CHAPTER 1

Population Dynamics

A female may survive to reproductive age, be fertilized, survive to deliver viable offspring, and then survive into the future. While the probabilities of these events are estimated by observations of populations and are not directly applicable to an individual member of a population, they do provide reliable information for a population in aggregate, which is consistent (in some probabilistic sense) with the Law of Large Numbers. How a population renews itself and thrives or declines is the subject of *renewal theory*. More generally, renewal theory describes dynamics of systems, such as populations or bank accounts, that have a feedback mechanism for propagating themselves into the future.

Although probabilities do not apply to an individual's path in a population, they have great influence on an individual's life. For most species, the relation between population size and its environment governs the quality (and viability) of life. On the other hand, humans have devised ingenious ways to increase the carrying capacity of earth, but even then these probabilities play direct roles in an individual's quality of life through formulation of public policy, life (insurance) tables, market analysis, etc., that are based on renewal theory.

The work in this chapter is devoted to modeling, by which is meant formulating a mathematical description of a system and then exploring it with mathematical analysis, computer simulations, and visualizations. In this chapter, we consider models of particular population phenomena in both nonrandom and random environments. Probability theory shows how to define randomness in ways that are reasonably faithful to observations, and yet can be analyzed using mathematical methods. The work of statistics is to interface the results of such models to data in specific applications. While some aspects of statistics are mentioned here, we focus on probabilistic aspects of models. Two approaches are taken here to modeling systems with noisy components: First, a nonrandom model is derived, and then we study the system when parameters are replaced by random processes. The second approach taken here involves modeling a phenomenon in probabilistic terms from the start, and in some cases deriving a nonrandom model from that using the Law of Large Numbers and the Central Limit Theorem. Both approaches are used in this book. It is worth noting now that chaotic dynamics are generated in many nonrandom models, and while chaotic solutions may appear to be random, they are distinct from random processes and are studied using other methods.

Another important aspect of modeling populations is the appearance of time delays; for example, the delay between the time of first infection of a human with parasites and the time that new parasites are produced by the human. Work in

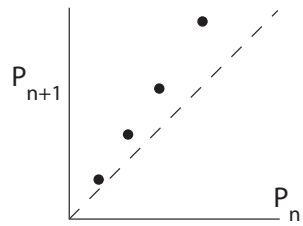

FIGURE 1.1. Reproduction data: From left the pairs (P_1, P_2), $(P_2, P_3), \ldots$ are plotted. The dashed line is a one-to-one line drawn for reference.

this chapter shows how time delays may be dealt with using renewal theory and population wave equations. These ideas are used throughout the book.

EXAMPLE ("Simple" Reproduction Theory). There is a simple graphical heuristic for describing renewal dynamics: It begins with the population's *renewal function*. Consider a population that is measured at regular sampling times, perhaps in synchrony with a reproductive cycle. Let the observed numbers be denoted by $P_1, P_2, \ldots$. We hypothesize that the number in the next generation is directly related to the number in the present generation, which we write as a mathematical relation

$$P_{n+1} = f(P_n), \tag{1.1}$$

where the renewal function f may not be known. To determine f from observations, we might try to describe its graph by plotting the observed samples $(P_1, P_2), (P_2, P_3), \ldots$. The result might look like that shown in Figure 1.1. To determine the reproduction function from these data, we would try to fit a curve to the observed points and use that curve to estimate f. In this case, a straight-line fit is the obvious first choice, and it can be found by using the least squares method. The result would be written as

$$P_{n+1} = rP_n \tag{1.2}$$

where the slope r, called the *renewal rate*, is estimated from the data. In this case, r appears to be approximately $r \approx 1.3$.

There are a number of difficulties with this approach that limit its usefulness. For example, the population size in the next generation might depend on more than the present population because several generations might contribute to reproduction. We study this and similar problems in this chapter.

Still, this simple heuristic gives insight to population behavior, and population theorists have speculated what various shapes of renewal functions are possible and what they might imply for a population's dynamics. Malthus (1798) proposed that a human reproduction function is linear as in Figure 1.1, where

$$f(P) = rP. \tag{1.3}$$

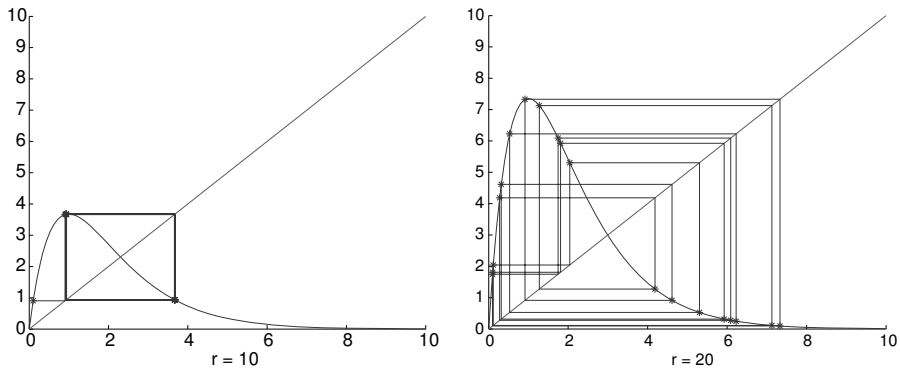

FIGURE 1.2. Ricker's model $P \to r\exp(-P)P$ cobwebbed. Left: $r = 10$. Right: $r = 20$. Shown also is the one-to-one reference line. In the top panel, the population approaches a stable oscillation where high and low population sizes are observed in alternate generations. In the bottom panel the population appears not to repeat itself, often coming near extinction and sometimes hitting near its peak reproduction value. These plots suggest that the model can exhibit dynamics that appears to be random.

Others, such as Verhulst (1849) (and later Beverton and Holt [**18, 21**]) speculated that the growth rate (r) gets smaller as population size increases, for example,

$$f(P) = \frac{r}{a+P}\,P. \tag{1.4}$$

Note that in this case the function $1/f(P)$ is a linear function of $1/P$, so this iteration is similar to Malthus's except it is for the reciprocals of population size. Later, Ricker (1957) speculated that reproduction of fish populations eventually tends to zero as the population increases, perhaps through cannibalism; for example,

$$f(P) = rPe^{-P/K}, \tag{1.5}$$

which peaks when $P = K$.

EXAMPLE (Cobwebbing Reproduction Curves). A useful method to determine the fate of the population for a known reproduction curve is called the *method of cobwebbing*. In this, the process begins with an initial population size P_1, and then the sequence $P_2 = f(P_1), P_3 = f(P_2) = f(f(P_1)), \ldots$ is determined graphically as shown in Figure 1.2. These plots are generated by the MATLAB®[1] program in Section 7.1.1.

EXAMPLE (Fibonacci's Model). A population's age structure may be taken into account directly by including reproduction information from previous generations. The simplest example that includes past generations in reproduction is *Fibonacci's model* (1202), where the number in each generation is related to the

[1]MATLAB® is a registered trademark of the MathWorks Inc.

numbers in the preceding two generations:

$$x_n = x_{n-1} + x_{n-2} \quad \text{for } n = 2, 3, \ldots. \tag{1.6}$$

If $x_0 = 1$ and $x_1 = 1$ are known, then $x_2 = 2, x_3 = 3, x_4 = 5, x_5 = 8, \ldots$. Fibonacci's model is sometimes referred to in the context of population growth where x_n denotes the births in the nth generation, which depends on the numbers of births in the previous two generations, each new birth exactly reproducing itself in the next and the one after that. The resulting births form the *Fibonacci sequence*, which is an integer analogue of geometric growth. We will analyze this simple model from various points of view in this chapter. This model also appears in studies of economics.[2]

These two examples are classified as being *discrete-event* models. They are examples of linear (Malthus (1.2) and Fibonacci (1.6)) models and nonlinear (Verhulst (1.4) and Ricker (1.5)) models for discrete-event renewal processes. Such models have been used in demographics, ecology, and economics to investigate a variety of dynamical processes, which we will study in detail in this chapter.

1.1. Population Renewal

Discrete-event models are easy to formulate but are usually difficult to study, partly because calculus is not available for them. As a result, many population models are cast in terms of continuous-time differential or integral equations, sometimes referred to as being models for *overlapping generations*, and calculus is used to study them. We first study an important class of continuous-time linear models.

