The Lotka Integral Equation as a Stable Population Model

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Abstract

In 1939, A.J. Lotka published a seminal paper [17] on Population Dynamics. He introduced Lotka Integral Equation, which is a continuous time population model with stable age structure. In this essay, we derive this deterministic, continuous time model known, alternatively, as the Fredholm Integral or the Volterra Integral equations of the second kind. We supply some methods for obtaining analytical and numerical solutions. Laplace transform and the extended trapezoidal rule are used. We highlight our results with practical examples and illustrations.

Contents

1. Introduction

Throughout recorded history, the interactions of populations have generated interesting mathematical problems. The possible exhaustion of the food supply or the importance of studying population interaction is seen when we consider the potential for the spread of a desease.

Knowing the size of a population becomes vital when economic or political decisions, for example, need to be made. For example, five thousand years ago, the Sumerians counted their population for taxation purposes.

A mathematical formulation of populations only started in the eighteenth century. In 1767, Leonhard Euler produced the first mathematical model of a human population. This was closely followed, in 1772 by Johann-Heinrich Lambert, using data on human mortality in London (1753–1758), who gave a mathematical formulation of the law of mortality. England has a rich source of data on populations, derived from a steady collection over centuries. In 1798, Thomas Malthus formulated the rate of growth of population size using a first-order differential equation.

The modern theory of the population dynamic started with Alfred James Lotka (1880–1949), an American Biophysicist. He worked in particular, on the stability of the age composition of a population. In 1907, he published an article [16] which contained two fundamental equations in the study of populations. The most important paper [21], which shall be considered as a rigorous first formulation on the subject of Population Mathematics was that published in 1911 by Lotka and F.R. Sharpe. In this essay, we will focus our attention on the integral equation he published in 1932. This equation tracks the rate of female births in the case of a stable population. We will use a Laplace transform to give the form of the analytical solution. Discretization of the equation by using the composite trapezoidal rule as led to the numerical solution. We then highlight our results using illustrations and practical examples.

2. Stable Population Theory

The stable population model has been for a long time a principal model in the theory of population. According to Nathan Keyfitz, one of the most important successors of Lotka, " The greatest single contribution to population theory."

In this chapter we discuss the concept of a stable population model. We introduce the life table method which leads to the determination of two fundamental functions in our discussion, the survivor function and the fertility function. We will through an example describe some properties of a stable population.

2.1 Life Table

Definition 2.1. *The life table is defined as a compilation of the age distribution of a population that provides an estimate of the probability that an individual will die by a certain age, used to compute life expectancy [1].*

This table provides a schedule of the deaths within a population as a function of age. It also specifies the survival function, which may then be combined with the fertility function. The life table is one of the tool, used in quantitative analysis and in estimation of populations.

2.1.1 Survivor And Fertility Functions

The survival function, also known as a survivor function, is a random variable that maps a set of events, which we associate with mortality, onto time.

Definition 2.2. *Let X be a continuous random variable with cumulative distribution function* $F(t)$ *and* $l(t)$ *the probability density function on the interval* $[0, \infty)$ *. Its survival function is equal to the probability,*

$$P_r\{X > t\} = \int_t^\infty l(x)\,dx = 1 - F(t)\,.$$

Property 2.3. *We have the following properties*

1. *Every survival function is monotone decreasing,*
2. *The survivor function is related to a continuous probability density function,*
3. *For any small number* $d\sigma$*, the probability that* X *is included in* $(\sigma, \sigma + d\sigma)$ *is equal to* $l(\sigma)d\sigma$*. That is,*

$$P_r(\sigma < X < \sigma + d\sigma) = l(\sigma)d\sigma\,.$$

Definition 2.4. *If X is a random variable for individual life times the probability that a newborn will survive between age x and $x + dx$, or the survivor function, the continuous case will be denoted by*

$$l(x)dx\,. \tag{2.1}$$

Let us consider the approach a demographer could take in the discrete case.
Assume that we have a large closed population of size N_0, all aged exactly 0 years. After x years, we will have N_x lives with $N_x \leq N_0$, due to mortalities. The probability ${}_tP_x$ of survival from exact age x to exact age $x + t$ will be, approximately equal to

$${}_tP_x \simeq \frac{N_{x+t}}{N_x}\,. \tag{2.2}$$

The survival function in the discrete case, denoted by l_x is defined such that

$${}_tP_x = \frac{l_{x+t}}{l_x}\,. \tag{2.3}$$

Our life table model will be applied in the following probabilistic sense. For a group of l_x individuals of age x, the expected number of individuals that will survive to age $x + t$ will be $l_{x+t} = {}_tP_x l_x$. An arbitrary value is assigned to l_0 which is known as the *radix*. By interpolation we can also find intermediary values if they are required for integration.

Definition 2.5. *The fertility function sometimes called the maternity function, is the function which gives the probability that newborn females, which survive to age x, give birth between x and $x + dx$. It expresses the age-specific rate of reproduction (related to an age group) and is defined by*

$$m(x)dx\,. \tag{2.4}$$

In general, the fertility expresses the reproductive performance of an individual (or a group) in a given population.

Definition 2.6. *The net maternity function, denoted by $g(x)$ is the probability density that an individual both survives to age x and gives birth then.*

Therefore,

$$g(x) = l(x)m(x)\,. \tag{2.5}$$

2.1.2 Tracking Method For Estimation

There are several methods to estimate the fertility function $m(x)$ and the survivor function $l(x)$. One possibility is to track a cohort of individuals from birth until the last individual of the group died. We provide the following example to illustrate this method.
The data below was collected from a population of Kaibab squirrels [2].

Year of survey	1	2	3	4	5	6	7
Population Size	58	26	14	10	5	2	0

We set the survivor function, l_0, initially equal to unity .The population is observed at regular time intervals, so we set $t = 0, 1, 2, 3, 4, 5, 6$. Let $x : 0 \leq x \leq 6$, be the age.
From (2.3) we have the survival rate $\;_tP_x = \dfrac{N_{x+t}}{N_x}$.
The death rate is defined by

$$_tQ_x = 1 - \;_tP_x \,. \tag{2.6}$$

The life table 2.1.2 is assembled as follows.
At time $t = 0$, there are 58 Kaibab born (x=0); at time t=1, their number is 26 and their age x=1.
Then

$$_1P_0 = \frac{26}{58} = 0.45 \quad \text{and} \quad _1Q_0 = 1 - \;_1P_0 = 0.55. \tag{2.7}$$

Notice that the lifetime of each Kaibab is wholly independent of the rest of the population. Therefore, the survival rate at $t = 1$ is the conditional probability

$$l_1 = \;_1P_0 l_0 = \frac{26}{58} 1 = 0.45 \,.$$

At time $t = 2$, we have 14 kaibab. The survival rate at time t=2, given that they survived at t=1 is

$$l_2 = \;_2P_1 \, l_1 = \frac{14}{26}\frac{26}{58} = \frac{14}{58} = 0.24 \,,$$

where $_2P_1 = \dfrac{14}{26} = 0.54$ and $_2Q_1 = 1 - \;_2P_1 = 0.46$.
Here we have adapted (2.3) to the form

$$l_x = \;_xP_{x-1} \, l_{x-1} \,.$$

We obtain Table 2.1.2

Age	Population Size	$_tP_x$	$_tQ_x = 1 -_t P_x$	l_x
0	58	–	–	1
1	26	0.45	0.55	0.45
2	14	0.54	0.46	0.24
3	10	0.71	0.29	0.17
4	5	0.50	0.50	0.09
5	2	0.40	0.60	0.03
6	0	0	1	0

Table 2.1.2. Life table for Kaibab population

From the life table (2.1.2), the survivor function l_x for the Kaibab squirrel is shown in Figure 2.1. We clearly see that the survivor function is monotone decreasing. This is a *general feature* of all survival functions. For human populations there is a maximum age ω such that $l(\omega)$ equals 0. Currently the record for human longetivity is 122 years, set by Jeanne Calment from France.

