Mathematical Models for Society and Biology

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ACADEMIC PRESS

An Elsevier Science Imprint

San Diego San Francisco New York Boston
London Sydney Toronto Tokyo

Sponsoring Editor	Barbara Holland
Editorial Coordinator	Tom Singer
Production Editor	Angela Dooley
Cover Design	Dick Hannus/Hannus Design Assoc.
Composition	International Typesetting and Composition
Printer	Hamilton Printing Co.
Cover Printer	Jaguar Advanced Graphics, Inc.

This book is printed on acid-free paper. ∞

Cover image: Mike Kelly/Getty Images

Academic Press
An imprint of Elsevier Science
525 B Street, Suite 1900, San Diego, California 92101-4495, USA
http://www.academicpress.com

Academic Press
Harcourt Place, 32 Jamestown Road, London, NW1 7BY, UK
http://www.academicpress.com

Academic Press
An imprint of Elsevier Science
200 Wheeler Road, Burlington Massachusetts 01803, USA
http://www.harcourt-ap.com

Library of Congress Catalog Number: 2001096949
International Standard Book Number: 0-12-085561-5

Printed in the United States of America
01 02 03 04 05 06 HP 9 8 7 6 5 4 3 2 1

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Preface

The book before you is a new upper-level undergraduate text that shows how mathematics can illuminate fascinating problems drawn from society and biology. The book assembles an unusual array of applications, many from professional journals, that have either not appeared before or that cannot be found easily in book form. Moreover the context of most chapters are current issues of real concern, and we distance ourselves from contrived "toy models" that are merely "academic" exercises. In this book mathematics follows from the problems and not the other way around, as is often the case in other works.

Mathematical modeling is viewed as an organizing principle that enables one to handle a vast and often confusing array of facts in a parsimonious manner. A model is useful when it reveals something of the underlying dynamics, providing insight into some complex process. Although models rarely replicate reality, they can serve as metaphors for what is going on in a simple and transparent manner, a bit of a caricature perhaps but informative nonetheless. The models chosen for this book all share these qualities.

Features

There are applications of interest in political science (Chapters 2 and 9); sociology (Chapter 1); economics (Chapters 7 and 9); ecology (Chapters 1, 7, and 8); public policy, in the municipalities, and management science (Chapters 3 and 4); molecular biology (Chapter 5); epidemiology (Chapter 6); and biochemistry and cell biology (Chapters 6 and 7), among other areas. No prior knowledge of any of these fields is assumed except what an interested layperson might pick up by reading the daily newspaper; any background that is needed to understand the problem is provided in the text.

A feature of the book is that several topics reappear in different guises throughout the text, thereby giving the student alternative perspectives on different facets of the same problem. A few unifying themes are woven throughout the book using fresh insights, and these result in a more cohesive presentation. This is discussed in a final section that gives an overview of the entire book and of the modeling process.

Prerequisites

As for prerequisites, I assume that a student has had the conventional training expected of a junior-level student including basic results from the multivariate calculus and matrix theory and some elementary probability theory and linear differential equations. More exotic material is explained in the text, as needed, and in the few places where relatively sophisticated tools are required I explain the results carefully and provide appropriate references to where details can be found.

Most chapters include a section that describes the relevant mathematical techniques needed later in that chapter, and there is a short appendix on conditional probability. In particular, there is a brief but fairly complete account of systems of differential equations in Chapter 6. An instructor may wish to expand on our treatment of these topics, depending on the preparation of the students.

In my opinion, the most interesting differential equation models ultimately require that solutions be obtained numerically, and it would be useful for students to have access to a simple language for computing orbits for systems of two and three nonlinear differential equations, such as those that occur in Chapters 6 through 8. In this book, all the computer generated solutions and accompanying graphics utilized MATLAB, Version 5.