1.1.1. The Renewal Equation. Let $B(t)$ denote the birth rate in a population at time t. This can be related to earlier birth rates in the following way: A portion of the births at time $t - a$ will survive to age a and produce offspring. Let $\lambda(a)$ denote the probability of survival to age a, and let $f(a)$ denote the fertility of those of age a. Then the *maternity function* $m(a)$ is the probability of survival multiplied by the expected number of births to those of age a: $m(a) = \lambda(a) f(a)$. Since B is a birth rate (i.e., dimensions births/time), the number of newborns in a cohort $(a, a + da)$ will be $B(a)da$. Adding the contributions from all births up to the present time t gives an integral equation that describes renewal of a population's birth rate:

$$B(t) = B_0(t) + \int_0^t m(a)B(t-a)da \equiv B_0(t) + \int_0^t m(t-t')B(t')dt' \tag{1.7}$$

where $B_0(t)$ is the birth rate at time t due to survivors from the initial time of the process, at $t = 0$.[3] In ordinary language, the number born a units ago is $B(t-a)da$, the proportion of them who survive to age a is $\lambda(a)$, and each of these survivors produces $f(a)$ offspring. The equation results when we add up all contributions to births at time t due to those who survived from earlier times. Note that the integral may be written in two different but equivalent ways. The second is derived from

[2] `http://www.branta.connectfree.co.uk/fibonacci.htm`

[3] A formula for $B_0(t)$ is derived in (1.19)

the first by the change of variables $a = t - t'$, so $da = -dt'$. This form of integral is referred to as being a *convolution integral*, and it defines a *linear time-invariant* (LTI) operation.[4]

If one would simulate the renewal equation on a computer, he would be faced with implementing a quadrature formula for evaluating the integral at each time step of the solution process. This is reasonably straightforward.

On the other hand, the renewal equation may be formulated directly as a discrete-event model, and in this way integrals are replaced by matrix multiplications. A discrete-event formulation of the renewal equation is described in Section 1.3.2.1. There is an interesting numerical analysis question about the relation between these two renewal models: The continuous-time model enables one to perform mathematical analysis, but simulating it requires a significant amount of numerical analysis, involving concepts about the relative and absolute errors, accuracy, and stability of computer algorithms. These issues pertain to the numerical solution of the continuous-time model, and not of the phenomenon being modeled. A major advantage of the continuous-time model is that through the use of calculus one can reveal how changing parameters in the model, such as λ, f, and B_0, will influence dynamics of the solution.

Discrete-event simulations describe a birth rate trajectory for a single choice of parameters, and further analysis is usually not possible. But the simulation may be repeated many times for various values of the parameters, and the resulting data set of solutions can be studied further. A discrete-event process can be "solved" on a computer by straightforward iteration without concern about numerical errors, other than small roundoff errors.[5] It is interesting that discrete-event models emerged well before calculus was invented, and they were replaced by continuous-time models to facilitate analysis of them. But now with developments in high-capacity computers, discrete-event models are returning; they can now be simulated and studied as desktop exercises. Moreover, by doing multiple simulations of a discrete-event model in which parameters are replaced by "random" elements, one obtains a huge database of outcomes that can be analyzed using data mining methodologies. Still, analysis of the continuous-time model may reveal how solutions depend on parameters, while the discrete-time model leaves only a mass of data to be digested by some means or another.

1.1.2. Transform Analysis of the Renewal Equation (LTI). The renewal equation (1.7) can be solved using a Laplace transform. The *Laplace transform*

$$\mathcal{L}(f)(s) \equiv \int_0^\infty e^{-st} f(t)dt,$$

[4]See `http://en.wikipedia.org/wiki/LTI_system_theory`. Note that mathematics majors often are not exposed to integral equations of this form. However, engineering students deal with them regularly, so the material is not beyond students at the undergraduate level.

[5]Of course if the size of the system is large, there arise other problems.

when this integral exists. This converts the problem from being in the time domain t to one in the frequency domain s.[6]

The Laplace transform is a fundamental tool in solving and analyzing mathematical models in science and engineering. For example, the renewal equation involves a convolution integral of the form

$$(f * g)(t) = \int_{-\infty}^{\infty} f(t-a)g(a)da,$$

where f and g are some integrable functions. (In the case of the renewal equation, $g(a) \equiv 0$ for $a < 0$.) A short computation from integral calculus shows that $\mathcal{L}(f * g)(s) = \mathcal{L}(f)(s) \times \mathcal{L}(g)(s)$.

Since the renewal equation is a convolution equation,

$$B(t) = B_0(t) + (M * B)(t)$$

where

$$M(a) = 0 \quad \text{for } a \leq 0$$

and $M(a) = m(a)$ for $a > 0$, it is amenable to the Laplace transform.

Applying the Laplace transform to the renewal equation gives

$$\mathcal{L}(B)(s) = \mathcal{L}(B_0)(s) + \mathcal{L}(M)(s)\mathcal{L}(B)(s).$$

Solving for the transform of B gives

$$\mathcal{L}(B)(s) = \frac{\mathcal{L}(B_0)(s)}{1 - \mathcal{L}(M)(s)}. \tag{1.8}$$

This may not seem to be a step forward. On one hand, something about B (viz., it's a Laplace transform) is written explicitly in terms of known things. But to complete the analysis, we must see how to recover B once its transform is known. That is, we must create the inverse Laplace transform and apply it to

$$\frac{\mathcal{L}(B_0)(s)}{1 - \mathcal{L}(M)(s)}.$$

The following observation suggests a shortcut to calculating the inverse Laplace transform:

$$\mathcal{L}(e^{at})(s) = \int_0^{\infty} e^{-st} e^{at}\, dt = \int_0^{\infty} e^{(a-s)t}\, dt = \frac{1}{s-a} \tag{1.9}$$

for any $s > a$. So, we may say that the inverse Laplace transform of $1/(s-a)$ is the function $\exp(at)$.

[6] If t is a time variable, then s must be in units of 1/time. In other problems the independent variable may be in units of length, and the transform variable has units of 1/length and it is then referred to as being a wave number.

1.1.2.1. *The Characteristic Equation.* For most of our applications here, the denominator in (1.8) will be a polynomial in the transform variable s. This can be factored and the result expanded using partial fractions. Then the calculation in (1.9) may be used.

The denominator is critical to this analysis and it tells us important things about how the birth rate will evolve: We seek its zeros

$$1 - \mathcal{L}(M)(s) = 0 \tag{1.10}$$

This equation is called the *characteristic equation* of the renewal equation.

We suppose here that

(H1) $m(a) \geq 0$ for $0 < a < \infty$, $\int_0^\infty m(a)da$ exists, $m(a) \to 0$ as $a \to \infty$, and $m(a) = 0$ for $a < 0$. The forcing function $B_0(t)$ is a continuous function having support in some finite interval $[0, A]$, that is, $B(t) \equiv 0$ for $t \geq A$.

We consider the renewal equation under hypothesis (H1), which greatly simplifies analysis.

We also assume that

(H2) The characteristic polynomial has the form of a factored polynomial,

$$1 - \mathcal{L}(M)(s) = (s - s_1)^{k_1}(s - s_2)^{k_2} \cdots (s - s_K)^{k_K},$$

whose roots are $s_1, s_2, \ldots, s_K$, which occur with multiplicities $k_1, k_2, \ldots, k_K$, respectively.

With these assumptions, we have from the calculation in (1.9) that

$$B(t) = \sum_{k=1}^{K} C_k e^{s_k t}, \tag{1.11}$$

which is a sum of exponentials whose amplification rates are the characteristic roots and whose amplitudes (C_k) may be calculated from the Laplace transforms of B_0 and $m(a)$. This procedure is described next, but the details are not needed to proceed with analysis of the renewal equation once we accept the result in (1.11).

A useful example has $m(a) = a^2 e^{-a}$ as in Figure 1.3, then $\mathcal{L}(M)(s) = 2(s + 1)^{-3}$. As a result,

$$B(t) = C_1 e^{1.26t} + O(e^{s^* t})$$

where $s^* < 0$. (Note that the roots are $s_1 = 2^{1/3} \approx 1.26$, $s_2 = 2^{1/3} e^{2\pi\imath/3} - 1$, and $s_3 = 2^{1/3} e^{-2\pi\imath/3} - 1$. The last two have negative real parts, so the terms they represent in the solution die out. Let $s^* = \Re(s_2)$.[7] Then $s^* < 0$.) The root s_1 is referred to as being the intrinsic growth rate of the population, and the stable birth rate is defined by C_1:

$$\lim_{t \to \infty} e^{-s_1 t} B(t) = C_1. \tag{1.12}$$

[7] A complex number s is written in terms of its real and imaginary parts, $s = \Re(s) + \imath\Im(s)$.

