Population Modelling
II. Non-Exponential Models

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Contents

1 Introduction to Population Modelling

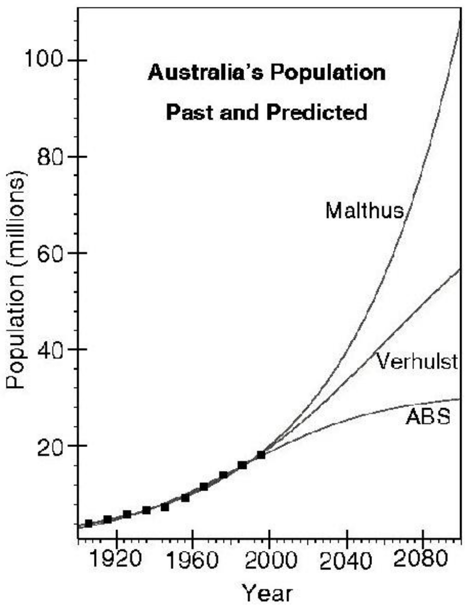
When mathematicians talk about playing with a model, chances are they don't mean a model plane or boat. They are probably talking about a mathematical model — a set of equations that describe in mathematics how a particular system works. There are mathematical models for many things, such as the planets revolving about the sun, heating iron ore in a blast furnace, pollution in a lake, how prices vary on the stock exchange, the spread of diseases and how populations (people, animals, bacteria, viruses, etc) change with time.

Population modelling started a long time ago, and one of the earliest modellers was Fibonacci (1170–1250). In his book *Liber abaci*, he modelled a rabbit population, starting with one pair of baby rabbits. If each adult pair of rabbits produces only one pair of baby rabbits each month, and if baby rabbits take one month to become adults, the numbers of pairs of rabbits in successive months are given by the famous Fibonacci numbers: 1, 1, 2, 3, 5, 8, 13, 21, and so on. The next number is found by adding the previous two numbers. Fibonacci numbers are also found elsewhere in Nature. If you look at a pine cone, you will find the 'petals' spiral in two directions. The number of petals it takes to go once around is almost always a Fibonacci number. The same thing occurs in pineapples, sunflowers and many other flowers.

Much later, Thomas Malthus (1766–1834) in England startled the world by predicting that food would run out sometime in the future, because of the rapid increase in the human population. Based on the data he had at the time, Malthus predicted that the world population would increase exponentially, doubling every 40 years, thereby increasing at a faster and faster rate. (Forty years is the current doubling time of the world's population.) If you start with the number 1 and keep doubling it, you will see an example of exponential growth.

The models of Fibonacci, Malthus and some other scientists all predict that the population will grow faster and faster. This is an alarming prospect, but does not seem to happen in experiments performed when there are limited resources, such as food and space to live in. Experiments with small animals and fungi in the laboratory, and with larger animals in fenced areas in the field show that as the resources start to run out, the reproduction rate reduces and the rate of growth slows down. The Belgian scientist Pierre Verhulst (1804–1849) while at the Belgian military school, the Ecole Royale Militaire, developed a model, called the logistic model, which took into account these observations. He introduced the idea of a 'carrying capacity' or maximum sustainable population that the environment will support.

We can illustrate the Malthus exponential model and the Verhulst logistic model by looking at the population of Australia since 1900. The small dark squares on the graph over the page show the Australian Bureau of Statistics (ABS) figures for the number of people in Australia (in millions) up until 1996. If we model these data with an exponential curve (the Malthus model), we get the top curve in the figure. The middle curve is the Verhulst model. Both these curves fit the population numbers up to the present time well, but predict quite different future populations.



According to the exponential (Malthus) model, the population will continue to grow at a faster and faster rate, with a predicted population of about 109 million people in the year 2100, and about 587 million people in 2200. The logistic (Verhulst) model predicts that the population will keep on growing, but at a slower and slower rate; the predicted population in 2100 is about 57 million people, and the population would level off eventually at about 83 million people.

The Australian Bureau of Statistics uses a mathematical model to predict the population of Australia well into the future to assist in planning for the number of people who will be living here. The predictions of its model are shown as the bottom curve in the figure. It has the shape of a logistic curve, but levels out much faster than the middle curve, predicting a population in 2100 of about 30 million people, and a maximum population of about 31 million.

Prediction is one powerful aspect of a mathematical model. By putting in the numbers we know, such as for the Australian population, we can predict what a population will be in the future, according to our model. Of course, the accuracy of our predictions depends on how good our model is, that is how well it describes the phenomena that affect population growth.

Another important use of a population model is to predict what will happen to the population if something changes, for example if the birth rate drops, if the number of immigrants is increased or decreased, or if, say in a war, many people die. Predicting changes in a population is particularly relevant to populations of animals, insects and plants which have become serious pests after being brought into Australia from overseas. These include rabbits, foxes, mice, cane toads and European carp among the animals, and prickly pear, Paterson's curse, salvinia, mimosa and scotch thistle, to name but a few of the plants. The populations of some of these have reached very high levels at times, causing serious problems for farmers and the environment.

Rabbits drinking at a waterhole before the introduction of myxomatosis (nma.gov.au).

How do we control such pests? Often there are a number of possible ways, but which one is best? Population models can be modified to include the effect of the release of a predator, the spread of a disease in the pest population, the effect of poisoning or some other control measure. It is then possible to use the models to predict what would happen to the population if the different control strategies were tried. The models can also be used to find the best way of carrying out a particular control measure. Sometimes the modelling is done together with small-scale experiments, but often only the mathematical model can be used because the experiments are too risky or too expensive.

In using a population model, we put the starting conditions and parameters (number of animals, how quickly they breed, etc) into our equations and predict the population at some later time. What if we change the starting conditions only slightly? We will end up with nearly the same final answer, right? Not necessarily. In some models, for example a variation on the Verhulst logistic model, with particular parameters, we find that the population does not change steadily towards some ultimate population, as we saw in modelling the Australian population, but changes rapidly and unpredictably with time. We say the model exhibits chaos: it loses its ability to predict, because a small change in the starting conditions produces a large change in how the population varies with time.

Population Modelling Series

Population Modelling I. Exponential Growth looks at simple exponential-growth models and problems; suitable for Years 7–9.

Population Modelling II. Non-Exponential Models looks at other types of population models, both continuous and discrete; suitable for Years 10–12.

Population Modelling III. SIR Epidemic Model works through a classic model of the spread of an epidemic; suitable for good students in Year 12 .