Acknowledgments

A number of colleagues at Stony Brook, past and present, have influenced the development of this book by their work at the interface between mathematics and the other sciences. Indeed, there is hardly a chapter in the book that doesn't incorporate, to some extent, the inspired research of a Stony Brook scientist. These include Akira Okubo of the Marine Sciences Research Center, Ivan Chase of the Sociology Department, Jolyon Jesty of the Health Sciences Hematology Department, William Bauer of Microbiology, Larry Slobodkin of Ecology and Evolution, and Larry Bodin of the Harriman School of Public Policy.

I want to extend my sincere thanks to the following individuals for their helpful reviews of my manuscript: Jayne Ann Harder, University of Texas, Austin, Bruce Lundberg, University of Southern Colorado, Thomas Seidman, University of Maryland, Robert White, North Carolina State University, Raleigh, Daniel Zelterman, Yale University.

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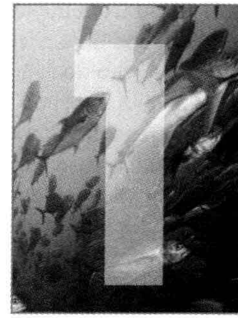
Crabs and Criminals



1.1. Background

A hand reaches into the still waters of the shallow lagoon and gently places a shell on the sandy bottom. We watch. A little later a tiny hermit crab scurries out of a nearby shell and takes possession of the larger one just put in. This sets off a chain reaction in which another crab moves out of its old quarters and scuttles over to the now empty shell of the previous owner. Other crabs do the same until at last some barely habitable shell is abandoned by its occupant for a better shelter, and it remains unused.

One day the president of a corporation decides to retire. After much fanfare and maneuvering within the firm, one of the vice presidents is promoted to the top job. This leaves a vacancy which, after a lapse of a few weeks, is filled by another executive whose position is now occupied by someone else in the corporate hierarchy. Some months pass and the title of the last position to be vacated is merged with some currently held job title and the chain terminates.

A lovely country home is offered by a real estate agency when the owner dies and his widow decides to move into an apartment. An upwardly mobile young professional buys it and moves his family out of the split-level they currently own after selling it to another couple of moderate income. That couple sold their modest house in a less than desirable neighborhood to an entrepreneurial fellow who decides to make some needed repairs and rent it.

What do these examples have in common? In each case a single vacancy leaves in its wake a chain of opportunities that affect several individuals. One vacancy begets another while individuals move up the social ladder. Implicit here is the assumption that individuals want or need a resource unit (shells, houses, or jobs) that is somehow better (newer, bigger, more status) or, at least, no worse than the one they already possess. There are a limited number of such resources and many applicants. As units trickle down from prestigious to commonplace, individuals move in the opposite direction to fill the opening created in the social hierarchy.

A chain begins when an individual dies or retires or when a housing unit is newly built or a job created. The assumption is that each resource unit is reusable when it becomes available and that the trail of vacancies comes to an end when a unit is merged, destroyed, or abandoned, or because some new individual enters the system from the outside. For example, a rickety shell is abandoned by its last resident, and no other crab in the lagoon claims it, or else a less fortunate hermit crab, one who does not currently have a shell to protect its fragile body, eagerly snatches the last shell.

A mathematical model of movement in a vacancy chain is formulated in the next section and is based on two notions common to all the examples given. The first notion is that the resource units belong to a finite number, usually small, of categories that we refer to as states and, second, that transitions take place among states whenever a vacancy is created. The crabs acquire protective shells formerly occupied by snails that have died and these snail shells come in various size categories. These are the states. Similarly, houses belong to varying price/prestige categories, while jobs in a corporate structure can be labeled by different salary/prestige classes.

Let's now consider an apparently different situation. A crime is committed and, in police jargon, the perpetrator is apprehended and brought to justice and sentenced to "serve time" in jail. Some crimes go unsolved, however, and of the criminals that get arrested only a few go to prison; most go free on probation or because charges are dropped. Moreover even if a felon is incarcerated, or is released after arrest, or even if he was never caught to begin with, it is quite possible that the same person will become a recidivist, namely, a repeat offender. What this has in common with the mobility examples given earlier is that here, too, there are transitions between states, where in this case "state" means the status of an offender as someone who has just committed a crime, or has just been arrested, or has just been jailed or, finally, has "gone straight" never to repeat a crime again. This, too, is a kind of social mobility and we will see that it fits the same mathematical framework that applies to the other examples.