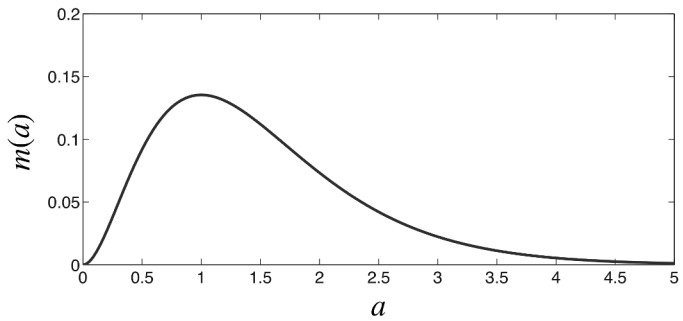

FIGURE 1.3. Maternity function $m(a) \propto a^2 \exp(-a)$. Age is in units of 7 years.

1.1.2.2. *Method of Residues.* This section describes the method of residues, and it requires some background in complex analysis. It may be skipped if one accepts the formula (1.11).

The solution B can be recovered by applying the inverse Laplace transform to both sides in formula (1.8) . This is defined by the contour integral

$$B(t) = \frac{1}{2\pi\imath} \int_{c-\imath\infty}^{c+\imath\infty} e^{st} \frac{\mathcal{L}(B_0)(s)}{1 - \mathcal{L}(M)(s)} \, ds$$

where $\imath = \sqrt{-1}$ and the contour ($\Re(s) = c$) is taken to lie to the right of all zeros of the characteristic equation.

The simplest case arises when the singularities are poles of finite order. With condition (H2) satisfied, the integrand can be expanded using partial fractions to give

$$B(t) = \frac{1}{2\pi\imath} \int_{c-\imath\infty}^{c+\imath\infty} e^{st} \mathcal{L}(B_0)(s) \sum_{m=1}^{M} \frac{R_m}{(s - s_m)^{k_m}} \, ds$$

where the numbers R_m are called the residues of the resolvent.

Recall Cauchy's formula for a function of a complex variable, say $F(z)$. Suppose that F is analytic near a point z_0. Then

$$F(z_0) = \frac{1}{2\pi\imath} \int_C \frac{F(z)}{z - z_0} \, da.$$

In the case of simple poles ($k_m = 1$ for $m = 1, 2, \ldots, M$), we have

$$\begin{aligned} B(t) &= \frac{1}{2\pi\imath} \int_{c-\imath\infty}^{c+\imath\infty} e^{st} \mathcal{L}(B_0)(s) \sum_{m=1}^{M} \frac{R_m}{(s - s_m)} \, ds \\ &= \sum_{m=1}^{M} R_m \mathcal{L}(B_0)(s_m) e^{s_m t}, \end{aligned}$$

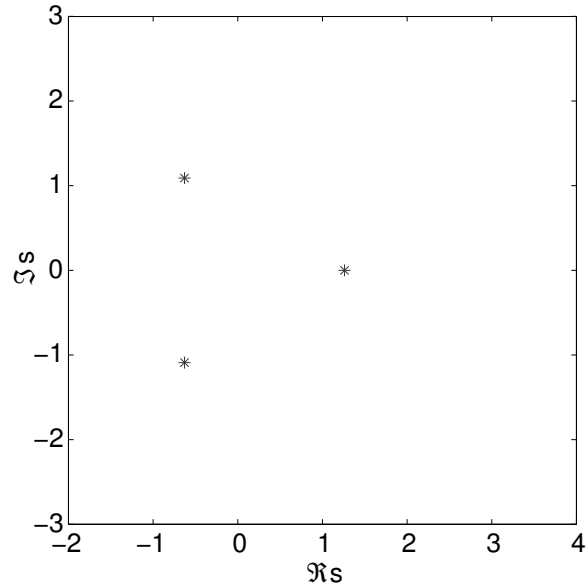

FIGURE 1.4. Characteristic roots for $m(a) = a^2 \exp(-a)$.

which shows the solution to be a linear combination of exponentials, each term having an amplification rate $\Re(s_m)$!

In the preceding example, the characteristic roots are proportional to the cube roots of unity. These are plotted in Figure 1.4. The contour of integration may be chosen to be any vertical line lying to the right of $\Re s = 2^{1/3}$. Figure 1.4 is generated by the MATLAB program in 7.1.2.

Detailed accounts of the Laplace transform are available [**50**].

1.1.2.3. *The Renewal Theorem.* The renewal theorem describes how solutions of the renewal equation behave for large time:

THEOREM (Renewal Theorem) *Let $x(t)$ solve the renewal equation*

$$x(t) = x_0(t) + \int_0^t m(a)x(t-a)da$$

where hypothesis (H1) *is satisfied. Then there is a unique real characteristic root s^* and*

$$\lim_{t\to\infty} e^{-s^*t}x(t) = x^*$$

where $x^* =$ residue of $\mathcal{L}(x_0)(s)/(1-\mathcal{L}(m)(s))$ at $s = s^*$. Moreover, all other characteristic roots satisfy $\Re(s) < s^*$.

An important corollary of the Renewal Theorem is that the solution $x(t)$ behaves (asymptotically) like an exponential; that is, in some sense

$$x(t) \approx e^{s^*t}x^*$$

for large times.

Since $c > \Re(s_m)$ for all $m = 1, 2, \ldots, M$, we can apply Cauchy's formula to each term to get $B(t)$ in the form of an exponential series:

$$B(t) = x^* e^{s^* t} + \text{slower growing or decaying terms.}$$

as predicted by the Renewal Theorem where $x^* = \operatorname{Res} \mathcal{L}(B_0)(s^*)$.

The exponent s^* is called the population's *intrinsic growth rate*, and x^* is called the *stable birth rate*. As a result, we may write

$$B(t) \approx x^* e^{s^* t}$$

and observe that the birth rate will grow (or decay) exponentially.

A convenient choice for m is a Pearson type II function $m(a) = ra^2 \exp(-\mu a)$, as illustrated in Figures 1.3 and 1.4 for $r = 1$, $\mu = 1$. Now because $\mathcal{L}(m)(s) = 2r(\mu + s)^{-3}$, the poles are at $s = (2r)^{1/3}\rho^n - \mu$ for $n = 1, 2, 3$, where $\rho = \exp(2\pi\imath/3)$ is the primitive third root of unity. The intrinsic growth rate in this case is $s = (2r)^{1/3} - \mu$.

Note that if μ is large, indicating especially high infant mortality, then death swamps the population renewal process. But if μ is not large, the birth rate can exhibit significant, but damped, oscillations.

Example: Bernardelli Waves: The Delta Function and Residues. In the extreme case where all reproduction is focused at one age, which occurs in many species of insects for example, we write

$$m(a) = \beta e^{-\mu a} \delta(a - a_0) \tag{1.13}$$

where δ is Dirac's *delta function*, and a_0 is the age at which reproduction occurs. Substituting this into the renewal equation gives

$$x(t) = x_0(t) + \int_0^t \beta e^{-\mu a} \delta(a - a_0) x(t - a) da.$$

The delta function is a generalized function that only makes sense when inside of an integral. For example, for any smooth function $F(a)$,

$$\int_{-\infty}^{\infty} \delta(a - a_0) F(a) da = F(a_0).$$

In this case, the renewal equation becomes

$$\begin{aligned} B(t) &= 0 && \text{for } t < a_0, \\ B(t) &= \beta e^{-\mu a_0} B_0(t - a_0) && \text{for } t = a_0. \end{aligned}$$

Plotting the birth rate ($B(t)$) as a function of t would reveal a series of spikes occurring at times $a_0, 2a_0, 3a_0, \ldots$, separated by intervals of no births. The sizes of the birth rates, say $B_n = B(na_0)$, can be found from the formula

$$B_n = \beta e^{\mu a_0} B_{n-1} = \cdots = (\beta e^{\mu a_0})^n B_0,$$

respectively, which is determined by simple back-substitutions. These numbers would grow if $\beta e^{\mu a_0} > 1$, that is, if each individual more than replaces himself. This phenomenon — that very narrow reproductive windows may cause wavelike birth rates — is referred to as *Bernardelli waves* [**18**].