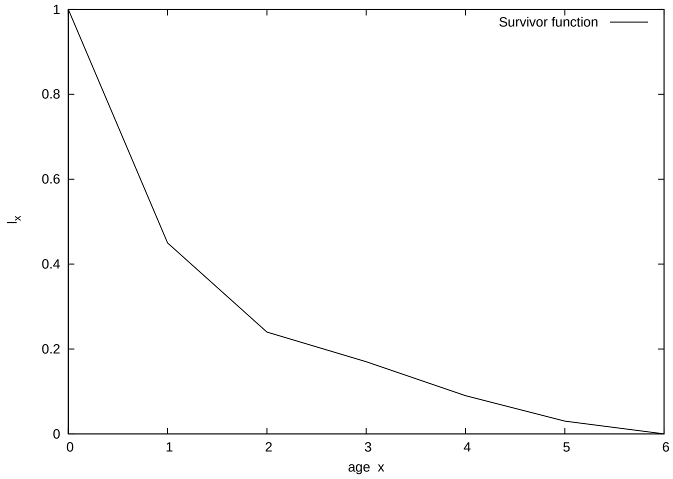


Figure 2.1: Life function l_x for the Kaibab squirrel

2.1.3 Estimation Of The Fertility Function

For the fertility function m_x is located between the some ages interval let $[\alpha, \beta]$, which represent the minimum age (menarche) and the maximum age (menopause) of reproduction. Let us now plot the fertility function using data from the life table below for the vole *Microtus agrestis* [9].

age x	1	2	3	4	5	6	7	8	9	10
m_x	0	0.6504	2.3939	2.9727	2.4662	1.7043	1.0815	0.6683	0.4286	0.3

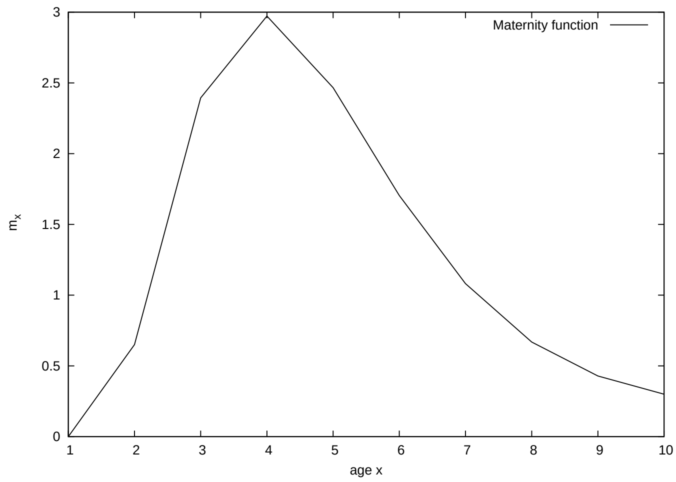


Figure 2.2: Maternity function m_x

As we might have expected, the graph shows that the maternity function varies over the interval and this can describe the behaviour of all fertility functions, even in the continuous case. The term fertility is used instead of birth rate when births are counted in relation to the number of women of reproductive age.

2.1.4 Sustainable And Stable Population

In the last 200 years the population of our planet has grown exponentially, at a rate of 1.9% per year. If it should continue at this rate, with the population doubling every 40 years, by 2600 we would all be standing literally shoulder to shoulder [12]. This concurs with Thomas Malthus' prediction in 1798 that populations are liable to grow to a point where their environment can not sustain them.

Definition 2.7. *A stable population is a population with an invariable age structure and a constant rate of growth.*

A stationary population with a zero growth rate is a special case of a stable population. The consequence of such a situation is that the absolute number of individuals of every representative age does not change over time.

Definition 2.8. *A sustainable population is one that is able to maintain a healthy number of individuals year after year.*

Any closed population without any migratory exchanges with the outside world, subjected to invariable fertility and mortality conditions over a long period, tends towards a stable condition with an invariable age structure and rate of growth.

The important concept of momentum for future population growth was introduced by Lotka to explain the problem of sustainability. In the case of the stable population model, the future growth of such a population is affected by the young age structure.

Population momentum is an effect which causes population growth. This phenomenon refers to the percentage of the population that are in their child-bearing years, who have not yet had children, and thus are scheduled to eventually have children, adding to the population through reproduction. For example, the higher the percentage of people aged 18 or less, the larger the population growth will be. This is due to the fact that there is such a large percentage of the population capable of having children, so the population will continue to grow. This is what is meant by population momentum. Here, the result of high fertility rate at some point occur when we have in a predominantly young population, which has yet to reach child-bearing age.

3. The Lotka Integral Equation

What happens if we start with, for example, a couple of parents and assume that the rate birth and death are constant? What can we say about the behaviour of that population for large t ? Does the size of this population depend on time or on the age structure? In his seminal paper [8], Euler gave some interesting answers to similar questions about populations. Upon its introduction, Lotka's model became a powerful tool to understand and analyse the dynamic processes of populations.

3.1 Derivation of the model

There are four different forms of Lotka's model [14]. In this chapter, we are going to give the derivation of the deterministic stable population model in continuous time, which takes the form of an integral equation. We will only include females in our model. First of all, we consider

$$B(t)\,dt,$$

as the differential number of female births during the small time interval $(t, t+dt)$. And we write also

$$F(x,t)\,dx,$$

as the differential number of females of ages between x and $x+dx$ at time t. We now use the age-specific survivorship and fertility in such populations as defined earlier in section 2 of the previous chapter.
We recall that $l(x)$ is the probability that an individual survives from ages 0 to x, with $m(x)\,dx$ representing the expected number of female offspring between the ages x and $x+dx$. Note that $l(x)$ and $m(x)$ are both assumed to be time independent.

Before continuing , we need to make a few assumptions. The functions $l(x)$ and $m(x)$ are considered to be continuous, piecewise smooth, and known. We define $F(x,0) = F_0$ to be the initial population density.

The number of female births $B(t)$, depends on the relation between the age, x, and the time, t. There are two cases:

Case 1: $x > t$
The females at initial time 0 have age $x-t$, since their age will be x after t years.Then some of these females will survive from age $x-t$ to x, with probability

$$\frac{l(x)}{l(x-t)}.$$

Case 2: $t > x$
The females who are born at time $t-x$, will survive to age x and give birth at that age. Thus,

some of these females will survive from age $t-x$ to x, with probability

$$B(x-t)\,l(x)\,.$$

To summarise,

$$F(x,t)=\begin{cases} B(x-t)\,l(x) & \text{for} \quad x<t, \\ F(x-t,0)\dfrac{l(x)}{l(x-t)} & \text{for} \quad x>t. \end{cases} \tag{3.1}$$

Multiplying the ultimate expressions by $m(x)$, the number of females born to females of any age can be calculated

$$B(t) = \int_0^\infty F(x,t)m(x)\,dx \tag{3.2}$$

$$= \int_0^t F(x,t)m(x)\,dx + \int_t^\infty F(x,t)m(x)\,dx \tag{3.3}$$

$$= \int_0^t B(t-x)l(x)m(x)\,dx + \int_t^\infty F(x-t,0)\frac{l(x)}{l(x-t)}m(x)dx\,. \tag{3.4}$$

For $x \in (t,\infty)$, we substitute $x-t$ by x, then

$$B(t) = \int_0^t B(t-x)l(x)m(x)\,dx + \int_0^\infty F(x,0)\frac{l(x+t)}{l(x)}m(x+t)dx\,. \tag{3.5}$$

Let

$$H(t) = \int_0^\infty F(x,0)\frac{l(x+t)}{l(x)}m(x+t)dx \tag{3.6}$$

and the net fertility function

$$g(x) = l(x)\,m(x)\,. \tag{3.7}$$

Then (3.5) becomes

$$B(t) = \int_0^t B(t-x)g(x)\,dx + H(t), \tag{3.8}$$

which is known as the basic *Lotka one-sex deterministic population model*.

3.2 Analytical Solution

3.2.1 The Lotka-Euler Characteristic Equation

We have demonstrated the derivation of the following integral equation

$$B(t) = \int_0^t B(t-x)g(x)dx + H(t), t \in [0,\infty)\ . \tag{3.9}$$

Notice that the unknown function $B(t)$ appears inside the integral, and the equation is clearly linear since the power of the function to be determined is one. It is important to point out that (3.9) is in the convolution form [13], and also that $g(x)$ and $H(t)$ are known. The existence proof of a solution for $B(t)$ can be found in Feller's paper [10].