2 Population Models and Problems

2.1 Rabbits and Fibonacci Numbers

Fibonacci (fib–on–archie), real name Leonardo Pisano (Leonardo of Pisa), was born in about 1170. He too thought about populations, but much earlier than Malthus. One of his problems concerning a rabbit population led to the famous Fibonacci numbers

$$1 \quad 1 \quad 2 \quad 3 \quad 5 \quad 8 \quad 13 \quad \ldots .$$

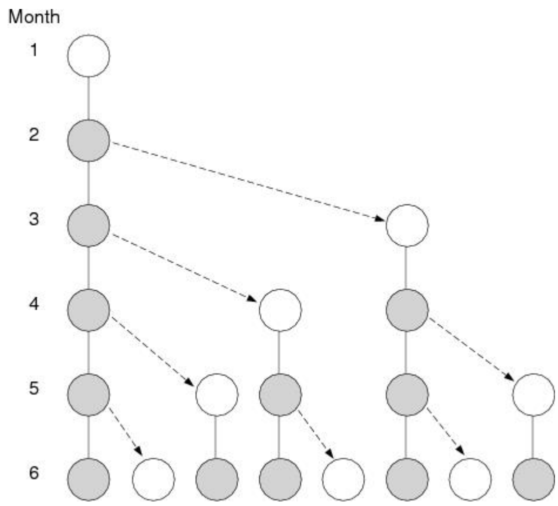
The Rule: Add the previous two numbers to get the next number.

Write down the first twenty Fibonacci numbers.

Look up Fibonacci numbers and how they relate to the *Golden Number* or *Golden Ratio* or *Golden Section* (architecture). Fibonacci numbers also turn up in Nature. See if you can find out where.

Here is Fibonacci's rabbit problem. See if you can understand why the Fibonacci numbers give the number of *pairs* of rabbits each month and answer the question. The diagram might help.

> A pair of new-born rabbits is put in a pen. *How many pairs of rabbits are there after a year if, every month, each adult pair produces a new pair?* The rabbits become adult one month after birth.



In the diagram, an open circle represents a *pair* of immature rabbits (too young to breed) and a shaded circle a *pair* of mature breeding rabbits. The arrows lead to offspring. Adding the number of circles for each month gives the number of pairs of rabbits — the Fibonacci numbers.

Note that the growth here is not exponential (we are not multiplying by a constant to obtain the next number), but the number of rabbits still increases rapidly.

2.2 Logistic Model

The Logistic Model arose from an attempt by Verhulst (Section 1) to come up with a more realistic population model than Malthus' exponential model. He reasoned that no organism grows withoutout bound, otherwise the Earth would be covered in this organism. Restrictions to growth are imposed by the need for food and space, so that the growth rate, assumed constant in the exponential model, must decrease as the population increases. Verhulst chose the simplest form for such a growth rate, a linear decrease with population: $k = a - bP$, where a and b are constants. This led to the so-called logistic curves (see Figure 1 above and Section 2.2.1 below), which start out like exponentials but eventually saturate or tend to a constant value.

2.2.1 Mathematical background

This section briefly outlines the steps to the Logistic Model in terms of differential equations. You can skip this if you haven't covered/encountered differential equations.

The assumption that the (instantaneous) rate of change (increase or decrease) in a population $P(t)$ at time t is proportional to the population at that time gives rise to the exponential differential equation

$$\frac{dP}{dt} = kP,$$

where the constant k is the growth (or decay) rate. Solutions are of the form $P(t)=P_0e^{kt}$, where $P_0=P(0)$ is the initial population.

Given that this leads to unlimited growth for positive k, Verhulst looked to the simplest modification to the growth rate k that would have it reducing as the population increased; this was $k=a-bP$, a linear form, where a and b are positive constants.

Putting this into the exponential differential equation above, re-arranging and renaming some constants gives the logistic differential equation

$$\frac{dP}{dt} = kP\left(1 - \frac{P}{K}\right),$$

where it turns out that K is the maximum sustainable population or carrying capacity.

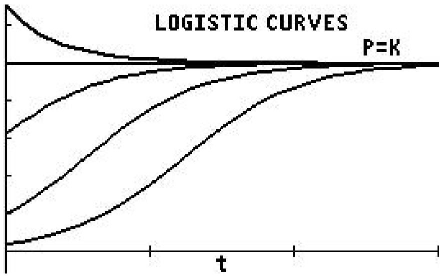
The solution to the logistic differential equation is

$$P(t) = \frac{KEe^{kt}}{Ee^{kt} - 1}, \tag{1}$$

where $E=P_0/(P_0-K)$, with $P_0=P(0)$ the initial population ($P_0 \neq K$).

If $P_0=K$, the solution is $P(t)=K$, a constant or equilibrium solution. $P(t)=0$ is the other equilibrium solution but not of great interest in population modelling other than acknowledging that it makes sense.

Some logistic curves are shown below.



Logistic curves are close to exponential for small t but, instead of increasing indefinitely like the exponentials, they level out and approach the constant value K asymptotically. Curves starting above the carrying capacity K decrease down to it asymptotically.

2.2.2 Logistic problem

A population $P(t)$ of fish in a pond is modelled by the logistic differential equation, Equation (1), with $k = 2.5$ and carrying capacity $K = 100$. Time t is measured in weeks. Initially there are 10 fish in the pond.

1. Graph $P(t)$ versus t for $0 < t < 5$.

2. How many fish are there after 1 week?

3. How long does it take the fish population to reach 80?

4. How many fish are there after a long time?

2.3 Discrete Logistic Model and Bacteria

Here we use a discrete version of the Verhulst or Logistic Model, called the Discrete Logistic Model, to predict the growth of a population of bacteria or kangaroos; in a discrete model, time goes in steps rather than being continuous, as it was in previous models. The model is in the form of a difference equation which tells you how to calculate the population in an hour's time if you know the population now:

$$P_{n+1} = A \times P_n \times (1 - P_n).$$

2.3.1 Bacteria

In this model, P_n is a measure of the population (in millions of bacteria) at the end of the nth hour and A is a number that depends on how fast the bacteria reproduce. For our calculations, we take $A =$ and the starting population $P_0 = 0.1$.

To calculate P_1, the population after 1 hour, put $n = 0$ and $P_0 = 0.1$ in the equation:

$$P_1 = 2 \times P_0 \times (1 - P_0) = 2 \times 0.1 \times (1 - 0.1) = 0.18.$$

To calculate P_2, the population after the second hour, put $n = 1$ in the equation:

$$P_2 = 2 \times P_1 \times (1 - P_1) = 2 \times 0.18 \times (1 - 0.18) = 0.2952,$$

and so on. After a few more steps (hours), you should find the population stabilises at a particular number. *What is the number?*

To speed up this process, on a calculator, type ([enter] ≡ [EXE])

0.1 → [alpha] P [enter]

2P(1−P) → P [enter]

This will give you the next value for P. If you now keep pressing [enter], the calculator will repeatedly execute the last line to give successive values for P.

Next let $A = 3.2$ and keep $P_0 = 0.1$:

0.1 → [alpha] P [enter]

3.2P(1−P) → P [enter]

and keep pressing [enter].

