Chapter 7

Modelling Population Structure

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"The sciences do not try to explain, they hardly even try to interpret, they mainly make models. By a model is meant a mathematical construct which, with the addition of certain verbal interpretations, describes observed phenomena. The justification of such a mathematical construct is solely and precisely that it is expected to work."

J. Von Neumann. (in Gleick, 1987)

INTRODUCTION

While some biologists may not agree with the first part of the above quotation, many would agree that modelling such phenomena is a useful way to gain understanding about biological systems. In this exercise you will use a computer model to learn how fecundity and survival help to determine the age and stage structure of populations.

WHAT ARE MODELS?

In general terms, a model is any abstraction or simplification of a system, and a system is any phenomenon having at least two separable components and some interaction between these components. For example, an ecosystem has various components, such as biotic and abiotic at the most fundamental level (Hall and Day, eds., 1977). Other definitions of models are:

A. Models are devices for predicting the behavior of a complicated, poorly understood system from the behavior of parts that are well understood.

B. Models are a formalization of our knowledge about a system.

Each of these definitions include points often alluded to by the critics of models, e.g., simplification and undue faith in the model and its predictions. A useful characterization of this discussion is given by James Gleick, in his book "**Chaos**":

"The choice is always the same. You can make your model more complex and more faithful to reality, or you can make it simpler and easier to handle. Only the most naive scientist believes that the perfect model is the one that perfectly represents reality. Such a model would have the same drawbacks as a map as large and detailed as the city it represents, a map depicting every park, every street, every building, every tree, every pothole, every inhabitant, and every map. Were such a map possible, its specificity would defeat its purpose: to generalize and abstract**..........**Whatever their purpose, maps and models must simplify as much as they mimic the world."

Given the simplification that does occur when models are formulated, the following analogy by Skellum (1971) is a useful caution to keep in mind:

"The application of mathematics to science bears some analogy to pictorial expression. The pen sketches out fine lines or the brush on damp paper yields all the gradations of light and shade, but in all cases much color and detail are lost. Only those who know how to relate what is seen to what gets drawn, know how to relate what has been drawn to what could have been seen. The uncertainties are always two-fold."

Perhaps in the context of this exercise models are best seen as an aid to understanding, and as an aid to testing our understanding of the factors that determine ecological processes. In this exercise we will construct a model that will help you to understand the components of population growth and structure and, through analysis of the results, to make an estimate of how well the system is understood.

There are many types of models, and different individuals classify models in different ways. Some types of models are Analytic, Dynamic, Matrix, Optimization, Multivariate, Stochastic and Simulation. In this exercise we will be concerned with a matrix model, which is a deterministic model in that it always gives the same answer (output), given the same input. This contrasts with a stochastic model, in which the output will differ with the same input. However, a matrix model may be made stochastic by generating random terms in place of a specific input. The random terms may be limited in scope so that they only cover a biologically reasonable range. It should be noted that many researchers believe that the stochastic model more closely mimics ecological reality, and some consider the chaotic model (see Gleick, 1987) to be most realistic.

THE MATRIX MODEL IS ONE KIND OF MODEL

What follows is an explanation of what the matrix model is, and how it operates mathematically. This is followed by an explanation of model construction, using the matrix model as an example.

A computer program to actually 'run' the model with different inputs and for varying lengths of time [generations] is available from the author and can be used on the Apple II and IIE, and some Apple IIGS, computers. However, commercially available programs which allow matrix manipulation may be equally suitable.

In most general terms the matrix model consists of a transition module and a current-state-of-affairs module. The transition module will be referred to as a transition matrix, and the current-state-of-affairs module will be referred to as a column vector, for reasons which will become apparent shortly. In operation, the model multiplies the column vector by the transition matrix, resulting in a new column vector which represents the updated state of affairs or, to put it another way, the state of affairs in the next time interval.

In the example to be used in this exercise, the transition matrix consists of numbers denoting birth and death rates of a population, usually on an age or stage specific basis, and the column vector gives the numbers in each age or stage class of the same population. Note: an ape class is a portion of the population defined by age, and a stage-class is a portion defined by some other criterion, such as size. When the matrix is "run" the transition matrix is multiplied by the column vector in a specific manner (outlined below), resulting in a new column vector which contains the numbers in the next generation.