We use (3.9) to determine the explicit form for $B(t)$, and also to answer the question about the behaviour of $B(t)$ for large t. If we assume that there is a restriction on the age of females (their age lie strictly between α and β) then $m(x) = 0$ unless $x \in [\alpha, \beta]$.
Furthermore, $H(t) = 0$ for $t \geq \beta$ since the additional number of female births due to all females already present at time $t = 0$ vanishes. We obtain the homogeneous equation

$$B(t) = \int_{\alpha}^{\beta} B(t-x)g(x)dx\,. \tag{3.10}$$

According to the linearity of the equation, we guess

$$B(t) = A\,e^{rt}\,. \tag{3.11}$$

We substitute (3.11) in (3.10), where A is an arbitrary constant that depends on the initial population, to obtain

$$A\,e^{rt} = \int_{\alpha}^{\beta} A\,e^{r(t-x)}g(x)dx\,.$$

Dividing both sides by $A\,e^{rt}$

$$\int_{\alpha}^{\beta} e^{-rx}\,g(x)dx = 1\,, \tag{3.12}$$

which is the *Euler-Lotka characteristic equation* for growth rate r .

Some numerical methods have been developed to find r. But in the general case where the integral (3.12) is over $[0, \infty)$, Caswell argued that all those numerical approaches are wrong [5], because r come from a continuous model. The numerical approaches are only convenient for the discrete Lotka model.

Theorem 3.1. *The Euler-Lotka equation has exactly one real solution $r = r_0$ (r_0 is called the Malthusian parameter).*

Proof. Let us consider the function,

$$\Phi(r) = \int_{\alpha}^{\beta} e^{-rx}\,g(x)dx = \int_{\alpha}^{\beta} e^{-rx}\,m(x)l(x)dx\,.$$

We notice that $\Phi(r) \to \infty$ as $r \to -\infty$, and $\Phi(r) \to 0$ as $r \to \infty$. Also $m(x)$, $l(x)$, $e^{-r\,x}$ are all simultaneously positive for $x \in (\alpha, \beta)$. Then, $\Phi^{'}(r) < 0$ and $\Phi^{''}(r) > 0$. Therefore, $\Phi(r)$ is a positive, continuous strictly decreasing, concave-up function of r, and it can cross the line $\Phi(r) = 1$ just once. □

The following theorem seen to be significant when we recall that $B(t)$ is a real number.

Theorem 3.2. *Any complex roots* $\{r_n\}$ *of the Euler-Lotka characteristic equation occur as complex conjugate pairs, and* $r_0 > \Re\{r_n\}$.

Proof. Consider now the complex roots, and we assume that $r_n = a + ib$ is one such root. Equation (3.12) becomes

$$\int_{\alpha}^{\beta} e^{[-(a+ib)x]} g(x)dx = 1\,.$$

By expansion of the left-hand side, and identification of the real and imaginary parts, we find that

$$\int_{\alpha}^{\beta} e^{-ax}\ \cos(bx) g(x)\, dx = 1\,, \tag{3.13}$$

$$\int_{\alpha}^{\beta} e^{-ax}\ \sin(bx) g(x) dx = 0\,. \tag{3.14}$$

Substitution of r_n by $\overline{r}_n$ in (3.12) leads to the same result. Then $\overline{r}_n$ is also a complex root of (3.12).
For some values of x in the range of integration of (3.12), we have

$$\cos(bx) < 1\,;$$

therefore,

$$\int_{\alpha}^{\beta} e^{-ax}\ \cos(bx) g(x)\, dx < \int_{\alpha}^{\beta} e^{-ax}\, g(x)\, dx\,.$$

Using (3.13) and the fact that r_0 satisfies (3.12), we compare the two results to finally confirm that $r_0 > \Re\{r_n\}$. □

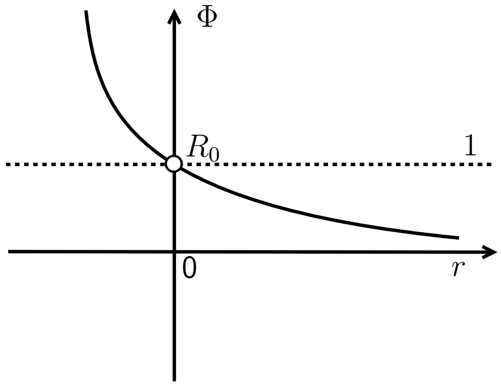
Using the result for the Theorem 3.1 and setting $r = 0$, we give the following important definition.

Definition 3.3. *The net reproductive rate is given by*

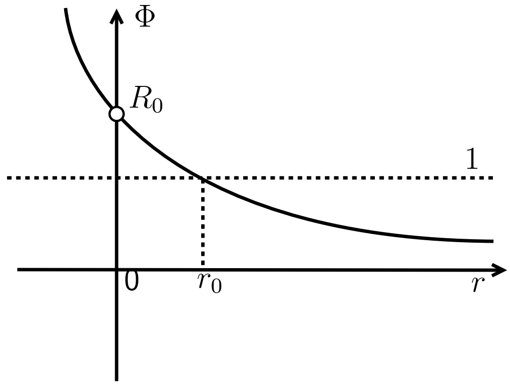
$$R_0 = \Phi(0) = \int_{\alpha}^{\beta} g(x) dx = \int_{\alpha}^{\beta} m(x)\, l(x) dx\,. \tag{3.15}$$

R_0 *gives the average number of daughters that will be born to a female now aged* 0 *during its entire lifetime, and is simply the product of the age-specific survivorship and fertility schedules, over all ages at which reproduction occurs.*

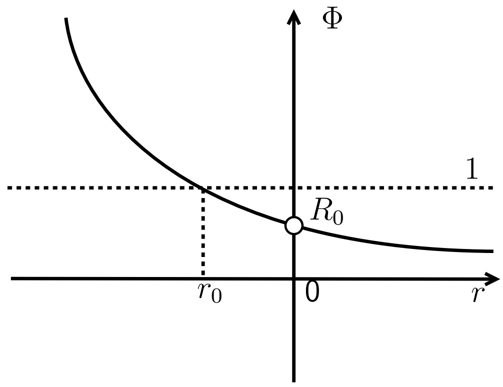
Computing the net reproductive rate R_0 is helpful when one wants to know if a population will grow or decay exponentially for different values of r. The illustration in Figure 3.1 leads us to make the following prediction. If $R_0 > 1$ (when $r_0 > 0$), then the population size increases; this is because each female produces more than one offspring during her lifetime. But if $R_0 = 1$ when $r_0 = 0$, the population size is constant, since a newborn female has to give birth to one female before dying. And if $R_0 < 1$ when $r_0 < 0$, the population size decreases.



(a) $R_0 = 1$ and $r_0 = 0$



(b) $R_0 > 1$ and $r_0 > 0$



(c) $R_0 < 1$ and $r_0 < 0$

Figure 3.1: Illustrations of the net reproductive R_0 and r_0.

3.2.2 Lotka's Solution

Note that (3.12) has infinitely many complex roots when the range of fertile age is finite [15]. To obtain the general form of the solution of (3.10), recall Theorem 3.1 and Theorem 3.2. Following Lotka, we consider only the case when all the roots of (3.12) are simple, the homogeneous linear integral (3.12) has a solution of the form

$$B(t) = A_0\, e^{r_0\, t} + \sum_{n=1}^{\infty} A_n\, e^{r_n\, t} \qquad \text{for} \quad t \geq \beta \quad \text{and} \quad r_n = a_n + i\, b_n\,, \tag{3.16}$$

where the first term is due to the Lotka real root, and the second term is arises from having complex roots.