You'll need to run the population for about 18 hours this time before it settles down. What happens here? *Draw a plot of population versus time.*

Now try $A = 3.8$ and $P_0 = 0.1$. This one is weird! The population varies wildly between 0.1 and 1, with no hope of prediction. *Plot this one too.* You've discovered chaos (the mathematical version).

What happens with other values of A and P_0?

The sequence grapher on a graphics calculator can be used to graph values of P_n vs n. The LOGISTIC program (Section 4.1) sets this up for you for the bacteria here and for the kangaroos in the next question.

2.3.2 Kangaroo management

Part of an UNSW Canberra Maths Lab adapted from *Stimulating Mathematical Interest with Dynamical Systems* by M.B. Durkin, The Maths Teacher 89, 242–24 (1996).

You are hired by the State Forestry Department, with your main task to assist in the management of the kangaroo population in a remote forest called Hamt Reserve. The possibility of culling of kangaroos in the reserve is under consideration.

The kangaroo population in the reserve is given by the Discrete Logistic Model, a difference equation,

$$P_{n+1} = 1.8P_n - 0.8(P_n)^2, \qquad (2)$$

where P_n is the number of kangaroos in the reserve at the end of year n in tens of thousands, i.e. *one unit of P equals 10,000 kangaroos.* At the end of 2005, there were 8000 kangaroos in the reserve ($P_0 = 0.8$).

The first task

As a training exercise, management asks you to model and report on a scenario containing several events that would affect the kangaroo population.

Write a short report on the outcome of the following scenario. The report should include a mathematical analysis with calculations, tables and/or graphs to substantiate your conclusions.

The scenario

- If there were no natural disasters in 2006, what would the kangaroo population be at the end of 2006? Do this and the following calculations manually (without a program) using Eq. (2).[1]
- Unfortunately, at the end of 2006, there was a short but fatal outbreak of the dreaded rootoxis which kills around 4000 kangaroos. What would the population of kangaroos be at the end of 2007? When would the kangaroo population recover to more than 9000 kangaroos if there were no more natural disasters?
- Following the rootoxis epidemic, on Christmas Day 2008 there was a forest fire in a nearby forest which resulted in 2000 kangaroos from that forest migrating into Hamt Reserve. What would the population of kangaroos in Hamt Reserve be at the end of 2009?
- After these two events, there were no more natural disasters. What would the kangaroo population be after a long time? The number here is the limiting capacity or maximum sustainable population of the reserve.

Effect of culling

Impressed by your previous report, management has now put you in charge of undertaking a feasibility study into whether culling of kangaroos is necessary/desirable in Hamt Reserve. Your analysis will be a crucial factor in the decision-making process.

Write a report addressing the following questions. Again, a mathematical analysis including calculations, tables and/or graphs is required to substantiate your conclusions. Add an executive summary for your boss, summarising your findings and making suitable recommendations.

1. What is the modified form of Eq. (2) if H kangaroo units are culled each year?

   We assume here, for simplicity, that all the kangaroos are killed close to the end of the year, otherwise the killing of the female kangaroos in particular would affect the number of births and deaths, and consequently the growth rate.

2. What would happen if 720 kangaroos were culled each year ($H = 0.072$), a value used in a nearby reserve? Assume the initial population is that given above for the year 2005, $P_0 = 0.8$. What is the long-term population?

   What if the initial population were $P_0 = 0.3$? $P_0 = 0.095$?

3. What would happen if 2400 kangaroos were culled each year ($H = 0.24$)? Assume again that $P_0 = 0.8$. What is the long-term population?

   What if the initial population were $P_0 = 1$? $P_0 = 1.5$?

4. What about $H = 0.2$? It turns out[2] that this is the largest number of kangaroos which could be culled annually without the kangaroos dying out in Hamt Reserve. Note that the initial population must be larger than 0.5. What is the long-term population in this case?

[1] *Calculator hint*: Store the initial population in memory P and repeatedly execute the calculation $1.8\text{P} - 0.8\text{P}^2 \rightarrow \text{P}$ by pressing enter / EXE the required number of times. Make sure you understand why this works.

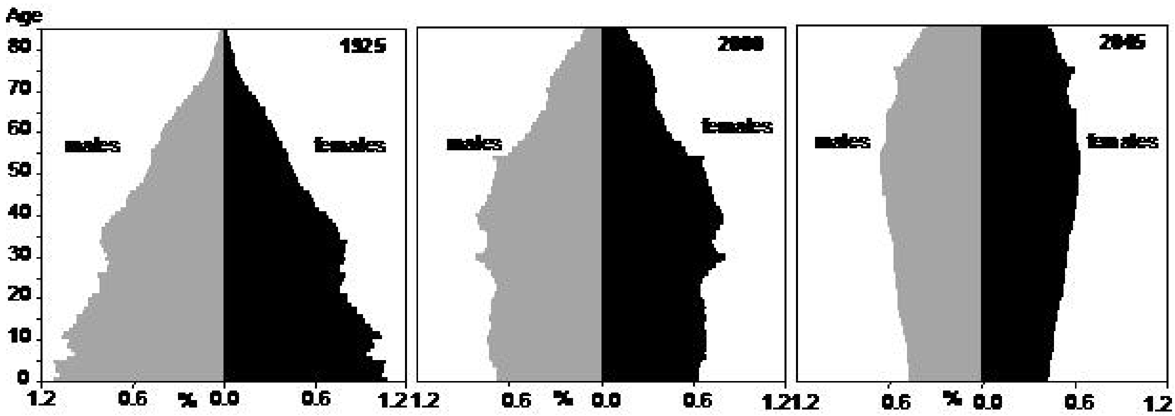
[2] Experiment and see — the LOGISTIC program (Section 4.1) might help here.

2.4 Population-Projection Matrices

In 2005, the Australian Government's Productivity Commission released its research report, *Economic Implications of an Aging Australia*[3]. Planners are concerned that the proportion of older people is increasing, which will put pressure on social services like health care. Also there may be fewer people in the working population to pay for the required services and pensions. The distribution of the population with respect to age is changing.

To describe the population we can divide it into age groups, for example into five-year groups, 0–5 years, 6–10 years, etc. It is also useful to split the population into males and females.

Here are some data taken from the Productivity Report.



From pyramid to coffin. Changing age structure of the Australian population, 1925–2045.

Some of the results are measured data (1925 and 2000), while those for 2045 are predictions. The trend is very clear, and we can see the "baby boomers" spreading through the population.

We follow this approach in the remaining examples in Section 2.4: splitting a population into age classes and seeing how these classes evolve over time.

2.4.1 Leslie matrices

The Leslie matrix is a discrete, age-structured model of population growth that is very popular in population ecology. It was invented by and named after Patrick H. Leslie.