One of the problems associated with models of social mobility is the difficult chore of obtaining data regarding the frequency of moves between states. If price, for example, measures the state of housing, then what dollar bracket constitutes a single state? Obviously the narrower we make a price category, the more homogeneous is the housing stock that lies within a given grouping. On the other hand, this homogeneity requires a large number of states, which exacerbates the data-gathering effort necessary to estimate the statistics of moves between states.

We chose the crab story to tell because it is a recent and well-documented study that serves as a parable for larger scale problems in sociology connected with housing and labor. It is not beset by some of the technical issues that crop up in these other areas, such as questions of race that complicate moves within the housing and labor markets. By drastically simplifying the criminal justice system we are also able to address some significant questions about the chain of moves of career criminals that curiously parallel those of crabs on the sandy sea bottom. These examples are discussed in Sections 1.3 and 1.4.

1.2. Absorbing Markov Chains

We began this chapter with examples of states that describe distinct categories such as the status of a felon in the criminal justice system or the sizes of snail shells in a lagoon. Our task now is to formalize this idea mathematically.

The behavior of individual crabs or criminals is largely unpredictable and so we consider their aggregate behavior by observing many incidents of shell swapping or by examining many crime files in public archives.

Suppose there are N states and that $p_{i,j}$ denotes the observed fraction of all moves from a given state i to all other states j. If a large number of separate moves are followed, the fraction $p_{i,j}$ represents the probability of a transition from i to j. In fact this is nothing more than the usual empirical definition of probability as a frequency of occurrence of some event. The N by N array $\mathbf{P}$ with elements $p_{i,j}$ is called a *transition matrix.*

To give an example, suppose that a particle can move among the integers $1, 2, \ldots, N$ by bouncing one step at a time either right or left. If the particle is at integer i it goes to $i+1$ with probability p and to $i-1$ with probability q, $p+q=1$, except when i is either 1 or N. At these boundary points the particle stays put. It follows that the transition probabilities are given by

$$p_{i,i+1} = p \quad \text{and} \quad p_{i,i-1} = q \quad \text{for } 2 < i < N-1$$

$$p_{1,1} = p_{N,N} = 1 \quad \text{and} \quad p_{i,j} = 0 \quad \text{for all other } j$$

The set of transitions from states i to states j is called a *random walk with absorbing barriers* and is illustrated schematically in Figure 1.1 for the case $N=5$.

A *Markov chain* (after the Russian mathematician A. Markov) is defined to be a random process in which there is a sequence of moves between N states such that the probability of going to state j in the next step depends only on the current state i and not on the previous history of the process. Moreover, this probability does not depend on when the process is observed. The random walk example is a Markov chain since the decision to go either right or left from state i is independent of how the particle got to i in the first place, and the probabilities p and q remain the same regardless of when a move takes place.

To put this in more mathematical terms, if X_n is a random variable that describes the state of the system at the nth step then prob$(X_{n+1} = j \mid X_n = i)$, which means "the conditional probability that $X_{n+1} = j$ given that $X_n = i$" is uniquely given

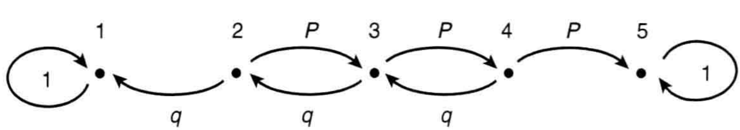


Figure 1.1. Schematic representation of a random walk.

by $p_{i,j}$. In effect, a move from i to j is statistically independent from all the moves that led to i and is also independent of the step we happen to stumble on in our observations. Clearly $p_{i,j} \geq 0$ and, since a move from state i to some other state always takes place (if one includes the possibility of remaining in i), then the sum of the elements in the ith row of the matrix $\mathbf{P}$ add to one:

$$\sum_{j=1}^{N} p_{i,j} = 1 \quad 1 \leq i \leq N$$

The extent to which these conditions for a Markov chain are actually met by crabs or criminals is discussed later. Our task now is to present the mathematics necessary to enable us to handle models of social mobility.