Example: Maternity Function (Pearson). The maternity function $m(a) = ra^2 \exp(-\mu a)$ was considered earlier. We found in equation (1.12) that

$$\text{stable birth rate} = C_1 \approx \lim_{t\to\infty} e^{-s_1 t} B(t) = \operatorname{Res} \mathcal{L}(B_0)(s_1),$$
$$s_1 = (2r)^{1/3} - \mu;$$

that is,

$$B(t) \approx e^{((2\tau)^{1/3}-\mu)t} B_0$$

for large values of t. The residue can be evaluated as described in the section on the method of residues.

1.2. Population Wave Equation

How can the distribution of the total population among the age groups be determined from knowing the birth rate? We do this by deriving an equation for the total population age distribution that keeps track of time and age: Let $P(a,t)$ denote the population density (organisms/age) of those having age a at time t. Age of humans is measured in terms of time since birth. In other species age may have quite different interpretations; for example, in bacteria, age might be proportional to its phase in the mitotic cycle.[8] To account for the possibility of nonchronological aging, we define the flux of organisms into age a at time t to be $\gamma(a,t)P(a,t)$, but age may be units of something other than time. The conservation equation for a population is

$$\frac{\partial P}{\partial t} = -\nabla \cdot \text{flux} + \text{sources} - \text{sinks}.$$

In the present case, there are no sources, the flux is given above, and the only sink is due to death, say the death rate of organisms of age a at time t is $\mu(a,t)$. Then

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial a}(\gamma(a,t)P(a,t)) - \mu(a,t)P(a,t). \tag{1.14}$$

If γ is a differentiable function, we may write

$$\frac{\partial P}{\partial t} + \gamma(a,t)\frac{\partial P}{\partial a} = -\left(\mu(a,t) + \frac{\partial \gamma}{\partial a}(a,t)\right)P(a,t).$$

We first consider the case of humans where $\gamma \equiv 1$:

$$\begin{gathered} \frac{\partial P}{\partial t} + \frac{\partial P}{\partial a} = -\mu(a,t)P(a,t) \\ P(0,t) = B(t), \quad P(a,0) = P_0(a), \end{gathered} \tag{1.15}$$

where we suppose that the birth rate $P(0,t)$ and the initial population age distribution $P_0(a)$ are known. This model enables us to study the age distribution at each time, since it shows how various cohorts progress through life and how they may contribute to the birth rate. The system (1.15) is referred to as being the *population wave equation* for the chronological age distribution, and it was derived independently by A. G. McKendrick and by H. von Foerster.

[8] Species where aging is proportional to the rate at which nutrients are taken up are considered in Section 1.2.5.

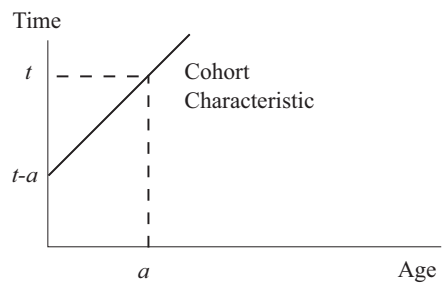

FIGURE 1.5. Lexis diagram showing aging of a cohort with time. The line starting at time $t - a$ moves up one age unit for each time unit, so at time t, the cohort has age a. The characteristic is a straight line having slope 1.0.

1.2.1. The Method of Characteristics. A basic tool in demography is (in one form or another) the Lexis diagram. This simply draws time versus age to show how cohorts move through age-time from birth. Its form is shown in Figure 1.5. The line in the Lexis diagram that a cohort travels on is called a *cohort characteristic curve*.

The method of characteristics provides a way to solve problem (1.15). We introduce a characteristic curve $(a, t) = (a(\tau), t(\tau))$ and a characteristic variable τ that are chosen so that the function

$$p(\tau) = P(a(\tau), t(\tau))$$

satisfies equation (1.15):

$$\frac{dp}{d\tau} = \frac{\partial P}{\partial a}\frac{da}{d\tau} + \frac{\partial P}{\partial t}\frac{dt}{d\tau} = \frac{\partial P}{\partial t} + \frac{\partial P}{\partial a} = -\mu(a(\tau), t(\tau))p(\tau)$$

provided we define the characteristic curve so that

$$\frac{da}{d\tau} = 1 \quad \text{and} \quad \frac{dt}{d\tau} = 1.$$

Thus, the characteristic curve is a straight line parameterized by τ and having direction numbers (1,1). Along the characteristic curve, the function $p(\tau) = P(a(\tau), t(\tau))$ must satisfy the differential equation

$$\frac{dp}{d\tau} = -\mu(a(\tau), t(\tau))p(\tau).$$

Two cases of interest depend on whether the characteristic curve starts at $t = 0$, $a = a_0$ (a cohort starting from the initial population) or at $t = t_0$, $a = 0$ (a cohort starting from new births at $t = t_0$). We first solve the problem along the characteristic curve starting at $(a_0, 0)$; namely,

$$a(\tau) = a_0 + \tau, \quad t(\tau) = \tau, \quad p(\tau) = p(0)\exp\left(-\int_0^\tau \mu(a_0 + s', s')ds'\right).$$

To relate this formula to the original distribution function P, we first eliminate τ by writing $t = \tau$ and $a = a_0 + t$. Substituting P for p gives

$$P(a,t) = P(a_0,0)\exp\left(-\int_0^t \mu(a_0+t',t')dt'\right).$$

Next, eliminate a_0 by observing that $a_0 = a - t$. The result is

$$P(a,t) = P_0(a-t)\exp\left(-\int_0^t \mu(a-t+t',t')dt'\right) \tag{1.16}$$

for $a > t$. This formula gives the solution of the population wave equation for $a > t$.

In the same way, but starting from $(0, t_0)$ we derive the formula

$$P(a,t) = B(t_0)\exp\left(-\int_0^a \mu(a',t_0+a')da'\right).$$

Since $t_0 = t - a$,

$$P(a,t) = B(t-a)\exp\left(-\int_0^a \mu(a',t-a+a')da'\right) \tag{1.17}$$

for $t > a$. This formula gives the solution of the population wave equation for $t > a$. Formulas (1.16) and (1.17) describe the population's age distribution for each time t.[9] Now, if the birth rate were known, for example by solving the associated renewal equation, then the population age distribution would be fully known using the solution of the population wave equation. This is helpful since it is not apparent from the renewal equation's solution how to construct the actual population distribution at any fixed time.

1.2.1.1. *Recovering the Birth Rate from the Age Distribution.* The method of characteristics shows how to derive a solution of the population wave equation given the initial population ($P(a,0)$) and given the birth rate ($B(t)$). How can the birth rate ($B(t)$) be found if the population age distribution $P(a,t)$ is known?

The birth rate is defined by the formula

$$B(t) = \int_0^\infty f(a,t)P(a,t)da,$$

where $f(a,t)$ is the expected number of births to a population member of age a at time t. Substituting in the solution we derived for P, we have

$$\begin{aligned} B(t) &= \int_0^\infty f(a,t)P(a,t)da \\ &= \left(\int_0^t + \int_t^\infty\right) f(a,t)P(a,t)da \\ &= \int_0^t f(a,t)\exp\left(-\int_0^a \mu(a',t-a+a')\right)B(t-a)da' + B_0(t), \end{aligned}$$

[9]Note that there may be a discontinuity in the age distribution along the cohort where $t = a$. This can be avoided by assuming that $P_0(0) = B(0)$, but this case may require further investigation, which is not carried out here.

where

$$B_0(t) = \int_t^\infty P_0(a-t)\exp\left(-\int_0^t \mu(a-t+t',t')dt'\right)da.$$

Now, the maternity function

$$m(a,t) = f(a,t)\exp\left(-\int_0^a \mu(a',t-a+a')\right)$$

may depend explicitly on time, and if so, we may not use the Laplace transform method to solve this equation.