We divide a population into a number of classes — here we shall assume three classes, referring to three age groups, young, adults and seniors, with respective numbers y, a and s. The population is then described by the vector or 3×1 column matrix

$$\boldsymbol{v} = \begin{bmatrix} y \\ a \\ s \end{bmatrix}.$$

[3]www.pc.gov.au/inquiries/completed/ageing/report

A 3×3 transition matrix $\boldsymbol{T}$ tells us how the population evolves. For example, if the population to start with is

$$\boldsymbol{v}_0 = \begin{bmatrix} y_0 \\ a_0 \\ s_0 \end{bmatrix},$$

after one cycle it is

$$\boldsymbol{v}_1 = \begin{bmatrix} y_1 \\ a_1 \\ s_1 \end{bmatrix} = \boldsymbol{T} \begin{bmatrix} y_0 \\ a_0 \\ s_0 \end{bmatrix} = \boldsymbol{T}\boldsymbol{v}_0.$$

In problems leading to a Leslie transition matrix:

- in each cycle, members of the other classes produce a certain number of new young in Class 1;
- a certain fraction of each class survives to move into the next class; the rest die;
- all members of the top class die.

This leads to a Leslie matrix $\boldsymbol{T}$ that is zero everywhere except possibly:

- along the top row after the first element — the birth rates for each class;
- in the elements along the diagonal parallel to and just below the main diagonal — the survival rates for each class.

$$\begin{bmatrix} 0 & * & * & * & * & \cdots & * & * \\ * & 0 & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & * & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & * & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & * & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & 0 & \cdots & * & 0 \end{bmatrix}$$

Leslie discovered these matrices in the 1940s when he pioneered this way of exploring how populations can develop. He taught himself matrix algebra while he was in hospital with TB.

Leslie matrices and beetles

(a) During each cycle, each adult beetle produces on average 2.75 young and each senior beetle produces on average 2.5 young; one quarter of the young beetles survive to become adults; and one half of the adult beetles survive to become seniors. In a Leslie-matrix problem, all the seniors die.

Find the Leslie transition matrix $\boldsymbol{T}$.

Good strategy: Write out the linear equations for y_1, a_1, s_1 in terms of y_0, a_0, s_0 and convert to matrix form.

(b) If we start with 40 young and no adults or seniors, show that after one cycle

$$\boldsymbol{v}_1 = \begin{bmatrix} y_1 \\ a_1 \\ s_1 \end{bmatrix} = \begin{bmatrix} 0 \\ 10 \\ 0 \end{bmatrix}.$$

You should have entered $\boldsymbol{T}$ into [A], the initial $\boldsymbol{v}$ into [B] and evaluated [A][B].

(c) Multiply repeatedly by $\boldsymbol{T}$ (the program POP (Section 4.2) helps here), and record $\boldsymbol{v}$ and the total population $P = y + a + s$ after 11, 12 and 13 cycles.

What happens to the total population? to the ratios of the numbers in the different classes?

2.4.2 Populations and oscillations

Workers other than Leslie had independently used matrix algebra in population models. The first was Harro Bernardelli, who published a paper in 1941 in the Journal of the Burma Research Society with the title *Population Waves.* Bernardelli's paper was unusual in focussing not on the eventual stability of the population structure, but on intrinsic oscillations in the population structure. He had observed oscillations in the age structure of the Burmese population between 1901 and 1931.

As an abstract model for such oscillations, he proposed a matrix model for the evolution of the population with

$$\boldsymbol{T} = \begin{bmatrix} 0 & 0 & 8 \\ 0.5 & 0 & 0 \\ 0 & 0.25 & 0 \end{bmatrix},$$

and showed by numerical calculations that this gave rise to apparently permanent oscillations in the age structure.

(a) By hand or using POP, with the vector $\boldsymbol{v}$ set initially to $\begin{bmatrix} 1 \\ 0.01 \\ 0.01 \end{bmatrix}$ (population in three age groupings in millions) and using Bernardelli's matrix $\boldsymbol{T}$, record the total population P at each cycle for 12 cycles. Plot P versus cycle number, joining up the points with straight lines. Discuss your findings.

(b) Repeat (a) using $\boldsymbol{T} = \begin{bmatrix} 0 & 0 & 5 \\ 0.7 & 0 & 0 \\ 0 & 0.5 & 0 \end{bmatrix}$. Describe your results in words. Explain.

2.4.3 Killer whales

Based on a Year-12 project set by Margaret MacLaughlan, St Francis Xavier College.

Teachers (and students) may find the POPMATX programs (TI-84/CE only; Section 4.3) useful (but not essential) for experimenting with the population-projection matrix.

Leslie matrices are just a special case of a more general population-projection matrix. In the more general case, animals in a class may remain in that class for more than 1 cycle. The probability that an animal remains in a particular class for any given cycle is an element on the diagonal of the matrix, immediately above the entry in the Leslie matrix, which gives the probability of moving to the next class in any given cycle.

Therefore we have a matrix whose elements along the top row give the fecundity or birth rate per animal per cycle for each class, whose diagonal elements give the probability of an animal remaining in a particular class in any cycle and whose elements below the diagonal give the probability of an animal moving to the next class in any cycle. The fact that the latter two numbers in any column do not add up to 1 means that some animals in each class die each cycle.

For female killer whales, we have four classes — yearlings (individuals in the first year of life), juveniles (past the first year, but not mature), mature females and post-reproductive females. The mean period in the juvenile stage is 13.4 years and in the mature stage 22.1 years, with an overall lifetime of 80–90 years. Details in Brault and Caswell, *Pod-specific demography of killer whales*, Ecology 74, 1444–1454 (1993).

The population-projection matrix for female killer whales is given below. The time for one cycle is one year.

$$\boldsymbol{T} = \begin{bmatrix} 0 & 0.0043 & 0.1138 & 0 \\ 0.9775 & 0.9111 & 0 & 0 \\ 0 & 0.0736 & 0.9534 & 0 \\ 0 & 0 & 0.0452 & 0.9804 \end{bmatrix}$$

1. A project you are involved in wants to re-introduce killer whales into an area of ocean from which they have disappeared. The project leader wants to know what is the best combination of juveniles and mature females to re-introduce, assuming an overall total of 50 (plus an appropriate number of adult males). You decide to model three options over 40 cycles (years).

(a) 50 female juveniles.

(b) 40 female juveniles and 10 mature females.

(c) 50 mature females.

What happens to the different population classes of female killer whales over time in each of these options (according to this model)? What is the best strategy for re-establishing the killer-whale population?

Hint: (*manual method*) If $\boldsymbol{T}$ is in matrix [A] and the initial population $\boldsymbol{v}_0$ is in the 4×1 matrix [B], executing the command [A] [B] $\to$ [B] $\big(\text{mat A mat B} \to \text{mat B}\big)$ and repeatedly pressing enter / EXE will generate successive population vectors $\boldsymbol{v}_1$, $\boldsymbol{v}_2$, $\boldsymbol{v}_3$, etc.[4] The symbol $\to$ stands for the sto key.