Let $\mathbf{P}^{(n)}$ be the matrix of probabilities $p_{i,j}^{(n)}$ of going from state i to state j in exactly n steps. This is conceptually different from the n-fold matrix product $\mathbf{P}^n = \mathbf{PP}\ldots\mathbf{P}$. Nevertheless they are equal:

Lemma 1.1 $\mathbf{P}^n = \mathbf{P}^{(n)}$

Proof: Let $n = 2$. A move from i to j in exactly two steps must pass through some intermediate state k. Because the passages from i to k and then from k to j are independent events (from the way a Markov chain was defined), the probability of going from i to j through k is the product $p_{i,k}p_{k,j}$ (Figure 1.2). There are N disjoint events, one for each intermediate state k, and so

$$p_{i,j}^{(2)} = \sum_{k=1}^{N} p_{i,k}p_{k,j}$$

which we recognize as the i, jth element of the matrix product $\mathbf{P}^2$. □

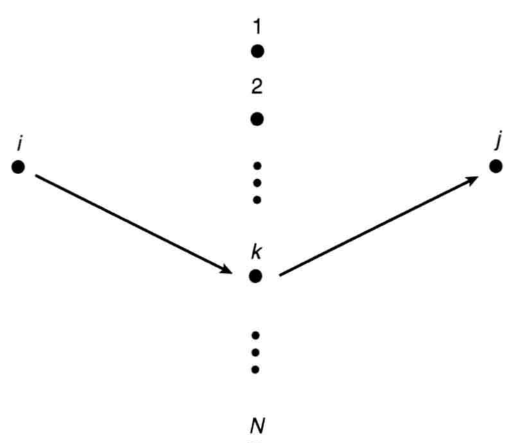


Figure 1.2. Two-step transition between states i and j through an intermediate state k.

We now proceed to the general case by induction. Assume the Lemma is true for $n-1$. Then an identical argument shows that

$$p_{i,j}^{(n)} = \sum_{k=1}^{N} p_{i,k} p_{k,j}^{(n-1)}$$

which is the i,jth element of $\mathbf{P}^n$.

A state i is called *absorbing* if it is impossible to leave it. This means that $p_{i,i} = 1$. In the random walk example, for instance, the states 1 and N are absorbing.

Two nonabsorbing states are said to communicate if the probability of reaching one from the other in a finite number of steps is positive. Finally, an *absorbing Markov chain* is one in which the first s states are absorbing, the remaining $N-s$ nonabsorbing states all communicate, and the probability of reaching every state $i \leq s$ in a finite number of steps from each $i' > s$ is positive.

It is convenient to write the transition matrix of an absorbing chain in the following block form:

$$\mathbf{P} = \begin{pmatrix} \mathbf{I} & \mathbf{O} \\ \mathbf{R} & \mathbf{Q} \end{pmatrix} \tag{1.1}$$

where $\mathbf{I}$ is an s by s identity matrix corresponding to fixed positions of the s absorbing states, $\mathbf{Q}$ is an $N-s$ by $N-s$ matrix that corresponds to moves between the nonabsorbing states, and $\mathbf{R}$ consists of transitions from transient to absorbing states. In the random walk with absorbing barriers with $N = 5$ states (Figure 1.1), for example, the transition matrix may be written as

$$\mathbf{P} = \begin{array}{c} \\ 1 \\ 5 \\ 2 \\ 3 \\ 4 \end{array} \begin{array}{c} \begin{array}{ccccc} 1 & 5 & 2 & 3 & 4 \end{array} \\ \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ \mathrm{q} & 0 & 0 & \mathrm{p} & 0 \\ 0 & 0 & \mathrm{q} & 0 & \mathrm{p} \\ 0 & \mathrm{p} & 0 & \mathrm{q} & 0 \end{pmatrix} \end{array}$$

Let f_i be the probability of returning to state i in a finite number of moves given that the process begins there. This is sometimes called the first return probability. We say that state i is recurrent or transient if $f_i = 1$ or $f_i < 1$, respectively. The absorbing states in an absorbing chain are clearly recurrent and all others are transient.