If the fertility f and death rate μ depend only on a and not on t, then

$$B(t) = \int_0^t f(a)P(a,t)da + \int_t^\infty f(a)P(a,t)da,$$

which, according to the solutions in (1.16)–(1.17), gives

$$\begin{aligned} B(t) = &\int_0^t f(a)B(t-a)\exp\left(\int_0^a -\mu(a')da'\right)da \\ &+ \int_t^\infty f(a)P(a-t,0)\exp\left(\int_0^t -\mu(a-t+t')dt'\right)da. \end{aligned}$$

As a result, we have

$$B(t) = \int_0^t f(a)B(t-a)\exp\left(\int_0^a -\mu(a')da'\right)da + B_0(t), \tag{1.18}$$

where

$$B_0(t) = \int_t^\infty f(a)P_0(a-t)\exp\left(\int_0^t -\mu(a-t+t')dt'\right)da \tag{1.19}$$

represents the residual births from the initial population. Equation (1.18) is the renewal equation where the maternity function is given by the formula

$$m(a) = f(a)\exp\left(-\int_0^a \mu(a')da'\right).$$

This shows that the population wave model is consistent with the renewal equation, and it identifies the components of the maternity function that are due to age-specific death and fertility rates.

1.2.2. Stable Age Distribution. Applying the Renewal Theorem to (1.18) implies that there is a unique dominant solution s^* of the characteristic equation

$$1 - \mathcal{L}(m)(s^*) = 0$$

and a number B^* such that

$$\lim_{t\to\infty} e^{-s^*t}B(t) = B^*.$$

Therefore, for each age $a > t$, we have that

$$P(a,t)e^{-s^*t} = e^{-s^*(t-a)}B(t-a)\exp\left(-\int_0^a \mu(a')da' - s^*a\right).$$

Taking the limit $t \to \infty$ in this equation shows that

$$P(a,t)e^{-s^*t} \to p^*(a)$$

where

$$p^*(a) = B^* \exp\left(-\int_0^a \mu(a')da' - s^*a\right),$$

which is called the *stable age distribution* of the population. This is stable in the sense that the relative ratio of population sizes in various cohorts remains constant (i.e., since e^{s^*t} cancels out of both numerator and denominator in the ratio,

$$\frac{\int_{a_0}^{a_1} P(a,t)da}{\int_0^\infty P(a,t)da} \approx \frac{\int_{a_0}^{a_1} p^*(a)da}{\int_0^\infty p^*(a)da}$$

for large times.

The stable age distribution is often plotted for each sex in a population to form the *age pyramid*. The age pyramid for a population is often used to describe the economic circumstances of a population [**6, 31**].

1.2.3. Total Population: Malthus's Model. The model (1.15) is also consistent with Malthus's model: If there is a constant death rate μ and a constant fertility f_0, then $m(a) = f_0 \exp(-\mu a)$, and

$$B(t) = B_0(t) + \int_0^t f_0 \exp(-\mu(t-a))B(a)da.$$

Differentiating this formula gives

$$\begin{aligned} \frac{dB}{dt} &= \frac{dB_0}{dt}(t) + f_0 B(t) - \mu \int_0^t f_0 \exp(-\mu(t-a))B(a)da \\ &= f(t) + (f_0 - \mu)B(t) \end{aligned} \tag{1.20}$$

where $f(t) = (dB_0/dt)(t) - \mu B_0(t)$. Equation (1.20) is a continuous-time version of Malthus's model of geometric population growth, but with an external forcing $f(t)$ that describes lingering contributions to growth from the initial population, and $f_0 - \mu$ represents the intrinsic growth rate of the population.

1.2.4. The Reproduction Window: Nonoverlapping Generations. For most species, there is a window of ages during which reproduction can take place. Figure 1.6 depicts this.

However, in many species reproduction is focused at essentially one age. We write this using a delta function as described earlier, say $m(a) = m_0\delta(a - a_0)$. In this case, all reproduction is focused on the single age $a = a_0 = a_1$ in Figure 1.6, and the renewal equation becomes

$$B(t) = B_0(t) + m_0 B(t - a_0).$$

Any member of the initial population having age greater than a_0 will not participate in further reproductions. Thus, we restrict attention to the case where $t > a_0$. We may look at the solutions stroboscopically: Let $B_n = B(na_0)$. Then

$$B_n = m_0 B_{n-1} = m_0^n B_0$$

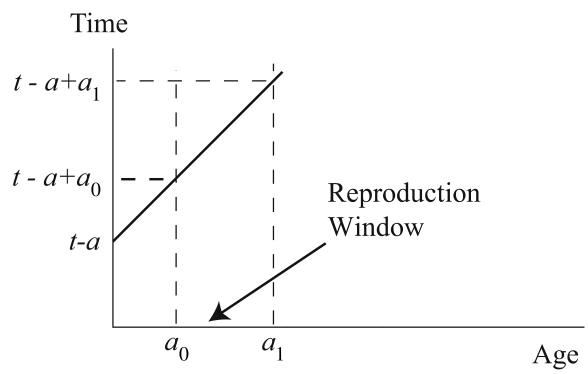

FIGURE 1.6. Lexis diagram showing the reproduction window, which spans the ages $[a_0, a_1]$. The offspring of a cohort beginning at time $t - a$ will be eligible for reproducing during the time interval $[t - a + a_0, t - a + a_1]$.

for $n = 2, 3, \ldots$, and $B_1 = m_0 B_0(a_0)$.

In this extreme case, there are no overlapping generations in the sense of multiple cohorts reproducing at the same time, since all reproduction occurs at only one age. However, if we replace the delta function in this investigation by a narrowly based pulse, say

$$\delta(a) \approx \frac{1}{h} \mathbb{1}_{(a_0, a_0+h)}(a)$$

for some small number h,[10] then we see that several age groups (namely those with ages between a_0 and $a_0 + h$) may reproduce. This leads to spreading out of the cohorts, which complicates keeping track of the population sizes, but the Renewal Theory does this nicely by identifying the stable growth rate and stable age distribution.

1.2.5. Nonchronological Aging. Many organisms age at rates depending upon the availability of nutrients or progress through some metabolic process, environmental conditions, etc. When conditions are not favorable, they may enter a state of stasis until things improve. For example, a particular bacterium typically goes through several phases on its way to cell division: G_1, where material is accumulated for synthesis of DNA; S, where synthesis occurs; G_2, where further materials are accumulated in preparation for division; and a brief mitotic interval of cell division. Happy cells might perform all of these feats within 20 minutes, but if suitable nutrients are scant or the environment is unfavorable, the process may need more time. Therefore, chronological time is not suitable for describing aging of such organisms. Rather we introduce a new variable a that describes the phase of the cell in its division cycle. Say $0 \leq a \leq 1$, and this unit interval is divided into subintervals G_1, S, G_2, and M, corresponding to the gaps, synthesis, and mitosis as described above.

[10]The function $\mathbb{1}_{(a_0, a_0+h)}(a) = 1$ for $a_0 < a < a_0 + h$, and is 0 otherwise.

Suppose that individuals of (nonchronological) age a at time t have numbers $P(a,t)$, and that they age at a rate $\gamma(a,t)$, which we suppose is a smooth function of (a,t). The resulting population wave equation was derived in (1.14).

This problem is, as for (1.15), supplemented with initial and boundary conditions:

$$P(a,0) = P_0(a), \quad P(0,t) = \int_0^\infty f(a,t)P(a,t)da \tag{1.21}$$

where $f(a,t)$ describes the fertility of those of age a at time t.

The problem (1.14), (1.21) may be reduced to a single integral equation for the birth rate $B(t) = P(0,t)$, but this will not be a convolution integral, so Laplace transform methods may not be useful for analyzing it. As a result there may be no analytical methods available for studying this integral equation for $B(t)$.

Example: Nonchronological Aging by Bacteria. An example of nonchronological aging is given by the growth of bacteria where we interpret age as being a phase of the cell cycle. The life cycle of a bacterium comprises

M: Mitosis (cell division and consequent appearance of two daughters),
G_1: Gap 1, where the cell accumulates resources in preparation for synthesis,
S: Synthesis, where the cell replicates all of its DNA, organelles, etc.
G_2: Gap 2, where the cell consolidates its holdings and accumulates materials needed for mitosis.