[4]You could also use the POP program (Section 4.2) directly on a TI-84/CE or, on a Casio 9860,

2. Does the trend in the total population depend on which option you choose?

3. The value of 0.1138 in the top row of $\boldsymbol{T}$ gives the number of live births per mature female per cycle (year). To what value could this birth rate fall before the total population starts to decrease?

This birth rate is clearly important for the overall survival of killer whales.

Hint: See the discussion in Section 4.3 on the eigenvalue λ_p of the matrix $\boldsymbol{T}$.

4. How sensitive is the population to the survival rates of yearlings (0.9775), juveniles (0.9111), mature females (0.9534) and post-reproductive females (0.9804)?

You might like to quantify your answers here by determining what percentage decrease in each rate is needed to stop the population growing.

Do your answers make sense?

change the last line of POP to mat B(1,1)+mat B(2,1)+mat B(3,1)+mat B(4,1). Run POP repeatedly by pressing [enter]/[EXE]. This will give you the total population directly. POPMATX4 also plots the populations.

3 Solutions

Diagrams here were done on a TI-84CE graphics calculator.

3.1 Rabbits and Fibonacci Numbers

The first twenty Fibonacci numbers are

1 1 2 3 5 8 13 21 34 55 89 144 233 377 610 987 1597 2584 4181 6765.

The Golden Number/Ratio/Section

The Golden Ratio (also called the Divine Proportion) is denoted by the Greek letter ϕ or τ. If a length is divided in the Golden Ratio $1:\phi$, the ratio of the longer part to the whole, $\phi:1+\phi$, is also the Golden Ratio. When used to construct a rectangle, this ratio was thought to make the rectangle pleasing to the eye. Hence the Golden Ratio occurs everywhere, and has supposedly been used to design buildings from the Parthenon to the United Nations building in New York, as well as by artists and musicians. It is closely connected with the Fibonacci series, and has a value of $(1+\sqrt{5})/2=1.61803\ldots$.

Fibonacci numbers are evident in particular (equi-angular or logarithmic) spirals which appear frequently throughout the natural world — in things as small as the double helix and other microscopic twisting structures, to the galaxies that move in equi-angular spirals. These spirals also account for gastropods growing while maintaining their shape. In order for all leaves on a stem to catch sunlight, they are arranged in equiangular spirals that incorporate the Fibonacci numbers. Other examples of this natural phenomenon include pine-cone seeds, flower petals, sunflower seeds, the horns of mountain goats, elephant tusks, lions' claws, scales in pineapples, and so on. Find out more at *www.mcs.surrey.ac.uk/Personal/R.Knott/Fibonacci/fib.html.*

How many pairs will there be in one year?

1. There is only one pair of immature rabbits during the first month.
2. At the beginning of the second month they mate, but there is still only 1 pair during the month.
3. At the beginning of the third month the female produces a new pair, so now there are 2 pairs of rabbits in the pen.
4. At the beginning of the fourth month, the original female produces a second pair, making 3 pairs in all in the pen.
5. At the beginning of the fifth month, the original female has produced yet another new pair, while the female born two months ago produces her first pair, making 5 pairs in all.

   and so on.

The number of pairs of rabbits after a year is the twelfth Fibonacci number, 144 pairs.

Why do the Fibonacci numbers appear as the number of rabbits in the pen each month?

If we let $f(n)$ be the number of pairs of rabbits in the pen at the start of the nth month, we will show that $f(1)=1$, $f(2)=1$ and $f(n)=f(n-1)+f(n-2)$, which is exactly the definition of the Fibonacci numbers.

We start in month 1 with one newly born pair, so $f(1)=1$.

There is also only 1 pair during month 2, since although the adults mate at the start of month 2, babies are not born until the start of month 3: $f(2)=1$.

Now look at the nth month.

All the rabbits from the previous month ($f(n-1)$ pairs of them) survive. Any rabbit (pair) that was alive 2 months ago is now able to produce a new pair; we assume they produce 1 and only 1 new *pair* per month. Thus, the number of newly born pairs is the same as the number of pairs alive 2 months ago, $f(n-2)$. The total number of rabbits this month is the sum of all the rabbits alive last month and those that are newly born this month, that is $f(n)=f(n-1)+f(n-2)$ — the definition of the Fibonacci numbers.

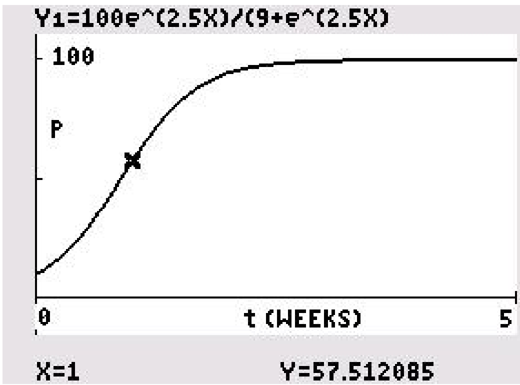
3.2 Logistic Problem

We have $P_0=10$ and $K=100$, so that $E=P_0/(P_0-K)=-\frac{1}{9}$.

The number of fish at time t weeks is therefore given by

$$P(t) = \frac{100e^{2.5t}}{9+e^{2.5t}}.$$

1.



2. How many fish are there after 1 week?

Read directly from your graph using trace or algebraically, the number of fish after 1 week is

$$P(1) = \frac{100e^{2.5}}{9+e^{2.5}} = 57.5 \quad \text{to 3 digits.} \tag{3}$$

There are 57 or 58 fish in the pond after 1 week.

3. How long does it take the fish population to reach 80?

Again you can do this from your graph of $P(t)$ by graphing $y = 80$, and finding its intersection $\left(\boxed{\text{calc}}/\boxed{\text{G-solv}}\right)$ with $P(t)$.

Algebraically, we need to solve $P(t) = 80$. Therefore,

$$\begin{aligned} \frac{100e^{2.5t}}{9 + e^{2.5t}} &= 80. \\ \therefore \quad \frac{e^{2.5t}}{9 + e^{2.5t}} &= 0.8. \\ \therefore \quad e^{2.5t} &= 0.8(9 + e^{2.5t}). \\ \therefore \quad 0.2e^{2.5t} &= 7.2. \\ \therefore \quad e^{2.5t} &= 36. \\ \therefore \quad t &= \frac{\ln(36)}{2.5} \\ &= 1.43 \quad \text{to 3 digits.} \end{aligned}$$

It takes about 1.43 weeks or about 10 days for the fish population to reach 80.

4. How many fish are there after a long time?

Again you can do this from your graph of $P(t)$ by tracing along it and remembering what K means.

There are 100 fish in the pond after a long time. This is the carrying capacity or maximum sustainable capacity of the pond according to the logistic model Equation (3).

Algebraically, multiplying numerator and denominator of Eq. (3) by $e^{-2.5t}$,

$$P(t) = \frac{100e^{2.5t}}{9 + e^{2.5t}} = \frac{100}{9e^{-2.5t} + 1}.$$

Now $e^{-2.5t}$ goes to 0 as $t \to \infty$, so $P(t) \to 100$.

