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Modelling Population Dynamics

Model Formulation, Fitting and Assessment using State-Space Methods

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Methods in Statistical Ecology

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Preface

In Borchers et al. (2002), a unifying framework was given for the plethora of methods for estimating the abundance of closed populations of animals. In Chap. 13 of that book, the bare bones of an approach to provide similar unification for open populations were provided. Here, we seek to put flesh on those bones. Our aims are to lay down an approach for defining and fitting a wide range of population dynamics models for those new to the field and to provide some coherence to the process of modelling population dynamics for more experienced practitioners.

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Authors' (Brief) Biographies

Ken Newman is a mathematical statistician for the United States Fish and Wildlife Service. His primary research interest is in the use of state-space models to model the population dynamics of fish and wildlife to answer scientific questions and to serve as management decision support tools.

Stephen Buckland is professor of statistics at the University of St Andrews and is also co-director of the UK National Centre for Statistical Ecology. His interest in modelling population dynamics dates from a project to develop a decision support system for managers of red deer populations in Scotland in the 1990s.

Byron Morgan is honorary professorial research fellow in the University of Kent and co-director of the National Centre for Statistical Ecology. He is interested in integrated population modelling, which accounts for data collected on different aspects of the demography of wild animals. A convenient component of this work is the use of state-space models for describing ecological time series.

Ruth King is a reader in statistics at the University of St Andrews. Her research interests include the development of population dynamics models and model fitting tools in both the classical and Bayesian frameworks. This particularly includes the application of hidden Markov (or state-space) models.

David Borchers is a reader in statistics at the University of St Andrews. His research involves developing general statistical models for estimating population density and distribution, integrating hidden state or latent variable models with various kinds of observation model.

Diana Cole is a senior lecturer in statistics at the University of Kent. Her primary research is on parameter redundancy or identifiability of models used in statistical ecology.

Panagiotis Besbeas is a lecturer in the Athens University of Economics and Business and also a part-time post-doctoral research associate within the National Centre for Statistical Ecology group in the University of Kent, Canterbury. His research includes integrated population modelling, recently including the importance of replication for error estimation, and new methods for measuring goodness of fit as well as for conducting model selection.

Olivier Gimenez is a senior scientist in statistical ecology at the Centre National de la Recherche Scientifique (CNRS) in France. His main research interest is animal demography using hidden structure models with contributions to the coexistence of humans and animals.

Len Thomas is a reader in statistics at the University of St Andrews and is director of the Centre for Research into Ecological and Environmental Modelling, an inter-disciplinary research centre at the university. He has two main research interests: (1) use of computer-intensive methods, particularly particle filters, to fit and compare state-space models of wildlife population dynamics; (2) development of methods and software for estimating animal population size and density.

Chapter 1
Introduction

This book was conceived as a companion volume to *Estimating Animal Abundance: Closed Populations* by Borchers et al. (2002), who gave a unifying framework for estimating the abundance of closed populations. We seek to do the same for estimating the abundance of open populations: populations subject to births, deaths and movement in and out of the population. We focus primarily on populations of large vertebrates, for which we will typically model dynamics within the framework of an annual cycle, and for which stochastic variability in the demographic processes is usually modest. We consider discrete time models in which animals can be assigned to discrete states such as age class, gender, population (within a metapopulation), or species (for multi-species models).

We go beyond estimation of abundance, however, as we are interested in understanding reasons for variation in abundance over time. Knowledge of abundances alone will seldom be sufficient for the ecologist or wildlife manager. For example, suppose one knew there were exactly 5,218, 6,319, and 7,438 individuals for three consecutive years. A natural question would be "*Why* are the abundances increasing?". More generally, the question is "What is causing, or driving, the population dynamics?". The answer will depend in some way on the underlying processes of birth or recruitment, survival and movement. These processes are typically of greater interest to ecologists and managers than abundance itself.

To quantify these processes requires the formulation and fitting of population dynamics models. The resulting fitted models will potentially yield both estimates of abundance and estimates of parameters characterizing the underlying processes, such as survival probabilities.

1.1 Background to the Book

Population dynamics models serve a wide variety of uses, including explaining previous population fluctuations as well as projecting future population abundances under hypothetical scenarios. We might for example wish to reintroduce an animal

that has become extinct locally. We then need to be confident that the reintroduced population is viable. Models are needed to make this assessment. Or perhaps we need to manage an exploited fish stock, and assess whether the level of take is sustainable. Another example is when we wish to manage a species of conservation concern, and perhaps reverse a declining trend. We would like models of the species and its environment to allow us to explore "what-if" scenarios on the computer before we experiment with the real population. If we can build a model that relates demographic processes to habitat, we can then explore options for modifying the habitat to the species' benefit. Perhaps we wish to assess the response of a species or community to climate change. To do this, we must model the population processes, and how these depend on climate. Yet another example is when a population is too large for the environment to support, so that habitat degrades, to the detriment of biodiversity in the region. We may then need models to indicate levels of culling needed to sustain the environment and its diversity.