Writing $e^{r_n\, t} = e^{a_n\, t}\,[\cos{(t\, b_n)} + i\, \sin{(t\, b_n)}]$ in (3.16), we understand that there is first an oscillation in the birth rate, but for large t, the behaviour of $B(t)$ is dominated by the real root r_0. In fact by assuming that the series $\sum_n \mid A_n \mid$ converge,

$$B(t) \;=\; A_0\, e^{r_0\, t} + \sum_{n=1}^{\infty} A_n\, e^{[(a_n + i\, b_n)\, t]} \tag{3.17}$$

$$B(t) \;=\; A_0\, e^{r_0\, t} \left[1 + \sum_{n=1}^{\infty} \frac{A_n}{A_0}\, e^{(a_n - r_0)\, t}\, e^{i\, b_n\, t}\right]. \tag{3.18}$$

But

$$|e^{(a_n - r_0\, t)} e^{i b_n t}| = e^{(a_n - r_0)\, t}$$

since have already proved, in Theorem 3.2, that $r_0 > a_n$ for all n,

$$e^{(a_n - r_0)\, t} \longrightarrow 0 \quad as \quad t \longrightarrow \infty\,.$$

Therefore,

$$B(t) \sim A_0\, e^{r_0\, t} \quad \text{for} \quad \text{large} \quad t. \tag{3.19}$$

3.2.3 The Stable Age Distribution

As we have seen in section 2.1.4, the notion of a stable age distribution becomes very important when we analyse the dynamics of a given population which involves a structured age population.

Definition 3.4. *The age distribution, also called the age composition, is the proportionate number of persons in successive age categories in a given population.*

Definition 3.5. *The stable age distribution is the age distribution which the population will reach if allowed to progress until there is no longer a change in the distribution.*

The existence of a stable age distribution was discovered by Euler [8]. Dealing with some questions about mortality and life expectancy, he showed an increasing birth rate is always geometric and does not depend on the initial conditions. Let us find the form of that distribution, and this will help demonstrate the very important point that Lotka is a stable population model. We start with the following observation. After the death of the initial group of females, the total number $F(x,t)\,dx$ of the population is made of the survivors of the $B(t-x)dx$ females born at time $t-x$. Then,

$$F(x,t)\,dx = B(t-x)\,l(x)\,dx\,, \text{and} \tag{3.20}$$

$$F(x,t) = B(t-x)\,l(x)\,. \tag{3.21}$$

Similarly if we denote by $N(t)$ the total number of population at time t, then

$$N(t) = \int_0^\infty B(t-u)\,l(u)\,du. \tag{3.22}$$

To determine the stable age distribution, we let $C(x,t)$ be the proportion of females in the age group $(x, x+dx)$ once the stable rate of growth has been reached. Therefore,

$$C(x,t) \equiv \frac{F(x,t)}{N(t)} = \frac{B(t-x)\,l(x)}{\int_0^\infty B(t-u)\,l(u)\,du} \tag{3.23}$$

$$\begin{aligned} C^*(x) &\equiv \lim_{t\to\infty} C(x,t) = \frac{A_0\,e^{r_0(t-x)}\,l(x)}{\int_0^\infty A_0\,e^{r_0(t-u)}\,l(u)\,du}, \\ &= \frac{A_0\,e^{r_0t}\,e^{-r_0x}\,l(x)}{A_0\,e^{r_0t}\int_0^\infty e^{r_0\,u}\,l(u)\,du} \end{aligned}$$

$$C^*(x) = \frac{e^{-r_0x}\,l(x)}{\int_0^\infty e^{-r_0u}\,l(u)\,du}. \tag{3.24}$$

This is asymptotically independent of time, which means that the population tends to a stable asymptotic age distribution (rigorous proof of the stability can be found in [21]). We know that $C^*(x)$ does not depend on t, and imposing $l(0)=1$ in (3.24) gives

$$C^*(0) = \frac{1}{\int_0^\infty e^{-r_0u}\,l(u)\,du}. \tag{3.25}$$

Then, asymptotically, the relation between the proportion of females of age x and newborns is

$$C^*(x) = C^*(0)\,e^{-r_0x}\,l(x). \tag{3.26}$$

The age structure of the population is clearly explained by (3.26). When $r_0 = 0$, we have a stationary population. But for $r_0 > 0$, the exponential function decreases, and then

$$C^*(x) < C^*(0)\,:$$

there is an excess of young females within the population. Otherwise, we are faced with an excess of old females.

Lotka [18] explained that the age distribution (3.26) is of the *fixed* form in the sense that, once established, it perpetuates itself. More than this, it is also *stable*, in the sense that if disturbed by a temporary change in the conditions of life (e.g. war, disease), it will spontaneously return upon restoration of normal conditions.

3.2.4 Solution Using Laplace Transform

In the previous section, we discussed the solution for $t \geq \beta$. We obtained some useful information about (3.9), but we didn't elaborate the method to find A_n, and we have yet to find a solution for $t < \beta$. We will use a Laplace transform to give the analytical form of the solution in the more general case. The most significant advantage of this method is that differentiation and integration become multiplication and division, respectively. This changes our integral equation to a polynomial equation, which is then much easier to solve.

Definition 3.6. *The Laplace transform $\mathcal{L}$ of a function $f(t)$, defined for all real numbers $t \geq 0$, is the function $\hat{f}(s)$, defined by:*

$$\mathcal{L}\left[f(t)\right](s) = \hat{f}(s) = \int_0^\infty e^{-st} f(t)dt, \quad s = a + ik \in \mathbb{C}. \tag{3.27}$$

For the range of convergence of (3.27) , $f(t)$ must satisfy the following two properties:

Property 3.7. *The function $f(t)$ is piecewise continuous on the interval $0 \leq t \leq T$ for any $T > 0$. This means that it has at most a finite number of discontinuities on any interval of finite length, and that both the left and the right limits exist at each point of discontinuity.*

Property 3.8. *The function $f(t)$ grows no faster than a simple exponential; that is, there exist two constants σ and M, depending on f, such that*

$$|f(t)| < M\,e^{\sigma t} \quad for \quad t \geq 0.$$

Then, the Laplace transform of $f(t)$ exists for $\Re\{s\} > \sigma$. In particular, if the smallest possible value for σ, σ_0, is taken, the condition $\Re\{s\} > \sigma_0$ defines the smallest possible range of convergence. Therefore for $a > \sigma_0$, $\lim_{t\to\infty} f(t)e^{-at} = 0$, but the same is not true for $a < \sigma_0$. The convergence area of the Laplace transform is shown below

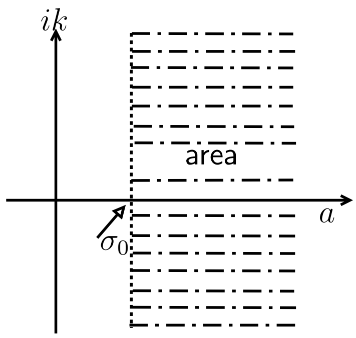


Figure 3.2: Convergence area for the Laplace Integral in the s-plane

Inverse Laplace Transform

The inverse Laplace transform that returns the original function is given by

$$f(t) = \frac{1}{2\pi i}\int_{k-i\infty}^{k+i\infty} e^{st}\hat{f}(s)ds, \quad t > 0, \tag{3.28}$$

where k is a real number so that the contour path of integration is in the region of convergence of $\hat{f}(s)$, which requires $k > \Re\{s_p\}$ for every singularity s_p of $\hat{f}(s)$.

Remark For the Lotka integral, $B(t-x)$ and $g(x)$ are in the special form. Thus

$$(B * g)(t) \equiv \int_0^t B(t-x)g(x)\,dx\,,$$

which is generally termed the Faltung (or convolution) of the two functions B and g. In fact the Laplace transform of a convolution (denoted by *) is the product of two Laplace transforms [13],

Hence

$$\mathcal{L}\left[B * g(t)\right](r) = \hat{B}(r)\hat{g}(r).$$

We are now ready to adapt the methods from [24] and [10] to give the analytical form of the Lotka model. By taking the Laplace transform of both sides in (3.9), we generate the algebraic equation,

$$\mathcal{L}B = \mathcal{L}g\mathcal{L}B + \mathcal{L}H, \tag{3.29}$$

$$\left[1 - \mathcal{L}g\right]\mathcal{L}B = \mathcal{L}H \tag{3.30}$$

$$\left[1 - \hat{g}(r)\right]\hat{B}(r) = \hat{H}(r) \tag{3.31}$$

Suppose that, in the right hand half of the complex plane, there is a straight line parallel to the imaginary axis on which $[1 - \mathcal{L}g]$ is non zero. If the equation of this line is $\Im\{r\} = k$, then

$$\hat{B}(r) = \frac{\hat{H}(r)}{[1 - \hat{g}(r)]}, \tag{3.32}$$

and the general analytical form of the solution is given by

$$B(t) = \frac{1}{2\pi i}\int_{k-i\infty}^{k+i\infty} \frac{\hat{H}(r)}{[1 - \hat{g}(r)]}e^{rt}dr. \tag{3.33}$$

This will yield the solution of (5.1). In fact, we can then also assume that $\dfrac{\hat{H}(r)}{[1 - \hat{g}(r)]}$ satisfies the conditions necessary to apply (3.28).