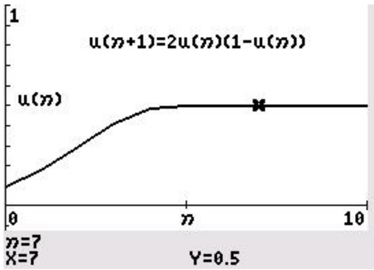
3.3 Discrete Logistic Model

3.3.1 Bacteria

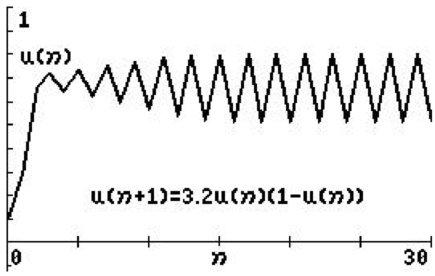
For the logistic difference equation

$$P_{n+1} = A \times P_n \times (1 - P_n),$$

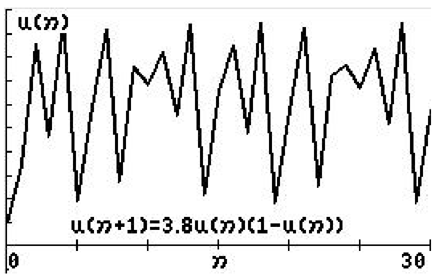
with $A = 2$ and starting population $P_0 = 0.1$, the population stabilises at 0.5.



With $A = 3.2$ and $P_0 = 0.1$, eventually the population alternates between 0.513 and 0.799. *Draw a plot of population versus time.*



$A = 3.8$ and $P_0 = 0.1$. This one is weird! The population varies wildly between 0.1 and 1, with no hope of prediction. *Plot this one too.*



You've discovered chaos (the mathematical version).

What happens with other values of A and P_0? Try them and see!

3.3.2 Kangaroo management

The calculation of the population P_n can be done manually on a calculator (following the calculator hint in the question) or by using the built-in sequence grapher, depending on the sophistication of your students and the type of calculator they have. The LOGISTIC program (Section 4.1) sets up the sequence grapher for the problem here.[5]

We have the logistic difference equation for the kangaroo population

$$P_{n+1} = 1.8P_n - 0.8(P_n)^2,$$

with $P_0 = 0.8$ corresponding to the (end of) year 2005.

Using this and incorporating the rootoxis outbreak in 2006 by subtracting 0.4 (4000 kangaroos) from the 2006 population, we have the following number of kangaroos in subsequent years.

Year	n	P_n	**Number of kangaroos**
2005	0	0.8	8000
2006	1	$0.928-0.4=0.528$	5280
2007	2	0.7274	7274
2008	3	0.8860	8860
2009	4	0.9668	9668

The number of kangaroos has recovered to 9668 by the end of the year 2009.

If we include the migration of 2000 kangaroos at the end of 2008, we have the following numbers.

Year	n	P_n	**Number of kangaroos**
2008	3	$0.8860+0.2=1.0860$	$10,860$
2009	4	1.0113	$10,113$
2010	5	1.0022	$10,022$
2011	6	1.0004	$10,004$
2012	7	1.0001	$10,001$
2013	8	1.0000	$10,000$

The population in the reserve at the end of 2009 would be $10,113$. In subsequent years, the population declines to the equilibrium or maximum sustainable population of $10,000$, the population after a long time.

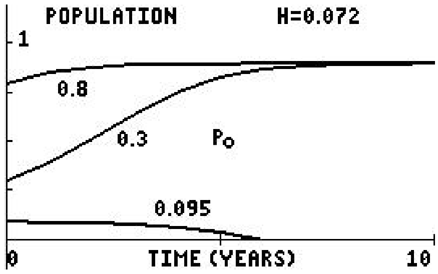
Effect of culling

1. If H kangaroo units are killed each year, this number is subtracted from the value for P_{n+1} that we calculated above, giving the difference equation

$$P_{n+1} = 1.8P_n - 0.8(P_n)^2 - H.$$

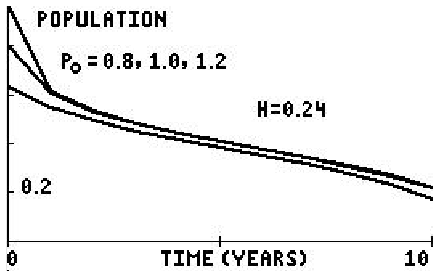
[5]The sequence grapher on the TI-84 (but not the CE) writes P_n in terms of P_{n-1}, so it is necessary to rewrite the difference equation as $P_n = 1.8P_{n-1} - 0.8(P_{n-1})^2$ if you use this method.

2. With $H = 0.072$ and an initial population of 0.8 units, the long-term population would be 0.9 units or 9000 kangaroos.

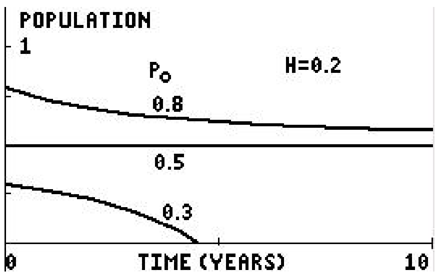


We find that[6] if the initial population is greater than 0.1 kangaroo units, the population will tend toward a stable value of 0.9. If the initial population is less than 0.1 kangaroo units, the population will tend to 0.

3. With $H = 0.24$, the population would die out, no matter what the initial population.



4. With $H = 0.2$, the long-term population would be 0.5 units or 5000 kangaroos, the maximum sustainable population with this level of hunting, provided that the initial population is greater than 5000. If the initial population is less than 5000, the population will die out.



If this level of hunting were chosen, any natural disaster that killed more than a few kangaroos after the population had levelled off at 5000 would bring the population to below 5000, and it would therefore die out. There is no margin for error with this level of hunting. In practice, a smaller value than 2000 would be chosen for the number of kangaroos killed annually, thereby leaving a margin to allow for natural disasters.

[6]Theory helps a lot here, but you can reach the same conclusions by experimenting with numbers on your calculator. Using the LOGISTIC program may help with this.

3.4 Population-Projection Matrices

3.4.1 Leslie matrices

(a) Writing out the equations for the three beetle age classes,

$$\begin{aligned} y_1 &= 0y_0 + 2.75a_0 + 2.5s_0 \\ a_1 &= 0.25y_0 + 0a_0 + 0s_0 \\ s_1 &= 0y_0 + 0.5a_0 + 0s_0 \end{aligned} \qquad \text{or} \qquad \begin{bmatrix} y_1 \\ a_1 \\ s_1 \end{bmatrix} = \begin{bmatrix} 0 & 2.75 & 2.5 \\ 0.25 & 0 & 0 \\ 0 & 0.5 & 0 \end{bmatrix} \begin{bmatrix} y_0 \\ a_0 \\ s_0 \end{bmatrix}.$$

Therefore, $\boldsymbol{T} = \begin{bmatrix} 0 & 2.75 & 2.5 \\ 0.25 & 0 & 0 \\ 0 & 0.5 & 0 \end{bmatrix}$.