Apparently, cells do not start synthesis until they have enough materials to complete it; that is, they do not stop synthesis of DNA once they have started it. Therefore, if a culture is starved of a vital nutrient, all cells that are in a gap phase will cease aging, but those in the synthesis phase will continue aging, eventually to accumulate at the start of the second gap phase. This mechanism is useful in synchronizing cell cultures [**5**]. In general, the characteristic curves will not be straight lines, but their progress reflects the levels of nutrition, environmental conditions, etc., as indicated in Figure 1.7.

1.2.6. Accounting for Other Time Delays. Time delays occur in almost all systems. We saw in the work on population waves and renewal that time delays can be accommodated in some quite sophisticated ways (e.g., as characteristics in a wave equation or as kernels in a convolution integral equation). Another collection of models starts with a differential equation but one that involves earlier values of the state variables, rather than only the present values. We consider Malthus's model with a time delay and solve it in two interesting cases.

Example: Malthus's Equation with Time Delays: Laplace Transform Solution. Malthus's model with a time delay may simulate the expected delay between conception and delivery of a live birth: In short, the population is assumed to change depending on what size it was τ time units before:

$$\frac{dx}{dt}(t) = gx(t-\tau) \tag{1.22}$$

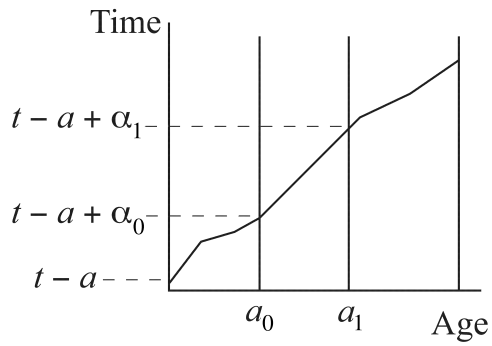

FIGURE 1.7. Lexis diagram for a bacterial population showing a nonlinear cohort characteristic that reflects a brief period of starvation occurring just before $t - a + \alpha_0$. The synthesis window spans the ages $[a_0, a_1]$. The offspring of a cohort beginning at time $t - a$ will be eligible for synthesis during the time interval $[t - a + \alpha_0, t - a + \alpha_1]$, where α_1 and α_2 are some functions of (a, t) that are determined in the method of characteristics.

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where g is a constant representing the intrinsic growth rate, and τ is the time delay in reproduction. This problem may be solved using Laplace transforms, since

$$\int_0^\infty e^{-st} \frac{dx}{dt}(t)dt = g \int_0^\infty e^{-st} x(t - \tau)dt$$

leads to the result that

$$\widetilde{x}(s) = \frac{\widetilde{\phi}(s)}{s + g \exp(-s\tau)} \quad \text{where} \quad \widetilde{\phi}(s) = \int_{-\tau}^0 e^{-st} x(t)dt,$$

which is assumed to be known. That is, we suppose that the population size is known on an interval of length τ, which we take to be $[-\tau, 0]$ for convenience of notation. The formula for $\widetilde{x}$ can be inverted using the method of residues as in Section 1.1.2. Now the equation for the characteristic values of s is

$$s + g \exp(-s\tau) = 0,$$

which is a transcendental equation to be solved for s. If we write $s = \alpha + \imath\beta$, then

$$\alpha + g \exp(\alpha\tau) \cos(\beta\tau) = 0, \quad \beta - g \exp(\alpha\tau) \sin(\beta\tau) = 0, \tag{1.23}$$

which must be solved simultaneously for α, β [**3**].

Example: Malthus's Equation with a Time Delay: Periodic Solutions. There is an interesting special case of (1.22) that highlights an important feature of differential-difference equations: Consider again

$$\frac{dx}{dt}(t) = gx(t - \tau). \tag{1.24}$$

The function $x(t) = \cos t$ solves equation (1.22) when $\tau = \pi/2$ and $g = 1$ since

$$\frac{d \cos t}{dt} = -\sin t = \cos\left(t - \frac{\pi}{2}\right).$$

This shows that time delays may drastically complicate a problem by introducing unexpected oscillations, and while this may be determined by solving the equations in (1.23) for α and β, these equations are not easy to solve. This example illustrates one complexity that time delays can create in a system, and it points out a largely unexplored aspect of Malthus's model. In particular, the general solution of equation (1.24) will have the form

$$x(t) = \sum_{j=1}^{\infty} x_j e^{s_j t},$$

where the numbers $\{s_j\}$ are the characteristic roots and the coefficients x_j are determined using the method of residues. This example shows that the dominant terms (i.e., the rightmost values of s_j) might be purely imaginary, so $x(t)$ is asymptotically periodic.

1.3. Discrete-Event Models

There are theories for discrete-event problems parallel to those developed in the preceding sections for continuous-time models. Discrete-event iterations arise in most applications in mathematics and science, and these have a general form that relates the state variables of the model at the next time step, say $P(n+1)$ in terms of the state variables at the present time step, $P(n)$:

$$\vec{P}(n) = F(\vec{P}(n-1)) \tag{1.25}$$

where the "time steps," the vector of state variables $\vec{P}$, and the system F have various interpretations. Three particular cases of interest in population mathematics are (1) linear models used in demographics, (2) the iteration of various nonlinear renewal processes in ecological systems, and (3) Markov chains, which are fundamental models in the theory and application of probability. We introduce here some of the basic methodologies for studying systems of these three types (1.25).

1.3.1. Discrete Renewal Equation. Time steps are selected in some way that is consistent with the biology of the system being studied, and the sequence

$$\{B_n\},$$

which describes the population's birth rate at those time steps, is to be determined given the sequence of maternity factors $\{m_k\}$. Using the same thinking as for the continuous-time case in (1.7), we consider the discrete renewal equation

$$B_n = \phi_n + \sum_{k=0}^{n} m_k B_{n-k} \tag{1.26}$$

for $n = 0, 1, 2, \ldots$. The maternity factor m_k measures the probability of survival to the kth age epoch multiplied by the fertility of those who reach that epoch.

Typically, the sequence $\{m_k\}$ will be finite, so $m_k = 0$ for $k \geq K$, for some number K. For example, in human populations, the epochs might be chosen to be of length 5 years, and $m_k = 0$ for $k \geq 11$, reflecting that fertility is effectively (for the population) 0 beyond age 55. We will see later how this renewal equation is related to the general form in (1.25).

1.3.1.1. *The z-transform.* We define the discrete Laplace transform of the sequence $\{B_n\}$ by the formula

$$\widehat{B}(z) = \sum_{n=0}^{\infty} B_n z^{-n}. \tag{1.27}$$

This is called the *z-transform* of the sequence $\{B_n\}$ [**37**], and it plays a role in analysis similar to that played by the Laplace transform for the renewal equation. We suppose that there is a number R such that the series

$$\sum_{n=0}^{\infty} |R^n B_n| \quad \text{and} \quad \sum_{n=0}^{\infty} |R^n m_n|$$

converge. Note that if C is a contour that encloses 0, then Cauchy's formula shows that

$$\frac{1}{2\pi\imath} \int_C z^{n-1}\, dz = \delta_n$$

where $\delta_n = 1$ if $n = 0$, $\delta_n = 0$ if $n \neq 0$. (This is kind of a nineteenth-century version of the Dirac delta function.) Therefore,

$$\frac{1}{2\pi\imath} \int_C z^{n-1} \widehat{B}(z) dz = B_n$$

for $n = 0, 1, 2, \ldots$, so we may recover the original sequence if we know its z-transform. The next step is to determine $\widetilde{B}(z)$ using the renewal equation (1.26).