Now let us have a closer look at expression (3.32), in an attempt to find a simple expression of $B(t)$. We can write the denominator as

$$1 - \hat{g}(r) = 1 - \int_0^\infty e^{-rt}g(t)dt. \tag{3.34}$$

The roots of equation (3.34) satisfy

$$1-\int_0^\infty e^{-rt}g(t)dt=0\,. \tag{3.35}$$

Using the fact that birth appears in the interval $[\alpha,\beta]$ leads to

$$1-\int_0^\infty e^{-rt}g(t)dt=1-\int_\alpha^\beta e^{-rt}g(t)dt. \tag{3.36}$$

Therefore the roots of (3.35) coincide with those for the Euler-Lotka equation (3.12).

- Assume that all the roots of $\hat{B}(r)$ are simple.

The following theorem is required for a series expansion of $\hat{B}$.

Theorem 3.9. *In order for the solution $B(t)$ to be representable in form (3.16), where the series converges absolutely for $t\geq 0$ and the r_n denotes the roots of the characteristic equation (3.35), it is necessary and sufficient that the Laplace transform $\hat{B}(r)$ admit an expansion of the form*

$$\hat{B}(r)\equiv\frac{\hat{H}(r)}{1-\hat{g}(r)}=\frac{A_0}{r-r_0}+\sum_{n=1}^{\infty}\frac{A_n}{r-r_n}, \tag{3.37}$$

and that

$$\sum_n |A_n|$$

converges absolutely.

The coefficients A_n are determined by

$$A_n=-\frac{\hat{H}(r_n)}{\hat{g}'(r_n)}. \tag{3.38}$$

In particular, it is necessary that $\hat{B}(r)$ be a one-valued function.

The proof of Theorem 3.9 can be found in [10].

$$B(t)=A_0\,e^{r_0\,t}+\sum_{n=1}^{\infty}A_n\,e^{r_n\,t},\forall t\geq 0. \tag{3.39}$$

To now find the expression of A_n, we recall that

$$\mathcal{L}\left(e^{r_0t}\right)(r)=\frac{1}{r-r_0}, \tag{3.40}$$

therefore

$$A_0 = \lim_{r \to r_0} \left[\frac{(r - r_0)\,\mathcal{L}\,(H)}{1 - \mathcal{L}\,(g)} + (r - r_0) \sum_{n=1}^{\infty} A_n\, e^{r_n\, t} \right], \tag{3.41}$$

$$A_0 = \lim_{r \to r_0} \left[\frac{(r - r_0)\,\mathcal{L}\,(H)}{1 - \mathcal{L}\,(g)} \right]. \tag{3.42}$$

We use $\mathcal{L}\,(g)\,(r_0) = \hat{g}(r_0) = 1$, and

$$\lim_{r \to r_0} \frac{\mathcal{L}\,(g) - 1}{r - r_0} = \left[\frac{d\mathcal{L}\,(g)}{dr} \right]_{r=r_0}. \tag{3.43}$$

By (3.41)

$$A_0 = - \left[\frac{\mathcal{L}(H)}{\frac{d\mathcal{L}(g)}{dr}} \right]_{r=r_0}. \tag{3.44}$$

And since $g(t) = 0$ for $t < \alpha$, $H(t)$ and $g(t)$ vanish when $t > \beta$,

$$\mathcal{L}\,[g(t)]\,(r) = \int_0^{\infty} e^{-rt} g(t)dt \tag{3.45}$$

$$= \int_{\alpha}^{\beta} e^{-rt} g(t)dt. \tag{3.46}$$

Knowing that

$$\frac{d\mathcal{L}(g)}{dr} = - \int_{\alpha}^{\beta} t e^{-rt} g(t)dt, \tag{3.47}$$

and

$$\mathcal{L}\,[H(t)]\,(r) = \int_0^{\infty} e^{-rt} H(t)dt \tag{3.48}$$

$$= \int_0^{\beta} e^{-rt} H(t)dt, \tag{3.49}$$

hence,

$$A_0 = \frac{\int_0^{\beta} e^{-r_0 t} H(t)dt}{\int_{\alpha}^{\beta} x e^{-r_0 x} g(x)dx}. \tag{3.50}$$

In the general form, we have

$$A_n = - \left[\frac{\mathcal{L}(H)}{\frac{d\mathcal{L}(g)}{dr}} \right]_{r=r_n}; \tag{3.51}$$

therefore

$$A_n = \frac{\int_0^{\beta} e^{-r_n t} H(t)dt}{\int_{\alpha}^{\beta} x e^{-r_n x} g(x)dx}, \text{ for all } n. \tag{3.52}$$

- Secondly some of the complex roots of (3.35) can have a multiplicity greater than one.

We use a partial fraction expansion each time $\hat{B}$ is meromorphic (holomorphic except at an isolated set of poles). Then (3.37) has the following partial fraction decomposition

$$\hat{B}(r) = \sum_{n=0}^{\infty}\left\{\frac{A_n^{(1)}}{r-r_n} + \frac{A_n^{(2)}}{(r-r_n)^2} + ... + \frac{A_n^{(\gamma(n))}}{(r-r_n)^{\gamma(n)}}\right\}, \tag{3.53}$$

$$\hat{B}(r) = \sum_{n=0}^{\infty}\sum_{k=1}^{\gamma(n)}\frac{A_n^{(k)}}{(r-r_n)^k}, \tag{3.54}$$

where an $\gamma(n)$ is the multiplicity of the n-th complex root. Finally the general form of the solution using inverse Laplace transform [6] is

$$B(t) = \sum_{n=0}^{\infty} e^{r_n t}\left\{A_n^{(1)} + A_n^{(2)}\frac{t}{1!} + ... + A_n^{(\gamma(n))}\frac{t^{\gamma(n)-1}}{(\gamma(n)-1)!}\right\}, \tag{3.55}$$

$$B(t) = \sum_{n=0}^{\infty} e^{r_n t}\sum_{k=0}^{\gamma(n)}\frac{A_n^{(k)}t^{k-1}}{(k-1)!}. \tag{3.56}$$

By the residue theorem, the coefficients $A_n^{(k)}$ are determined by

$$A_n^{(k)} = \frac{1}{(\gamma(n)-k)!}\left\{\frac{d^{(\gamma(n)-k)}}{dr^{(\gamma(n)-k)!}}\left[\hat{B}(r)(r-r_n)^{\gamma(n)}\right]\right\}_{r=r_n} \tag{3.57}$$

4. Numerical Solution

In this section, we generate a method to approximate the solution of the linear Lotka integral equations by using the extended trapezoidal rule.

4.1 Extended Trapezoidal Rule

Proposition 4.1. *The* extended trapezoidal rule *is a method for approximating a definite integral by evaluating the integrand at n points. Let $[a, b]$ be the interval of integration with a partition $a = x_0 < x_1 < \ldots < x_n = b$. The formal rule is then given by*

$$\int_a^b f(x)\,dx \;\approx\; \frac{1}{2}\sum_{i=1}^{n}(x_i - x_{i-1})\left[f(x_{i-1}) + f(x_i)\right].$$

Remark The *composite trapezoidal rule* can also be applied to a partition which is uniformly spaced (i.e. $x_i - x_{i-1} = h$ for all $i \in \{1, \ldots, n\}$). In this case the formal rule is given by

$$\int_a^b f(x)\,dx \;\approx\; \frac{h}{2}\left[f(a) + 2\sum_{i=1}^{n-1} f(a + ih) + f(b)\right] \tag{4.1}$$

Proof The composite trapezoidal rule uses the ordinary trapezoidal rule on each subinterval

$$\begin{aligned}\int_a^b f(x)\,dx &= \sum_{i=1}^{n}\int_{x_{i-1}}^{x_i} f(x)\,dx \\ &\approx \frac{1}{2}\sum_{i=1}^{n}(x_i - x_{i-1})\left[f(x_{i-1}) + f(x_i)\right].\end{aligned}$$

4.2 Convergence

In order to verify that the method we use is convergent, the fundamental theorem of numerical analysis must be satisfied. This explains the choice of the trapezoidal method to discretize the Lotka model.