(b) $\boldsymbol{T}\begin{bmatrix} 40 \\ 0 \\ 0 \end{bmatrix} = \begin{bmatrix} 0 \\ 10 \\ 0 \end{bmatrix}$.

(c)

After cycle	$\boldsymbol{v}$	Total pop'n
1	$\begin{bmatrix} 0 \\ 10 \\ 0 \end{bmatrix}$	10
2	$\begin{bmatrix} 27.5 \\ 0 \\ 5 \end{bmatrix}$	32.5
⋮	⋮	⋮
11	$\begin{bmatrix} 17.320 \\ 4.305 \\ 2.184 \end{bmatrix}$	23.809
12	$\begin{bmatrix} 17.299 \\ 4.330 \\ 2.153 \end{bmatrix}$	23.781
13	$\begin{bmatrix} 17.289 \\ 4.325 \\ 2.165 \end{bmatrix}$	23.779

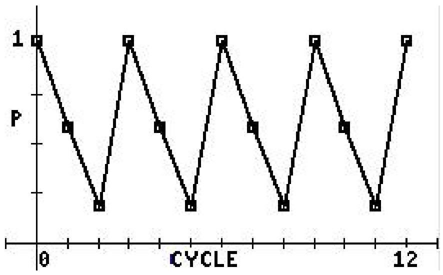
The total population seems to be stabilising at a little under 24, and the ratios of the populations in the 3 classes at about 8 : 2 : 1. Divide the first two numbers by the third (smallest) number to see this.

3.4.2 Populations and oscillations

(a) After 1 cycle: $\begin{bmatrix} 0 & 0 & 8 \\ 0.5 & 0 & 0 \\ 0 & 0.25 & 0 \end{bmatrix} \begin{bmatrix} 1 \\ 0.01 \\ 0.01 \end{bmatrix} = \begin{bmatrix} 0.08 \\ 0.5 \\ 0.0025 \end{bmatrix}$, so $P = 0.5825$.

From successive cycles, we build up a table.

Cycle	0	1	2	3	4	5	6	···
Pop'n	1.02	0.5825	0.185	1.02	0.5825	0.185	1.02	···

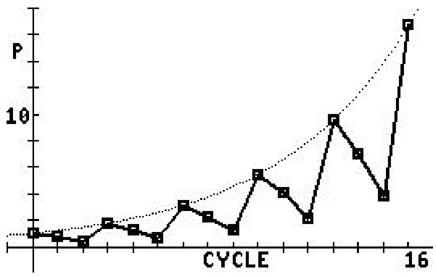


The population is oscillating or going in waves, with no overall growth or decline.

A group of young must first become adults (with a survival rate of 0.5) and then seniors (with a survival rate of 0.25) before producing a new group of 8 young; the process then repeats itself. The overall survival rate between young and seniors of $0.5 \times 0.25 = 1/8$ is balanced by a birth rate of 8, so that the overall population is not growing or declining.

(b) The populations are now 1.02, 0.755, 0.41, 1.785, 1.321, 0.718, 3.124, 2.312, 1.256, 5.467, 4.046, 2.197, 9.566, 7.081, 3.846, 16,741, ...

The population is oscillating, but growing overall. The birth rate of 5 and the survival rate of $0.7 \times 0.5 = 0.35$ gives an overall growth rate of 1.75 (dashed line).

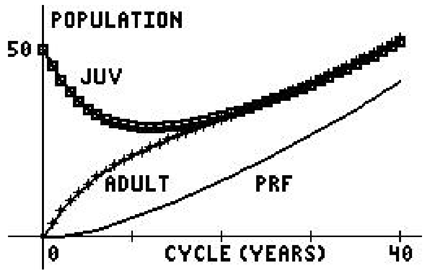


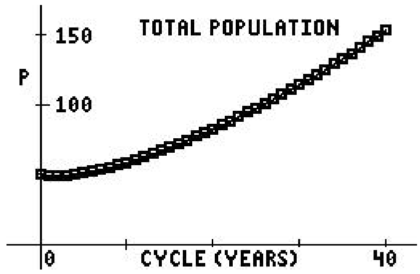
3.4.3 Killer whales

1. A project you are involved in wants to re-introduce killer whales into an area of ocean from which they have disappeared. The project leader wants to know what is the best combination of juveniles and mature females to re-introduce, assuming an overall total of 50 (plus an appropriate number of adult males).

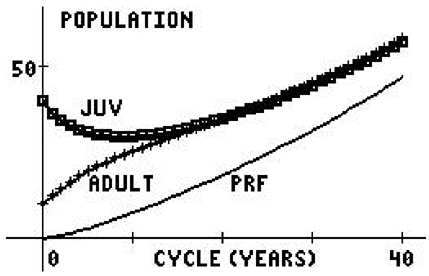
You model three options, with the resulting plots shown below. The left-hand plots show the populations of juvenile females (squares), mature females (crosses) and post-reproductive females (PRF: thin line); the right-hand plots show the total population (including yearlings), both as functions of the number of cycles (1 cycle = 1 year).

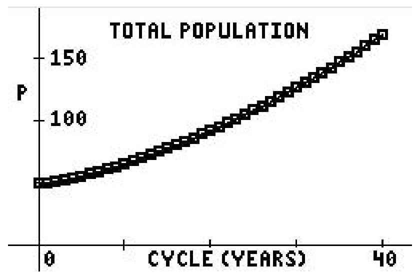
(a) 50 juveniles.



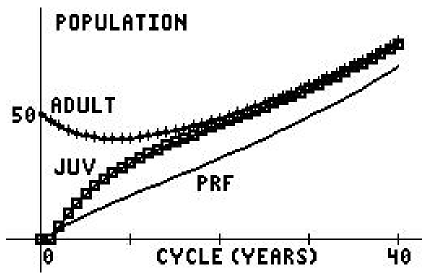


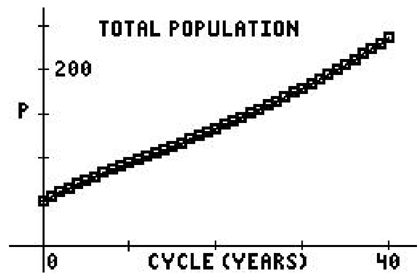
(b) 40 juveniles and 10 mature females.





(c) 50 adult females.





What happens to the different population classes of female killer whales over time in each of these options (according to this model)? What is the best strategy for re-establishing the killer-whale population?

After about 15 years, in all three options, there are approximately equal numbers of juvenile and mature females and this remains the case, both populations are increasing; the greater the inital number of mature females, the greater the numbers of both juvenile and mature females at any given cycle. The number of post-reproductive females follows a similar trend in all three options.[7]

[7] The ratios of the populations in the different classes are those of the components of the eigenvector of the population-projection matrix corresponding to λ_p.