A calculation similar to that for the continuous-time renewal equation shows that

$$\widehat{B}(z) = \widehat{m}(z)\widehat{B}(z) + \widehat{\phi}(z)$$

where

$$\widehat{\phi}(z) = \sum_{n=0}^{\infty} \phi_n z^{-n}, \quad \widehat{m}(z) = \sum_{n=0}^{\infty} m_n z^{-n},$$

are the z-transforms of $\{\phi_n\}$ and $\{m_n\}$, respectively. As a result,

$$\widehat{B}(z) = \frac{\widehat{\phi}(z)}{1 - \widehat{m}(z)} \quad \text{and so} \quad B_n = \frac{1}{2\pi\imath} \int_C z^{n-1} \frac{\widehat{\phi}(z)}{1 - \widehat{m}(z)}\, dz.$$

In this way, we have found a formula for the sequence in terms of the data ϕ and the maternity factors $\{m_k\}$. The poles of the numerator ($\widehat{\phi}(z)$) and the roots of the

denominator determine the nature of the residues, and the solution may be written in terms of the residues as

$$B_n = \sum_{k=1}^{K} A_k z_k^n,$$

where the characteristic roots are $\{z_1, z_2, \ldots, z_K\}$,[11] which are the solutions of the characteristic equation

$$\widehat{m}(z) = 1.$$

1.3.1.2. *Example: Fibonacci's Model.* As an example, we consider the Fibonnaci sequence where $B_0 = 1$, $B_1 = 1$ and for $n = 2, 3, \ldots$,

$$B_n = B_{n-1} + B_{n-2}.$$

Substituting in $B_n = z^n$ gives

$$z^2 - z - 1 = 0,$$

so there are two characteristic roots,

$$z_1 = \frac{1+\sqrt{5}}{2}, \quad z_2 = \frac{1-\sqrt{5}}{2}.$$

It follows that

$$B_n = A_1\left(\frac{1+\sqrt{5}}{2}\right)^n + A_2\left(\frac{1-\sqrt{5}}{2}\right)^n, \tag{1.28}$$

where A_1 and A_2 are free constants that can be used to meet initial conditions. In fact, in this case the initial conditions are $B_0 = A_1 + A_2 = 1$ and

$$B_1 = A_1 z_1 + A_2 z_2 = 1,$$

so

$$A_1 = \frac{z_2 - 1}{z_2 - z_1}, \quad A_2 = \frac{z_1 - 1}{z_1 - z_2}.$$

This calculation is justified next.

Consider the renewal equation

$$B_{n+2} = aB_{n+1} + bB_n$$

where a and b are fixed numbers. The z-transform for this model is calculated in the following steps:

$$z^2 z^{-n+2} B_{n+2} = az z^{-n-1} B_{n+1} + bz^n B_n,$$

$$z^2 \sum_{n=0}^{\infty} z^{-n+2} B_{n+2} = az \sum_{n=0}^{\infty} z^{-n-1} B_{n+1} + b \sum_{n=0}^{\infty} z^n B_n,$$

$$z^2 \sum_{k=2}^{\infty} z^{-k} B_k = az \sum_{k=1}^{\infty} z^{-k} B_{n+1} + b \sum_{n=0}^{\infty} z^n B_n,$$

[11] In most cases in population theory, $\widehat{m}(z)$ is a finite polynomial in z, and so we indicate a finite set of roots here.

$$z^2\left(\sum_{k=0}^{\infty} z^{-k} B_k - B_0 - z^{-1} B_1\right) = az\left(\sum_{k=0}^{\infty} z^{-k} B_{n+1} - B_0\right) + b\sum_{n=0}^{\infty} z^n B_n,$$

$$z^2(\widehat{B}(z) - B_0 - z^{-1} B_1) = az(\widehat{B}(z) - B_0) + b\widehat{B}(z),$$

$$(z^2 - az - b)\widehat{B}(z) = z^2 B_1 - (az + z^2)B_0.$$

Therefore,

$$B_n = A_1 z_1^n + A_2 z_2^n$$

where z_1, z_2 are the two roots of the equation $z^2 - az - b = 0$. The constants A_1 and A_2 can be determined from the initial data

$$B_0 = A_1 + A_2, \quad B_1 = A_1 z_1 + A_2 z_2.$$

1.3.2. Demographics: Connecting Theory to Discrete-Event Census Numbers. The connection between the discrete renewal equation (1.26) and the general system (1.25) that models the population distribution among ages is accomplished by deriving a discrete-event version of the population wave equation. Consider the population described above where there are K age classes. Denote the numbers in these age classes at various times by the column vectors

$$\vec{P}_n = \text{col}(P_{1,n}, P_{2,n}, \ldots, P_{K,n})$$

for $n = 0, 1, 2, \ldots$, where

$$P_{k,n} = \text{number of people in the } k^{\text{th}} \text{ age group at time } n.$$

This is the discrete-event analogy to the population density function $P(a,t)$ in population wave equation (1.15). Let $f(a)$ denote the number of births expected per unit time per population member of age a. Suppose that $f(a) = 0$ for $a > A$. We divide the ages from 0 to A into K equal intervals, to be consistent with the epochs chosen for the renewal equation, say $[0, a_1), [a_1, a_2), \ldots, [a_{K-1}, a_K)$ where $a_j = jA/K \equiv jh$. For example, if the census interval is 5 years, we may take $A = 11$ and $a_j = 5j$ for $j = 1, 2, \ldots, 11$.

Let λ_j denote the probability of surviving from age interval $[a_{j-1}, a_j)$ to $[a_j, a_{j+1})$. Then the birth rate is described by the discrete-event model

$$B_{0,n} = B_{0,0} + \sum_{k=1}^{K} \beta_k P_{k,n}$$

where

$$\beta_k = \frac{1}{h}\int_{kh}^{(k+1)h} f(a)da$$

is the average fertility over a census interval. The age distribution vectors $\vec{P}_n = (P_{1,n}, P_{2,n}, \ldots, P_{K,n})^\mathsf{T}$ for $n = 1, 2, 3, \ldots,$[12] describe the dynamics of the population's age structure as time progresses.

1.3.2.1. *Leslie Matrix.* Each of the older cohorts changes only through death, $P_{n+1} = \lambda_n P_{n-1}$, but the first cohort (that is, the number of newborns) is related to the others through the birth rates. Setting $P_0 = B_0$, we may write

$$\begin{pmatrix} P_{0,n} \\ P_{1,n} \\ \vdots \\ P_{K,n} \end{pmatrix} = \begin{pmatrix} \beta_1 & \beta_2 & \beta_3 & \cdots & \beta_K \\ \lambda_1 & 0 & 0 & \cdots & 0 \\ 0 & \lambda_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & \lambda_{K-1} & 0 \end{pmatrix} \begin{pmatrix} P_{0,n-1} \\ P_{1,n-1} \\ \vdots \\ P_{K,n-1} \end{pmatrix}. \tag{1.29}$$

Using obvious vector notation, we write

$$\vec{P}_n = L\vec{P}_{n-1} \tag{1.30}$$

where the matrix

$$L = \begin{pmatrix} \beta_1 & \beta_2 & \beta_3 & \cdots & \beta_K \\ \lambda_1 & 0 & 0 & \cdots & 0 \\ 0 & \lambda_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & \lambda_{K-1} & 0 \end{pmatrix} \tag{1.31}$$

is called Leslie's matrix [**31**]. Equation (1.30) is the discrete-event analogue of the population wave equation (1.15), and this model is of the form in equation (1.25). By applying successive back-substitutions, we get that

$$\vec{P}_n = L^n \vec{P}_0.$$

Incidentally, the first component of $\vec{P}_n$ is B_n, the birth rate, and it is easily seen that the full model reduces to a renewal equation for $\{B_n\}$, since the other components of $\vec{P}_n$ can be eliminated using Gaussian elimination.

The eigenvalues of the matrix L are determined by solving the characteristic equation

$$0 = \det \begin{pmatrix} \beta_1 - \nu & \beta_2 & \beta_3 & \cdots & \beta_K \\ \lambda_1 & -\nu & 0 & \cdots & 0 \\ 0 & \lambda_2 & -\nu & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & \lambda_{K-1} & -\nu \end{pmatrix} \tag{1.32}$$

for ν. The matrix L is similar to an upper block triangular matrix (its Jordan canonical form [**45**]) whose diagonal elements are the characteristic roots or the eigenvalues of L. Let $\Lambda_j = \lambda_1\lambda_2\cdots\lambda_j$. Then the characteristic equation becomes

$$(-1)^K \beta_K \Lambda_{K-1} + \nu\beta_{K-1}\Lambda_{K-2} + \cdots + \nu^K = 0,$$

[12] If V is a matrix, then V^T denotes the transpose of V. If V is a row vector with N columns, then V^T is a column vector having N rows.

and the coefficients in this polynomial are exactly the maternity factors described in the discrete renewal equation. There is one dominant real characteristic root, and all the rest fall within or on a circle in the complex plane whose radius is the dominant root [**18**].