The number of returns to state i, including the initial sojourn in i, is denoted by N_i. This is a random variable taking on values $1, 2, \ldots$. The defining properties of a Markov chain assure that each return visit to state i is independent of previous visits and so the probability of exactly m returns is

$$\text{prob}(N_i = m) = f_i^{m-1}(1 - f_i) \tag{1.2}$$

The right side of (1.2) is known as a *geometric distribution* and it describes the probability that a first success occurs at the mth trial of a sequence of independent Bernoulli trials. In our case "success" means not returning to state i in a finite number of steps. The salient properties of the geometric distribution are discussed in most introductory probability texts and are reviewed in Exercise 1.5.1.

The probability of only a finite number of returns to state i is obtained by summing over the disjoint events $N_i = m$:

$$\text{prob}(N_i < \infty) = \sum_{m=1}^{\infty} \text{prob}(N_i = m) = \sum_{m=1}^{\infty} f_i^{m-1}(1 - f_i) = \begin{cases} 0 & \text{if } i \text{ is recurrent} \\ 1 & \text{if } i \text{ is transient} \end{cases}$$

With probability one, therefore, there are only a finite number of returns to a transient state.

In the study of Markov chains the leading question is what happens in the long run as the number of transitions increases. The next result answers this for an absorbing chain.

Lemma 1.2 *The probability of eventual absorption in an absorbing Markov chain is one.*

Proof: Each transient state can be visited only a finite number of times, as we have just seen. Therefore, after a sufficiently large number of steps, the process is trapped in an absorbing state.

The submatrix $\mathbf{Q}$ in (1.1) is destined to play an important role in what follows. We begin by recording an important property of $\mathbf{Q}$: □

Theorem 1.1 *The matrix* $\mathbf{I} - \mathbf{Q}$ *has an inverse.*

Proof: From Lemma 1.1 the elements of the matrix product $\mathbf{Q}^n$ represent the probability of a transition in exactly n steps from some transient state $i > s$ to some other transient $j > s$. From Lemma 1.2, $\mathbf{Q}^n$ must go to zero as n tends to infinity. □

Let $\mathbf{u}$ be an eigenvector of $\mathbf{Q}$ with corresponding eigenvalue λ. It follows immediately that $\mathbf{Q}^n\mathbf{u} = \lambda^n\mathbf{u}$. But, since $\mathbf{u}$ is fixed, the vectors $\mathbf{Q}^n\mathbf{u}$ go to zero as n increases, which implies that λ^n also goes to zero. Hence $|\lambda| < 1$. This shows that 1 is never an eigenvalue of $\mathbf{Q}$ or, to put it another way, the determinant of $\mathbf{I} - \mathbf{Q}$ is nonzero. This is equivalent to the invertibility of $\mathbf{I} - \mathbf{Q}$.

We turn next to a study of the matrix $(\mathbf{I} - \mathbf{Q})^{-1}$. Our arguments may seem to be a bit abstract but actually they are only an application of the idea of conditional probability and conditional expectation.

Let $t_{i,j}$ be the average number of times that the process finds itself in a transient state j given that it began in some transient state i. If j is different from i then $t_{i,j}$ is found by computing a conditional mean, reasoning much as in Lemma 1.1.

In fact, the passage from i to j is through some intermediate state k. Given that the process moves to k in the first step (with probability $p_{i,k}$) the mean number of times that j is visited beginning in state k is now $t_{k,j}$. The unconditional mean is therefore $p_{i,k}t_{k,j}$ and we need to sum these terms over all transient states since these correspond to disjoint events (see Figure 1.2):

$$t_{i,j} = p_{i,s+1}t_{s+1,j} + \cdots + p_{i,N}t_{N,j}$$

In the event that $i = j$, the value of $t_{i,i}$ is increased by one since the process resides in state i to begin with. Therefore, for all states i and j for which $s < i, j \leq N$,

$$t_{i,j} = \delta_{i,j} + \sum_{k=s+1}^{N} p_{i,k}t_{k,j} \tag{1.3}$$

where $\delta_{i,j}$ equals one if $i = j$, and is zero otherwise. In matrix terms (1.3) can be written as $\mathbf{T} = \mathbf{I} + \mathbf{QT}$, where $\mathbf{T}$ is the $N - s$ by $N - s$ matrix with entries $t_{i,j}$. It follows that $\mathbf{T} = (\mathbf{I} - \mathbf{Q})^{-1}$.