Population dynamics models play a central role in adaptive resource management (Williams et al. 2007) where managers are experimenting with different management actions to produce desired population responses. Models are used to predict the consequences of management actions such as habitat modifications or predator removal. After-the-fact comparisons of model predictions to observed outcomes are also made. The strength of evidence for alternative models, i.e. competing explanations for the effects of actions, can be assessed to determine which explanations are more consistent with the data.

In all of the above examples, we need to address risk. This means that we need to quantify uncertainty in our model predictions. It is not enough therefore to develop mathematical models of animal dynamics. We also need to allow for the main sources of uncertainty in these models: demographic and environmental stochasticity; observation or sampling errors in our data; and model or structural uncertainty (Williams et al. 2001). Without these elements, a mathematical model of population dynamics is merely a tool of theoretical ecologists, with little to offer wildlife managers. Similarly, purely empirical models for trend, fitted to time series of data, have little predictive power, because they ignore the population processes that drive change, so cannot predict change with any degree of confidence. In this book, we develop an approach that allows models for population dynamics to be embedded within a full inferential framework, giving the predictive and explanatory power of mathematical process models, coupled with statistical tools for quantifying uncertainty.

The main steps involved are as follows. First, we formulate a model of the population dynamics. We provide a building block strategy for this, allowing quite complex models to be assembled from simple components. For convenience of model formulation, we use matrices to define these building blocks, which allows us also to relate our approach to the well-developed field of matrix population models (Caswell 2001). However, our fitting algorithms are not restricted to such models, and we can readily extend our models in various ways. We develop the tools needed for model formulation, and show how they provide a more general framework than is possible with matrix models.

Second, we formulate the population dynamics model as a hidden process model. If the model is first-order Markov, it is termed a *state-space model*. The states might reflect gender, age, geographic region, or other characteristics that define different sub-populations that might be subject to different dynamics. The state equation defines how the population updates stochastically through time. These processes are generally hidden because we cannot observe the entire population—we typically have counts or estimates of the population or of some component of the population at certain points in time. Hidden process models give great flexibility in defining both the systematic and the random components of the population dynamics model.

Third, we define how our observations relate to the states, through an observation equation. The random component of this equation relates to observation error, while the systematic component defines a "mapping" between the observations and the states.

As an aside, we note that partitioning the population dynamics model into two components, namely the underlying hidden state process and the observation model, has practical advantages. One advantage is that theories about the dynamics can be kept separate from the sampling and estimation issues; thus, for example, the subject matter specialist can focus attention on the underlying dynamic processes of survival and birth, postulating alternative theories largely independent of the data collection procedures. Sample size determination can also be partitioned into problems to determine the number of years to sample and problems to determine the sampling intensity within a given year, and trade-offs between different combinations of sample sizes can be more clearly determined.

Fourth, we address how the hidden process model may be fitted to time series of observations. We consider three primary approaches. The Kalman filter allows us to fit a model quickly, at the expense of assuming that the errors in both the state equation and the observation equation are normally distributed, and that the expectation of the state vector at one time point is a linear function of the state vector at the previous time point. We also give two computer-intensive methods which can be implemented within a Bayesian framework to give much greater flexibility. The first of these is Markov chain Monte Carlo (MCMC), and the second is sequential Monte Carlo methods.

Finally, we discuss model selection, goodness-of-fit, model averaging, parameter redundancy, and other issues related to model assessment and uncertainty.

In subsequent chapters, we consider different methods of assessing wild animal populations, and how these can be combined with hidden process modelling to allow the dynamics of the populations to be modelled. We first address the case where closed-population assessment methods are used at each of several time points, and a population dynamics model fitted to the time series of abundance estimates. This may be viewed as an extension of the robust design approach of Pollock (1982). Next, we consider open population assessment methods, and how these may be integrated with hidden process models. Finally, we look at the case when there are multiple data sources. These methods are illustrated through examples, and R or WinBUGS code is provided for most examples, allowing users to modify the code for their own purposes.

1.2   Book Website

Computer code for our examples is available at the book website, www.creem.st-and.ac.uk/modpopdyn. The code can be used as a learning aid to re-run the analyses of this book, and can also be used as a template for the user to generate code to analyse his or her own data.