In terms of the best strategy for re-introducing killer whales, it probably comes down to cost. Clearly the best option, according to the model, is to introduce all mature females but it could take quite a long time (and be expensive) to breed up a sufficient number, given it takes at least 14 years to maturity. Releasing all juveniles, a much cheaper option, runs the risk that not enough of the inexperienced juveniles survive long enough to establish a sustainable population. Some combination of juvenile and mature females may be the best option.

2. Does the trend in the total population depend on which option you choose?

In the three options with different initial populations, the trend is the same: the overall female population increases. However, the greater the inital number of mature females, the greater the total population at any given cycle. The fact of an increase in total population (and the eventual ratios of the populations in the four classes) does not depend on the initial populations in each of the classes.

3. The value of 0.1138 in the top row of $\boldsymbol{T}$ gives the number of live births per mature female per cycle (year). To what value could this birth rate fall before the total population starts to decrease?

This birth rate is clearly important for the overall survival of killer whales.

Experimenting with different values of the birth rate for mature females, either manually or using POPMATX4, shows that the population becomes steady when the value is about 0.055 ($\lambda_p \approx 1$), i.e. about 48% of the observed value. For birth rates less than 0.055, the total population will decline.

4. How sensitive is the population to the survival rates of yearlings (0.9775), juveniles (0.9111), mature females (0.9534) and post-reproductive females (0.9804)?

The female population is more sensitive to the survival rates than the birth rates, especially that of the mature females. Reducing the value of 0.9534 for mature females to 0.905 (a reduction of only 5%) is enough to stop the population growing.

For the other classes, the corresponding values are: yearlings 0.9775 down to 0.49 (50%); juveniles 0.9111 down to 0.82 (10%). The growth or otherwise of the population is unaffected by the survival rate of post-reproductive females.

4 TI-84/CE Population-Modelling Programs

Programs are available on the (free) CD *Graphics Calculator Activities* by Peter McIntyre and Margie Smith, or from Peter McIntyre at pdmcintyre@icloud.com.

4.1 LOGISTIC/LGSTCE — populations of bacteria or kangaroos

Sets up the graphics for a population of bacteria obeying the discrete logistic equation (Section 2.3.1) or for a population of kangaroos obeying the discrete logistic equation with culling (Section 2.3.2).

Use: Run the program. Select BACTERIA or KANGAROOS. Input the appropriate parameters at the prompts ($0 < \mathrm{u}(0) < 1$ for the bacteria). The program plots population versus cycle number (time). Use the arrow keys to trace the graph or press [enter] to return to the main menu.

When the program has finished, choose QUIT from the main menu. Here you can either keep the equations for manual plotting (e.g. with a different [window]; Option 1) or you can have the equations and other settings deleted (Option 2). If you choose Option 1, when you have finished rerun the program, QUIT and select Option 2 to tidy up.

4.2 POP — population-matrix multiplication

Also available for the Casio 9860.

Multiplies a column vector $\boldsymbol{v}$ (populations in different classes) by a matrix $\boldsymbol{T}$ (transition or population-projection matrix), displays the new $\boldsymbol{v}$ and the sum of the components of $\boldsymbol{v}$ (total population).

Use: Store the 3×3 matrix $\boldsymbol{T}$ in matrix A and the 3×1 column matrix $\boldsymbol{v}$ in matrix B. Run the program for the first step. Press [enter]/[EXE] repeatedly for subsequent steps. Press [on] [1] (Quit) to stop the program.

The TI-84/CE program actually works for $n\times n$ transition matrices $\boldsymbol{T}$ and $n\times1$ column matrices $\boldsymbol{v}$. Just store the matrices and run the program

4.3 POPMATX3, POPMATX4, POPMATXM — population matrix modelling

POPMATX3 and POPMATX4 calculate and plot as a function of cycle number (time) the numbers in 3 and 4, respectively, age classes of a population which is modelled using a Leslie matrix or other population-projection matrix. POPMATXM calculates and displays as a function of cycle number (time) the numbers in m age classes of a population. It also gives the ratios of the individual populations.

If $\boldsymbol{v_0}$ is the 3×1, 4×1 or $m\times1$ matrix containing the initial population values and $\boldsymbol{P}$ is the corresponding square population-projection matrix, the population after 1 cycle is given by $\boldsymbol{v_1} = \boldsymbol{P}\boldsymbol{v_0}$, after 2 cycles by $\boldsymbol{v_2} = \boldsymbol{P}\boldsymbol{v_1} = \boldsymbol{P}^2\boldsymbol{v_0}$, and so on. The population after n cycles is then $\boldsymbol{v_n} = \boldsymbol{P}\boldsymbol{v_{n-1}} = \boldsymbol{P}^n\boldsymbol{v_0}$.

Use: Put (in the relevant program) your 3×3, 4×4 or $m\times m$ population-projection matrix $\boldsymbol{P}$ (Leslie matrix or equivalent) in matrix A and the initial populations in the different age classes in the 3×1, 4×1 or $m\times1$ matrix B.

Run the program and input the number of cycles for which you wish to calculate the populations. The program will do the calculations.

POPMATX3 and POPMATX4 plot the graphs of the populations versus cycle number (time). These programs pause in [trace] mode so that you can analyse the graphs. The arrow keys allow you to move along a graph or from graph to graph. Which graph the cursor is on is indicated at the top left of the screen.

Pressing [enter] then gives a plot of the total population versus cycle number. Again you can [trace] this graph. Displayed on this graph is the largest eigenvalue λ_p of the population-projection matrix. The long-term total population varies as λ_p^n, where n is the cycle number. Therefore, if $\lambda_p > 1$, the population increases; if $\lambda_p = 1$, the population is steady; if $\lambda_p < 1$, the population decreases.

Pressing [enter] again ends the program.

Once POPMATX3 and POPMATX4 have finished, you can replot and [trace] any or all of the graphs of the individual populations versus cycle by selecting the appropriate plot in the [y=] menu. You can change the window either manually in the [window] menu or using [zoom] [9] (ZoomStat).[8]

POPMATXM does the calculations (but no plots) for an $m\times m$ matrix $\boldsymbol{P}$ and a $m\times1$ matrix containing the initial population values.

The data generated in the programs are stored in lists which can be accessed by pressing [stat] Edit. Scrolling across will show the lists not initially on the screen.

Run the POPMXCLR program to finish up. It deletes the matrices and lists used in/generated by the POPMATX programs, turns off the plots and resets the lists you will see when you press [stat] Edit.

POP, POPMATX3, POPMATX4, POPMATXM and POPMXCLR are contained in the group file POPMATX.84g.

[8] To plot the graph of the yearling population, you will have to change the Ylist in one of the plots using [statplot] ([2nd] [y=]).