Theorem 4.2 (Dahliquist Equivalent Theorem [22])**.** *A numerical method is convergent if and only if it is consistent and stable.*

For a numerical method to be considered consistent means that its order is greater than one. Stability is satisfied when the errors introduced at any particular time step cannot grow unboundedly over time. To verify those properties, we start by finding the order of the error.

Let $I = \int_a^b f(x)\,dx$ and $\tilde{I} = \dfrac{h}{2}\left[f(a) + f(b)\right]$.

In the algorithm, the user defines a tolerance ε such that $C = |I - \tilde{I}| < \varepsilon$. If this condition is satisfied, then the estimation is exact; otherwise, we reduce the step.

To find the local error of the trapezoidal method, we expand $f(x)$ by using a Taylor expansion around a.

$$f(x) = f(a) + f^{'}(a)(x-a) + \frac{f^{''}(a)}{2}(x-a)^2 + \frac{f^{'''}(a)}{3!}(x-a)^3 + ... \quad (4.2)$$

$$= f(a) + f^{'}(a)(x-a) + \frac{f^{''}(\theta)}{2}(x-a)^2 \quad (4.3)$$

where $\theta,\ x \in [a,b]$.

By integrating (4.3) over $[a,b]$, we obtain

$$I = \int_a^b f(x)\,dx = hf(a) + \frac{h^2}{2}f^{'}(a) + \frac{h^3}{12}f^{''}(\theta). \quad (4.4)$$

For $x = b$ in (4.2),

$$f(b) = hf(a) + \frac{h^2}{2}f^{'}(a) + \frac{h^3}{12}f^{''}(\theta). \quad (4.5)$$

Thus

$$I - \tilde{I} = (\frac{h^3}{12} - \frac{h^3}{4})f^{''}(\theta) = \frac{h^3}{12}f^{''}(\theta). \quad (4.6)$$

Local error is of third order, which guarantees the convergence of our method, by Theorem 4.2.

The global error of (4.2) is approximately

$$\frac{h_N^3}{12}f^{''}(\theta)N = (b-a)\frac{h_N^2}{12}f^{''}(\theta)$$

with $\theta \in [a,b]$. We conclude that the extended trapezoidal method is globally of second order in h_N. Increasing the number of subintervals by two corresponds to an improvement in the accuracy of our result by four.

4.3 Discrete Form Of Lotka Model

Let us now apply the method we described above to the Lotka integral equation.

$$B(t) = \int_0^t B(t-x)g(x)dx + H(t), \quad (4.7)$$

$$= \int_0^t B(x)g(t-x)dx + H(t). \quad (4.8)$$

We also set

$$K(t,x) = B(x)g(t,x), \tag{4.9}$$

where $g(t,x) = g(t-x)$, $t \in [0,T]$ and $x \in [0,t]$.

Consider t_i as a partition for the time interval $[0,T]$, $i = 0,...,N$ and x_j as a partition for the age interval $[0,t]$, $j = 0,1,...,i-1$.

The step $h = x_j - x_{j-1}$, then $x_j = x_0 + jh$.

$$\begin{aligned} B(t_0) &= \int_0^{t_0} K(t_0,x)dx + H(t_0), & (4.10)\\ B(t_0) &= H(t_0). & (4.11)\end{aligned}$$

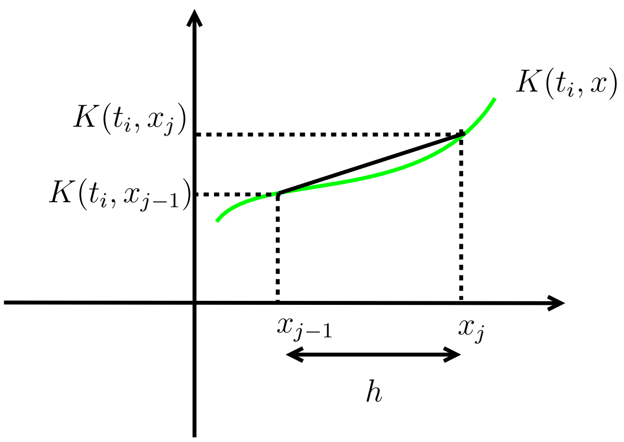


Figure 4.1: Trapezoid method

We can approximate,

$$\begin{aligned} B(t_i) &= \int_{t_0=0}^{t_i} K(t_i,x)dx + H(t_i) & (4.12)\\ &\simeq \frac{h}{2}\left[K(t_i,t_0) + 2\sum_{j=1}^{i-1} K(t_i,x_j) + K(t_i,t_i)\right] + H(t_i) & (4.13)\\ B(t_i) &\simeq \frac{h}{2}\left[B(t_0)g(t_i,t_0) + 2\sum_{j=1}^{i-1} B(x_j)g(t_i,x_j) + B(t_i)g(t_i,t_i)\right] + H(t_i). & (4.14)\end{aligned}$$

We make the following approximations: $B(t_i) \simeq B_i$, $B(x_j) \simeq B_j$ and $g(t_i, x_j) \simeq g_{ij}$.

Now we can rewrite (4.2) in the form

$$(1 - \frac{h}{2} g_{ii}) B_i = \frac{h}{2} B_0 g_{i0} + h \sum_{j=1}^{i-1} B_j g_{ij} + H_i. \tag{4.15}$$

4.4 Algorithm to Compute Lotka Integral

User supplied by two external functions:

$g(t, x) = g(t - x)$: net maternity function of females class age x at time t.

$H(t)$: contribution of birth due to female already present at time t.

$B_i =$ numerical solution at t_i

$N =$ number of points

$T =$ period

$h = \dfrac{T}{N} =$ step

$x_0 = 0 \quad =$ Lower boundary of age

$t_0 = 0 \quad =$ Initialise time

Initial condition $B_0 = H_{t_0}$

For $i = 1$ to N

$t_i = t_0 + ih$

Compute the $\sum_{j=1}^{i-1} B_j g_{ij}$

$sum = 0$

for $j = 1$ to $i - 1$

$x_j = x_0 + jh$

$sum = sum + B_j * g(t_i, x_j)$

Compute the numerical function

$$B_i = \left[\frac{h}{2} B_0 * g(t_i, x_0) + h * sum + H(t_i\right] * \left[1 - \frac{h}{2} g(t_i, x_i)\right]^{-1}. \tag{4.16}$$

Python code to compute the Lotka Integral equation model of a stable population, can be found in [20].