In this example, a 5x5 matrix (5 columns and five rows) is used which is multiplied by a 1x5 (1 column and 5 rows) matrix. As indicated above, these matrices are called, respectively, the transition mamx and the column vector. The transition matrix contains the survival and fecundity values of the population being studied, and the column vector the current age or stage distribution of the same population at time **t.** To "run" the model the two matrices are multiplied together; the product is the age or stage distribution in the next time interval, t+1. The survival and fecundity values in the transition matrix can be held constant over time, or changed at each new time interval. For example, one may wish to change survival values over time if there is evidence that survival is density dependent, and that the population density is changing.

Some definitions of terms used below may be necessary:

Stable age distribution - the same proportions exist in each age class (or stage class) from one time period to the next time period; the population may be increasing or decreasing when this condition exists.

Constant age distribution - The same numbers exist in each age class from one time period to the next time period; the population neither increases nor decreases when this condition exists.

Lambda (λ) - Denotes the factor by which the population must be multiplied in order to obtain the next time periods' population.

Finite rate of increase - The rate at which the population increases from one time period to the next time period; equivalent to (λ).

Intrinsic rate of increase (r) - The rate of population increase over an infinitesimally small period of time. (r) is also defined as the number of individuals added to the population per individual per unit of time. When a stable age distribution has been attained, the following relationship holds between (λ) and (r):

$N_{(t+1)} = \lambda Nt$ and since $N_{(t+1)}$ also equals $e^r N_{(t)}$, one can see that $(\lambda) = e^r$

HOW DOES THE MATRIX MODEL WORK?

What follows is an example of how the computer multiplies the transition matrix and the column vector together:

Transition Matrix					Column Vector
A	B	C	D	E	1
V	O	O	O	O	2
O	W	O	O	O	3
O	O	X	O	O	4
O	O	O	Y	Z	5

A-E = Fecundity values
V-Z = Survival values

1-5 designate age or stage classes

To multiply these two matrices, proceed as follows:

1. Multiply 1xA, 2xB, 3xC, 4xD, and 5xE and sum the products; this sum is the new value for age (or stage) class 1, at time <u>t+1</u>.

2. Multiply 1xV, 2x0, 3x0, 4x0, and 5x0 and sum the products; this sum is the new value for the age (or stage) class 2, at time <u>t+1</u>.

3. Continue in this manner until new values have been obtained for each age or stage class. The sum of the age or stage class values at any time is the size of the population at that time. The proportion in an age class can be found by dividing the number in each age class by the size of the population at that time. The finite rate of increase (λ) can be found, once a stable age distribution has been reached, by dividing population size at time t by the size at time <u>t+1</u>. The requirement of a stable age distribution is necessary in order for the finite rate of increase to be applicable for more than the two generations for which it was calculated.

Since Lambda (λ) is the finite rate of increase, the potential harvest that a population can sustain without decreasing in numbers can be calculated simply as:

$$H = \text{Harvest} = 100\ \frac{\lambda - 1}{\lambda}$$

H is the proportion that can be taken from each age class of the entire population. In practice, more could be taken from an age class with high mortality relative to other age classes, if the harvest could be done prior to the occurrence of most of the mortality. This is so because by definition most of the members of this age class will die anyway.

HOW IS A MODEL CONSTRUCTED?

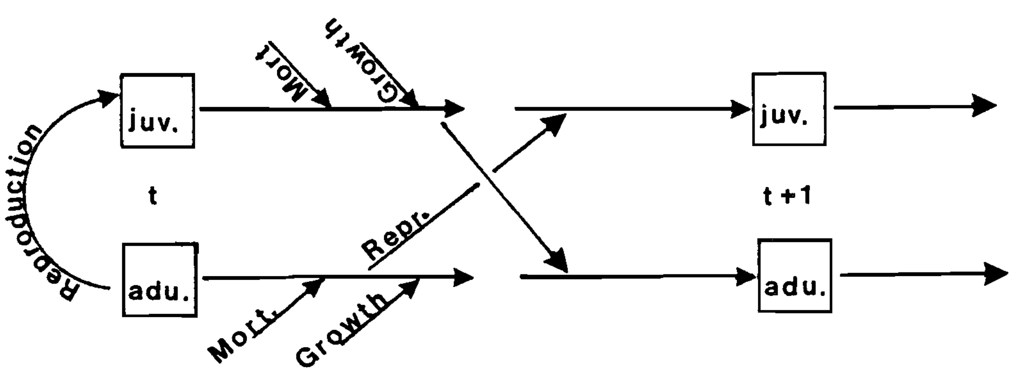
Despite the plethora of models, the process of constructing a model is similar for all, and is as follows:

1. A conceptual stage
2. A diagrammatic stage
3. A mathematical stage
4. A computer stage

The conceptual stage is one that mentally limits and describes the system. What is preying on what, which physical factors may be important and which are not, what can be included and excluded from consideration.