1.3   Related Books

As noted above, this book is a companion to Borchers et al. (2002). They give a unifying framework for methodologies for estimating the abundance of closed populations, and we seek to do the same for open populations. Population dynamics play a crucial role in open population modelling, yet methods for assessing the abundance of open populations have for the most part had no embedded model of these dynamics. Such embedded models are central to the methods of this book.

This book also complements the book on Bayesian analysis for population ecology by King et al. (2009). They focus on the underlying ideas associated with Bayesian analyses of ecological data and the corresponding methods to fit Bayesian models. There is an emphasis on mark-recapture-recovery data for open populations. Case studies are used to illustrate the methods, including state-space models, the use of covariate information (including dealing with missing data), multi-state data, integrated data analyses, random effects models and closed capture-recapture models. Computer codes are provided for examples, using both WinBUGS and R.

Williams et al. (2001) offer near encyclopedic coverage of many of the better known population dynamics models for animal populations as well as the wide variety of statistical procedures used to estimate abundance (for closed and open populations) and parameters of population dynamic processes. Integration of population process models with observation models is by and large not addressed, however.

Caswell (2001) uses matrices to model population dynamics, e.g., Leslie matrices to characterise survival and reproduction. Matrices, strictly speaking, imply linear models, although Caswell formulates non-linear extensions to the basic matrix model. We find matrix models to be useful for formulating state-space models and present many examples in Chap. 2.

Royle and Dorazio (2008) cover hierarchical models for ecological systems. In common with this book, they use both frequentist and Bayesian methods, and show how to combine explicit models of ecological system structure or dynamics with models of how ecological systems are observed. They apply the principles of hierarchical modelling to problems in population, metapopulation, community and metacommunity systems, whereas we focus on modelling population dynamics, and estimating population abundance.

Two classic fisheries science and management books, Hilborn and Walters (1992) and Quinn and Deriso (1999), describe a wide variety of methods and models for characterising fish population dynamics. These models and methods are often used for non-fish species. Both books also discuss the distinction between process variation and observation error, but at the time the books were written, the handling of both types of error simultaneously was not common practice.

Written for researchers and graduate students in statistics, ecology, demography, and the social sciences, McCrea and Morgan (2014) provide an up-to-date overview of capture-recapture methods. It covers model development and diagnostics. The authors use illustrative data sets drawn from a range of different areas and indicate available software for classical and Bayesian inference.

We use Bayesian methods for fitting many of the models of this book. Books that provide an introduction to Bayesian methods for ecologists are McCarthy (2007) and Link and Barker (2009). Kéry and Schaub (2012) focus on using `WinBUGS` to model population dynamics. They show how to fit Bayesian state-space models using mark-recapture or mark-recovery data, and they also provide example code for integrated population modelling, and for modelling counts.

1.4   Roadmap to the Book

After reading this chapter, we recommend that Chap. 2 be read next, which provides a path for those familiar with classic Leslie and Lefkovitch matrix models to a building-block approach to (a) constructing situation-specific matrix models and (b) formulating the skeleton of state-space models. Chapters 3–5 are the methodological core of the book giving general definitions of SSMs, methods for fitting SSMs, and then suggestions for formulation, or re-formulation, and assessment of SSMs. Chapters 6–9 are largely stand-alone chapters and can be read in any order, although there is some cross-reference between these chapters. Chapter 10 summarizes the book and can be read at any time.

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.

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

$$\phi_1$$
$$n_{1,t-1} \dashrightarrow u_{1(s),1,t}$$
$$\phi_2$$
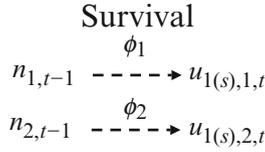$$n_{2,t-1} \dashrightarrow u_{1(s),2,t}$$

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 $E(u_{1(s),1,t}) = n_{1,t-1}\phi_1$ young and $E(u_{1(s),2,t}) = n_{2,t-1}\phi_2$ adults to survive through year t. The arrows are dashed to indicate that the processes are stochastic, so that in general $E(u_{1(s),j,t}) \neq u_{1(s),j,t}$ 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

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

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, $E(u_{1(s),j,t})$ 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

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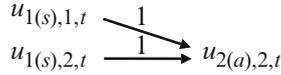
Age incrementation

$u_{1(s),1,t}$

$u_{1(s),2,t}$ $\xrightarrow{\quad 1 \quad}$ $u_{2(a),2,t}$

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 $E(u_{2(a),2,t}) \equiv u_{2(a),2,t}$. 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.)

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

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