4.4.1 Accuracy Of The Code Programme

We use the following integral equation from [23] to test the accuracy of our numerical methods.

$$B(t) = \int_0^t (x-t)B(x)dx + e^t. \tag{4.17}$$

Solving analytically yields to

$$B(t) = \frac{1}{2}\left(e^x + \cos(t) + \sin(t)\right). \tag{4.18}$$

We have the following plot:

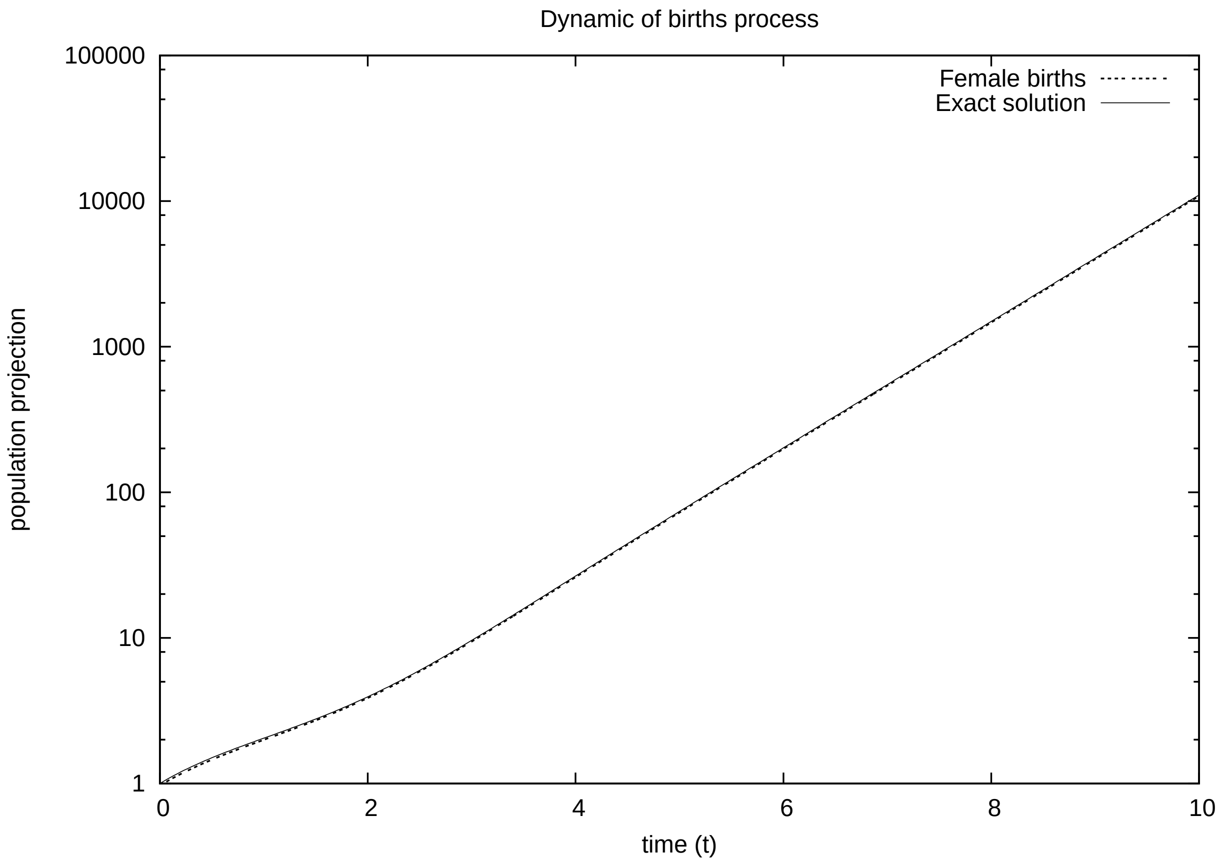


Figure 4.2: Plot of the numerical and the exact solutions

We have also plotted the relative error which is less than 5%.

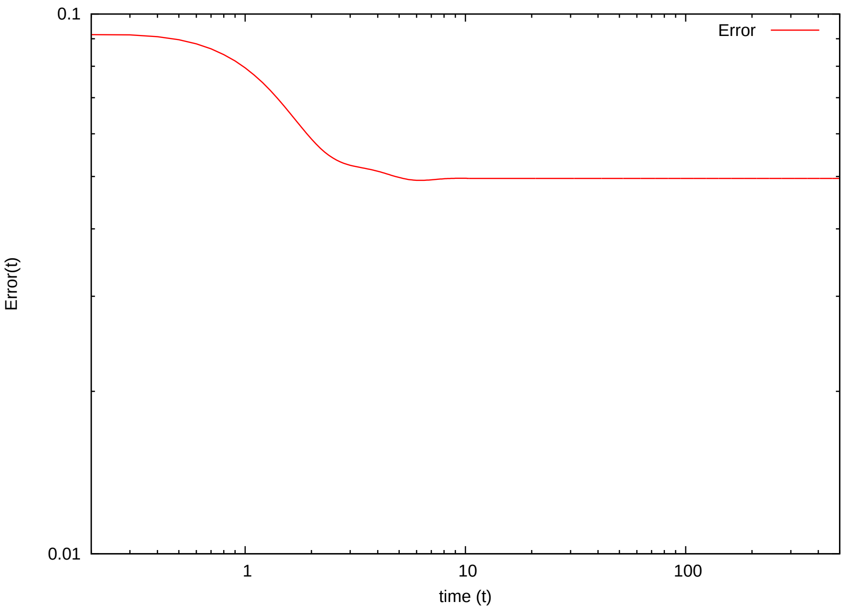


Figure 4.3: Plot of the Relative Error using logscale

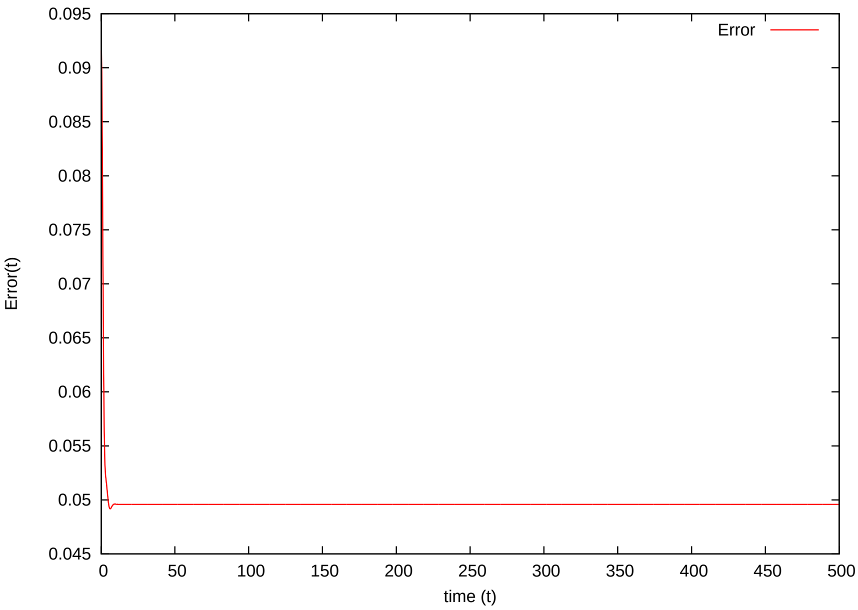


Figure 4.4: Plot of the Relative Error

5. Application

Stable population theory is an indirect method of demographic estimation, which makes use of partial information and reasonable assumptions. A typical example of the use of this method is to deduce mortality in populations where births and deaths are not well-recorded. To do an indirect computation and analysis in the case that direct data are lacking, one can model the data using the appropriate Pearson distribution curve. The formulation of these curves was pioneered by Karl Pearson in 1893. Let us consider one of these curve in the case of the birth process, in the particular form chosen by Lotka [10].

5.1 PEARSON Type II–curve

$$B(t) \;=\; \int_0^t B(t-x)g(x)\,dx + H(t). \tag{5.1}$$

We consider (5.1) for the case

$$g(t) = H(t) = P_{II}(t) = \frac{1}{2}t^2e^{-t}, \text{and} \tag{5.2}$$

$$\mathcal{L}\left[P_{II}(t)\right](r) \;=\; \int_0^\infty \frac{1}{2}t^2e^{-t}e^{-tr}dt, \tag{5.3}$$

$$= \frac{1}{2}\int_0^\infty t^2e^{-(1+r)t}dt. \tag{5.4}$$

To guarantee convergence, we need $\Re\{1+r\} = \Re\{1+a+ib\} = 1+a > 0$.

Then, $|t^2e^{-(1+a)t}| \to 0$ when $t \to \infty$. Using integration by part twice we obtain

$$\mathcal{L}\left[P_{II}(t)\right](r) = \hat{P}_{II}(r) = \frac{1}{(r+1)^3}. \tag{5.5}$$

By simple calculus, the roots of the characteristic equation,

$$\hat{P}_{II}(r) = 1, \tag{5.6}$$

are $r_0 = 0$, $r_1 = \frac{-3}{2} + \frac{i\sqrt{3}}{2}$, $r_2 = \frac{-3}{2} - \frac{i\sqrt{3}}{2}$.