In the diagrammatic stage pencil is put to paper, and the relationships considered in the conceptual stage are drawn, for example, in block diagrams.

The illustration below is an example of a block diagram for the change in numbers of a hypothetical seaweed population, over time.



Adu = Adult Juv = Juvenile

In the mathematical stage the numerical relationships between the variables are defined, and this is followed by the actual construction of the model. These steps are shown below, in the context of the matrix model.

First, the transition matrix is constructed for a hypothetical species of seaweed:

To determine mortality of the seaweeds, 100 individuals of five age classes were tagged and monitored every year for three years. Earlier observations had determined that individuals rarely survived beyond five years. The following data were obtained:

AGE CLASS	SURVIVORSHIP DATA TIME PERIOD (Years)			FECUNDITY DATA[1] (Zygotes per plant)		
	1	2	3	1	2	3
0-1	0.10	0.15	0.10	0	0	0
1-2	0.60	0.55	0.70	20	15	10
2-3	0.75	0.70	0.80	75	80	30
3-4	0.50	0.40	0.40	80	85	90
4-5	0.00	0.00	0.01	100	95	110

[1]All figures to be multiplied by $1x10^4$

Which of these figures are to be used? Year 1, year 2, or should they be averaged? One way of utilizing the data is to use the figures for year 1, and then see if the model will predict the correct data for years 2 and 3; the predictions can be checked since the second and third year data are available.

Why are the survivorship values in the last age class (4-5 years) essentially zero?

Additional work in the seaweed community over subsequent years supplied the following information on the numbers in the population at times t, t+1, and t+2:

	AGE CLASS 1	2	3	4	5	
NUMBERS/M2	500	45	27	18	10	t
	200	60	37	25	10	t + 1
	700	50	40	15	20	t + 2
	1245	278	45	32	12	t + 3

Using the previously discussed generalized matrix model as a guide, the figures for the first year are inserted into the transition mamx and the column vector as follows:

TRANSITION MATRIX					COLUMN VECTOR
0	20	75	80	100	500
0.1	0	0	0	0	45
0	0.6	0	0	0	27
0	0	0.75	0	0	18
0	0	0	0.50	0	10

The results of running the model for three generations are as follows:

Age Class	Year 2	Year 3	Year 4
1	5365	5545	15612
2	50	537	555
3	27	30	321
4	20	20	23
5	9	10	10
	5471	6142	16522

HOW IS THE COMPUTER PROGRAM USED?

This is a good time to become familiar with the computer program, by using the above data to run the model. (The comments below refer to the program available from the author.) Insert the diskette, start the computer, and follow the instructions on the screen.

1. Insert the data into the model;
2. Practice saving the transition matrix to disk;
3. Try viewing the model when presented with that option;
4. Run the model for three consecutive years and compare your third year data in the column vector with that of your neighbor or check with the instructor,
5. Run the model for 30 years (using the continuous run option) and again check your data;
6. Explore the option to calculate lambda (λ), and determine whether the population has reached a stable age distribution.

Questions you might consider are;

1. How can you get rid of the 'pile-up' of organisms in the first age class?
2. What property of the model causes this 'pile-up to occur?
3. Is the 'pile-up' biologically reasonable?
4. What is the biological assumption which, if true, would account for the accumulation of organisms in that first age class?
5. How accurate is the model in predicting the age structure of the following years population?
6. How close do the predicted numbers have to be to the actual numbers before you consider the model a success?
7. How would a stage-specific model differ from the above age-specific model?

In attempting to answer the above questions, keep the following assumptions of the matrix model in mind:
1. Reproduction occurs in an age class before any mortality occurs.
2. Fecundity and mortality are constant over the time period of the model.
3. A relatively simple life history is assumed (gametic or zygotic, as opposed to an alternation of generations).

All of these assumptions can be ignored with more complex matrix models, but these are not considered here.

CONSTRUCTING YOUR OWN MODEL

The last step of this exercise is for you to construct a model, based on what you think are reasonable numbers for fecundity and survivorship, for the organism of your choice. Run it for at least 40 generations and determine lambda, **r,** and the potential harvest rate. If there is time, report results to the class, and include a rational for the numbers you choose for fecundity and survivorship.

One variant on the above exercise is to start as though your population were colonizing a new habitat, as in a newly congealed lava flow. Think carefully about the structure of the column vector! Also, you might wish to test whether your population is more sensitive to changes in fecundity than survivorship.

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