Let t_i be a random variable that gives the number of steps prior to absorption, starting in state i. The expected value of t_i is

$$E(t_i) = \sum_{j=s+1}^{N} t_{i,j} \tag{1.4}$$

which is the ith component of the vector $\mathbf{Tc}$, where

$$\mathbf{c} = \begin{pmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{pmatrix}$$

and $\mathbf{T} = (\mathbf{I} - \mathbf{Q})^{-1}$. Vector $\mathbf{Tc}$ has $N - s$ components and the ith one can therefore be interpreted as the average number of steps before absorption when a chain begins in transient state i.

The probability $b_{i,j}$ that absorption occurs in state $j \leq s$, given that it began in some transient state i, can now be computed. Either state j is reached in a single step from i (with probability $p_{i,j}$) or there is first a transition into another transient state k and from there the process is eventually absorbed in j (with probability $b_{k,j}$). The reasoning is similar to that employed earlier. That is, since the moves from i to k and then from k to j are independent by our Markov chain assumptions, we sum over $N - s$ disjoint events corresponding to different intermediate states k:

$$b_{i,j} = p_{i,j} + \sum_{k=s+1}^{N} p_{i,k} b_{k,j} \quad s < i \le N, \ j \le s \tag{1.5}$$

In matrix terms (1.5) becomes $\mathbf{B} = \mathbf{R} + \mathbf{QB}$, where $\mathbf{R}$ and $\mathbf{Q}$ are defined in (1.1).

Now let $h_{i,j}$ be the probability that a transient state j is ever reached from another transient state i in a finite number of moves. If j differs from i then evidently

$$t_{i,j} = h_{i,j} t_{j,j}$$

and, because we must add one to the count of $t_{i,j}$ when $i = j$, in all cases one obtains

$$t_{i,j} = \delta_{i,j} + h_{i,j} t_{j,j}. \tag{1.6}$$

In matrix terms this is expressed as $\mathbf{T} = \mathbf{I} + \mathbf{HT}_{\text{diag}}$, where $\mathbf{T}_{\text{diag}}$ is the matrix whose only nonzero elements are the diagonal entries of $\mathbf{T} = (\mathbf{I} - \mathbf{Q})^{-1}$ and $\mathbf{H}$ is the matrix with entries $h_{i,j}$. Therefore

$$\mathbf{H} = (\mathbf{T} - \mathbf{I})\mathbf{T}_{\text{diag}}^{-1}$$

Note, for later use, that $h_{i,i} = f_i$.

Relations (1.1) through (1.6) will be used in the remainder of this chapter.

1.3. Social Mobility

The tiny hermit crab *Pagarus longicarpus* does not possess a hard protective mantle to cover its body and so it is obliged to find an empty snail shell to carry around as a portable shelter. These empty refuges are scarce and only become available when its occupant dies.

In a recent study of hermit crab movements in a tidal pool off Long Island sound (see the references to Chase and others in Section 1.6) an empty shell was dropped into the water in order to initiate a chain of vacancies. This experiment was repeated many times to obtain a sample of over five hundred moves as vacancies flowed from larger to generally smaller shells. A Markov chain model was then constructed using about half this data to estimate the frequency of transitions between states, with the other half deployed to form empirical estimates of certain quantities, such as average chain length, that could be compared with the theoretical results obtained from the model itself. The complete set of experiments took place over a single season during which the conditions in the lagoon did not alter significantly. Moreover each vacancy move appeared to occur in a way that disregarded the history of previous moves. This leads us to believe that a Markov