We notice that $r_0 > \Re\{r_n\}$, and that r_1 , r_2 are complex conjugates.

$$\hat{B}(r) = \frac{A_0}{r-r_0} + \frac{A_1}{r-r_1} + \frac{A_2}{r-r_2}, \tag{5.7}$$

According to equation (3.51),

$$A_n = \left[\frac{1}{3}(r+1)\right]_{r=r_n}, \text{ for } \quad n = 0,1,2. \tag{5.8}$$

We have

$$\hat{B}(r) = \frac{1}{3r} - \frac{\frac{1}{6} - \frac{i}{2\sqrt{3}}}{s + \frac{3}{2} - \frac{i\sqrt{3}}{2}} - \frac{\frac{1}{6} + \frac{i}{2\sqrt{3}}}{s + \frac{3}{2} + \frac{i\sqrt{3}}{2}}; \tag{5.9}$$

Recall that

$$\mathcal{L}\left[e^{-\zeta t}\right](r) = \frac{1}{(r+\zeta)}. \tag{5.10}$$

The solution is

$$B(t) = \frac{1}{3}e^{r_0 t} - \frac{1}{6}e^{r_1 t} + \frac{i}{2\sqrt{3}}e^{r_1 t} - \frac{1}{6}e^{r_2 t} - \frac{i}{2\sqrt{3}}e^{r_2 t} \tag{5.11}$$

$$= \frac{1}{3} + \frac{1}{2}e^{-\frac{3}{2}t}\left[-\frac{1}{3}\left(e^{i\frac{\sqrt{3}}{2}t} + e^{-i\frac{\sqrt{3}}{2}t}\right) + \frac{i}{\sqrt{3}}\left(e^{i\frac{\sqrt{3}}{2}t} - e^{-i\frac{\sqrt{3}}{2}t}\right)\right] \tag{5.12}$$

$$B(t) = \frac{1}{3} - e^{-\frac{3}{2}t}\left[\frac{1}{3}\cos\left(\frac{\sqrt{3}}{2}t\right) + \frac{1}{\sqrt{3}}\sin\left(\frac{\sqrt{3}}{2}t\right)\right] \tag{5.13}$$

5.1.1 Expected Number of Birth per female each month

time t	Expected birth $B(t)$
0	0
0.0833333333333	0.00319462947406
–	–
0.333333333333	0.0398318701449
0.416666666667	0.0572947572395
–	–
9.75	0.333333202287
9.83333333333	0.333333234927
9.91666666667	0.333333262157
10.0	0.333333284674

At the beginning we observed that the expected birth $B(t)$ fluctuate, but it start to converge at time $t = 10$.
From the table, of births for each age class consider population over a period of one month, $1/12$ of a year. The following plot is obtained.

Analysis of the Model
As we predicted, after a number of time intervals the proportion of individuals reaches an equilibrium: a stable population model. And for large t, we have

$$B(t) \simeq \frac{1}{3}e^{r_0 t} = \frac{1}{3} \simeq 0.333333333,$$

The birth process depends on the real root $r_0 = 0$, and this correspondingly true for a stationary population.

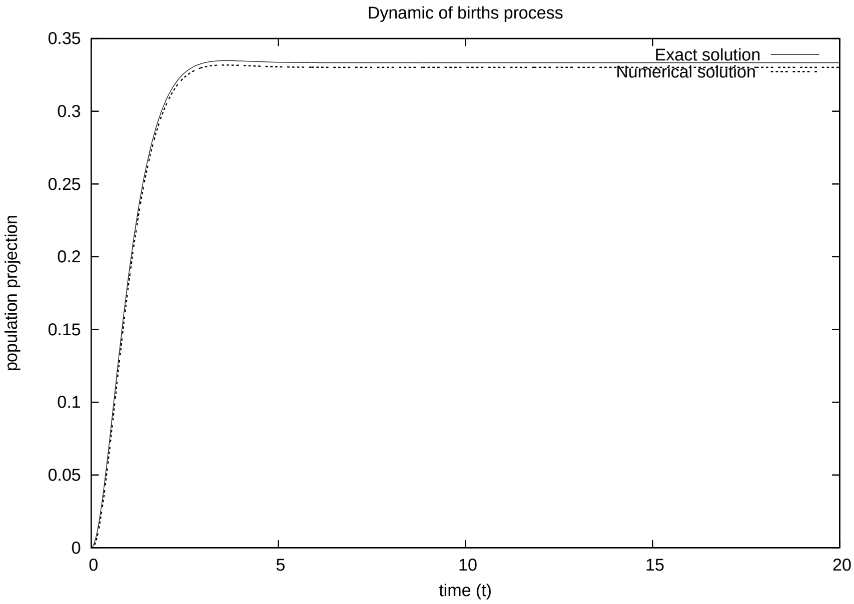


Figure 5.1: Plot of $B(t)$ and B_t

Figure 5.1 shows the relative error,

$$\frac{|B(t) - B(t_i)|}{|B(t)|}$$

as a function of the required value t. The relative error is 1%, this explain the accuracy of the method we use.

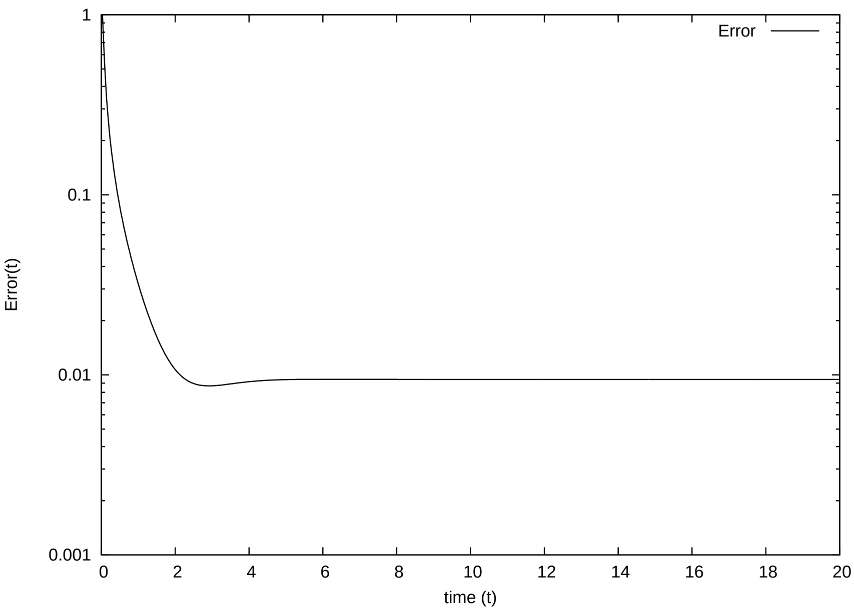


Figure 5.2: Plot of the error

6. Conclusion

In this essay, we derived the Lotka Integral equation in the linear case as a continuous time model, under the assumption that the age structure and the fertility rate are both constant. We started by looking at Lotka's solution, which considers all the roots of the Euler characteristic equation to be simple. Though building Lotka's solution helps to understand Lotka Integral equation, it assumed that the reproduction was restricted to a population member aged under a given boundary. This restriction represents a limitation of the model which we bypass in our treatment in this essay. We in fact extend the solution to account for all possible ages or times, rendering it more general. We then build complete analytical and numerical solutions using, respectively, Laplace Transform and the extended trapezoidal rules. The study of the numerical solution error with respect to the analytical solution shows that both solutions coincide.

In fact, the dynamics of populations can not be completely described by the stable population model as a Lotka Integral Equation, because in real situations, there are changes in the fertility rate and age structure over time. Therefore, the model is best suited for analysing the dynamics of a closed population. Complex phenomena can be simulated through this model by using the appropriate hypotheses. In industrial process control, for example, the renewal equation is obtained by replacing the fertility and mortality, respectively, by the flux in and the flux out.

Further research may be undertaken in order to understand an unstable population model which is more realistic. One could, for example, derive a nonlinear stochastic model which completely captures the random behaviour of such a population. For the purposes of this essay, however, and within its short timeframe we have dealt with an idealised population. Nevertheless, we hope we have managed to give the reader some useful insight into, and sparked their interest in, this fascinating area.

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