1.3.2.2. *Spectral Decomposition.* If the matrix L is diagonalizable, then it has a simple spectral decomposition, say

$$L = \sum_{i=1}^{K} \lambda_i \Pi_i$$

where $\{\Pi_i\}$ is a collection of K $(K \times K)$-matrices that satisfy the projector conditions

$$\Pi_i \Pi_i = \Pi_i \quad \text{and} \quad \Pi_i \Pi_j = 0_K \quad \text{for } i \neq j$$

where 0_K is the $(K \times K)$-zero matrix. Then

$$L^k = \sum_{i=1}^{K} \lambda_i^k \Pi_i .$$

The importance of this decomposition is that complicated multiplications of $(K \times K)$-matrices can be reduced to much simpler multiplications of K numbers. If the initial population distribution is

$$\vec{P}^* = \begin{pmatrix} P_0 \\ P_1 \\ \vdots \\ P_K \end{pmatrix},$$

then the population distribution after n time steps is

$$L^n P = \lambda_1^n \Pi_1 P^* + O(\|\lambda_2/\lambda_1\|^n) \quad \text{or} \quad \lambda_1^{-n} L^n P \to \Pi_1 P^*,$$

which vector is the called the *stable age distribution* of the population. A similar result follows if L is not diagonalizable, but the argument for this is beyond the level of this book [**6**].

The following MATLAB program gives an interesting illustration of the fate of a single founder cohort when there are eight age classes and a reproduction window of three age groups:

$$L = \begin{pmatrix} 0 & 0 & 0 & 1 & 1 & 1 & 0 & 0 \\ 0.9 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.8 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.7 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.6 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.4 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.3 & 0 \end{pmatrix}. \tag{1.33}$$

MATLAB calculates the eigenvalues of this matrix to be

$$0.0, 0.0, 0.9907, 0.1772 \pm \imath 0.8522, -0.7774, -0.2838 \pm \imath 0.4226.$$

So the intrinsic growth rate is 1.12. Note that the next largest eigenvalue has a significant imaginary part, so we expect damped oscillations to appear in the emerging age structure.

$$
(1.34)\qquad
\begin{array}{cccccccccc}
TIME & \rightarrow & & & & & & & & \\
1.0000 & 0 & 0 & 0.7200 & 0.5040 & 0.3024 & 0.5184 & 0.7258 & 0.6895 & 0.6781 \\
0 & 0.9000 & 0 & 0 & 0.6480 & 0.4536 & 0.2722 & 0.4666 & 0.6532 & 0.6205 \\
A\ 0 & 0 & 0.7200 & 0 & 0 & 0.5184 & 0.3629 & 0.2177 & 0.3732 & 0.5225 \\
G\ 0 & 0 & 0 & 0.5040 & 0 & 0 & 0.3629 & 0.2540 & 0.1524 & 0.2613 \\
E\ 0 & 0 & 0 & 0 & 0.3024 & 0 & 0 & 0.2177 & 0.1524 & 0.0914 \\
0 & 0 & 0 & 0 & 0 & 0.1512 & 0 & 0 & 0.1089 & 0.0762 \\
\downarrow\ 0 & 0 & 0 & 0 & 0 & 0 & 0.0605 & 0 & 0 & 0.0435 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.0181 & 0 & 0
\end{array}
$$

The first column in (1.34) gives the initial age distribution: All are newborn. As time increases to the right, the initial cohort diminishes through death, and in the last class accounted for here, it is 0.018. The birth rate, given in the first row, is increasing, but note the oscillation in it. Eventually all age classes are occupied; in this sense, the generations overlap. The program in 7.1.3 illustrates Leslie's matrix.

1.3.2.3. *Example: The Leslie-Fibonnaci Model.* These developments may be illustrated using Fibonacci's model (1.6): Leslie's matrix for this model is

$$L = \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix}.$$

The eigenvalues are

$$\lambda_1 = \frac{1+\sqrt{5}}{2} \quad \text{and} \quad \lambda_2 = \frac{1-\sqrt{5}}{2},$$

and this matrix can be written in the form of its spectral decomposition

$$L = \lambda_1 \Pi_1 + \lambda_2 \Pi_2$$

where the projection matrices Π_1 and Π_2 may be constructed using the left and right eigenvectors of L. These are determined by solving the equations

$$L \begin{pmatrix} a \\ b \end{pmatrix} = \lambda_{1,2} \begin{pmatrix} a \\ b \end{pmatrix}$$

for a, b. Solutions are

$$\begin{pmatrix} \lambda_1 \\ 1 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} \lambda_2 \\ 1 \end{pmatrix},$$

respectively. Similarly, the left eigenvectors are, respectively,

$$(\lambda_1, 1), \quad (\lambda_2, 1).$$

We define the projection matrices by the formulas

$$\Pi_1 = \frac{1}{\lambda_1^2 + 1} \begin{pmatrix} \lambda_1 \\ 1 \end{pmatrix} (\lambda_1, 1), \quad \Pi_2 = \frac{1}{\lambda_2^2 + 1} \begin{pmatrix} \lambda_2 \\ 1 \end{pmatrix} (\lambda_2, 1).$$

These matrices satisfy the projection conditions

$$\Pi_1 \Pi_1 = \Pi_1, \quad \Pi_2 \Pi_2 = \Pi_2, \quad \Pi_1 \Pi_2 = \Pi_2 \Pi_1 = 0,$$

and

$$L = \lambda_1 \Pi_1 + \lambda_2 \Pi_2.$$

Note that

$$L^n = \lambda_1^n \Pi_1 + \lambda_2^n \Pi_2 = \lambda_1^n \left(\Pi_1 + \left(\frac{\lambda_2}{\lambda_1} \right)^n \Pi_2 \right) \to \lambda_1^n \Pi_1$$

as $n \to \infty$, since $|\lambda_2/\lambda_1| < 1$. This is interpreted as saying that if the initial population distribution is

$$P^* = \begin{pmatrix} 1 \\ 1 \end{pmatrix},$$

then the population approaches a stable age distribution:

$$\lambda_1^{-n} L^n \begin{pmatrix} 1 \\ 1 \end{pmatrix} \to \Pi_1 P^* \propto \begin{pmatrix} \lambda_1 \\ 1 \end{pmatrix} \quad \text{as } n \to \infty.$$

The stable age distribution refers to the relative sizes of the cohorts; in this case the steady ratio of the first cohort to the second is λ_1, even as the population grows geometrically.

This analysis identifies two important parameters used by demographers: First, there is the eigenvalue λ_1, which describes an intrinsic growth rate (the largest amplification of possible components), and second, the ratio λ_2/λ_1, which describes the rate at which a population will converge to its stable age distribution.

1.3.3. Summary of Population Models.

Name	*Continuous*	*Discrete Event*
Malthus	$dP/dt = rP$	$P_{n+1} = (1 + rh)P_n$
Logistic	$dP/dt = rP(1 - P/K)$	$P_{n+1} = \frac{rP_n}{1+P_n/K}$
Wave	$\partial P/\partial t + \partial P/\partial a = -\mu P$ $P(0,t) = B(t), P(a,0) = P_0(a)$	$\vec{P}_{n+1} = L\vec{P}_n$ $L = \begin{pmatrix} \beta_0 & \dots & \beta_M \\ \lambda_1 & \dots & \dots \\ \vdots & \ddots & \vdots \\ 0 & \dots & 0 \end{pmatrix}$
Nonchronological Aging	$\partial P/\partial t + (\partial/\partial a)(\gamma(a,t)P) = -\mu(a,t)P$ $P(0,t) = B(t),\ P(a,0) = P_0(a)$	$\vec{P}_{n+1} = L_n\vec{P}_n$ $L = \begin{pmatrix} \beta_{0,n} & \dots & \beta_{M,n} \\ \lambda_{1,n} & \dots & \dots \\ \vdots & \ddots & \vdots \\ 0 & \dots & 0 \end{pmatrix}$
Renewal	$B(t) = B_0(t) + \int_0^t m(a)B(t-a)da$	$B_n = \phi_n + \sum_{j=1}^M m_j B_{n-j}$
Nonlinear Renewal	$B(t) = B_0(t) + \int_0^t m(a)F(\widetilde{P}(t))B(t-a)da$ $\widetilde{P}(t) = \int_0^\infty P(a,t)da$	$P_{n+1} = rP_n f(P_n)$