\mathbf{M}_{B,B,t}$ and $\mathbf{M}_{B,A,t}$. The probability of movement is assumed to be a function of the difference in densities for the two populations,

$$\mu_{A\to B,t} = \frac{1}{1 + \exp\{\gamma_0 + \gamma_1(D_{A,t} - D_{B,t})\}} \tag{2.30}$$

where $D_{A,t} = \sum_i u_{i,1(s),t}/A_A$ is the density of animals in population A just before movement occurs, expressed as the total number of survivors, $\sum_i u_{i,1(s),t}$, where summation is over the five states for animals in population A, divided by the size A_A of the area occupied by population A. We define $D_{B,t}$ similarly. A model for $\mu_{B\to A,t}$ may be defined in the same way.

The next process is age incrementation. Thus we have $E(\mathbf{u}_{3(a),t}|\mathbf{u}_{2(m),t}) = \mathbf{A}\mathbf{u}_{2(m),t} = \begin{bmatrix} \mathbf{A}_A & \mathbf{0}_{3\times5} \\ \mathbf{0}_{3\times5} & \mathbf{A}_B \end{bmatrix} \mathbf{u}_{2(m),t}$ where $\mathbf{0}_{3\times5}$ is a 3×5 matrix of zeros, and

$$\mathbf{A}_A = \mathbf{A}_B = \begin{bmatrix} 1\,0\,0\,0\,0 \\ 0\,0\,1\,1\,0 \\ 0\,1\,0\,0\,1 \end{bmatrix}. \tag{2.31}$$

Thus, the state vector now has three elements for each population, corresponding to second-year females, older females, and males in their second year or older.

We now define a model for generating new births. Only females can give birth, and one-year-old females (just entering their second year) have a lower birth rate than older females. Thus we have $E(\mathbf{u}_{4(b),t}|\mathbf{u}_{3(a),t}) = \mathbf{B}\mathbf{u}_{3(a),t} = \begin{bmatrix} \mathbf{B}_A & \mathbf{0}_{4\times3} \\ \mathbf{0}_{4\times3} & \mathbf{B}_B \end{bmatrix} \mathbf{u}_{3(a),t}$ where $\mathbf{0}_{4\times3}$ is a 4×3 matrix of zeros, and

$$\mathbf{B}_A = \mathbf{B}_B = \begin{bmatrix} \rho_1 & \rho_2 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}. \tag{2.32}$$

Thus ρ_1 is the probability that a one-year-old female gives birth, while ρ_2 is the probability that an older female gives birth.

Finally, we need a process model for assigning sex to the new-born animals. Suppose the probability that a new-born animal is female is α. If we considered that it was reasonable to assume that $\alpha = 0.5$, we would just fix it at this value. Otherwise, we can retain it as an unknown parameter to be estimated. In the latter case, we would like to include some data in the likelihood on observed proportion of females for a representative set of births. We can now write $E(\mathbf{n}_t|\mathbf{u}_{4(b),t}) \equiv E(\mathbf{u}_{5(c),t}|\mathbf{u}_{4(b),t}) = \mathbf{C}\mathbf{u}_{4(b),t} = \begin{bmatrix} \mathbf{C}_A & \mathbf{0}_{5\times4} \\ \mathbf{0}_{5\times4} & \mathbf{C}_B \end{bmatrix} \mathbf{u}_{4(b),t}$ where $\mathbf{0}_{5\times4}$ is a 5×4 matrix of zeros, and

$$\mathbf{C}_A = \mathbf{C}_B = \begin{bmatrix} \alpha & 0\,0\,0 \\ 1-\alpha & 0\,0\,0 \\ 0 & 1\,0\,0 \\ 0 & 0\,1\,0 \\ 0 & 0\,0\,1 \end{bmatrix}. \tag{2.33}$$

We now have a fully specified (deterministic) population dynamics model, but we have not yet addressed how the states relate to our data. Suppose we have annual estimates of number of adults (one-year-old or older) generated from aerial surveys of each population at the time of breeding. There is no information on age or sex. Then the expected observation equation for year t is

$$E[\mathbf{y}_t|\mathbf{n}_t] = \mathbf{O}\mathbf{n}_t \tag{2.34}$$

where $\mathbf{y}_t$ is a vector of length two, corresponding to an estimate of adult abundance in population A and population B, and

$$\mathbf{O} = \begin{bmatrix} 0\,0\,1\,1\,1\,0\,0\,0\,0\,0 \\ 0\,0\,0\,0\,0\,0\,0\,1\,1\,1 \end{bmatrix}. \tag{2.35}$$

The complete (deterministic) model for the population dynamics and the observation process is summarized as follows.

$$E[\mathbf{n}_t|\mathbf{n}_{t-1}] = \mathbf{L}_{t-1}\mathbf{n}_{t-1} = \mathbf{CBAM}_t\mathbf{S}_{t-1}\mathbf{n}_{t-1} \tag{2.36}$$

$$E[\mathbf{y}_t|\mathbf{n}_t] = \mathbf{O}\mathbf{n}_t. \tag{2.37}$$

The expected abundance at time t was written as a Leslie matrix operation, conditional on the previous abundance, i.e. $\mathbf{L}_{t-1}\mathbf{n}_{t-1}$. A look at each of the five component matrices indicates the complexity of the resulting matrix $\mathbf{L}_{t-1}$, a matrix that is relatively easily constructed by thinking in terms of sequential sub-processes, but near impossible to construct otherwise.