

# Notes on Coale (1957)

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## 1 Introduction

Coale’s paper is about stable population theory, which is ultimately organized around what is known as “the characteristic equation.” This is the fundamental tool of age-structured demography. The characteristic equation combines the schedule of age-specific mortality, the schedule of age-specific fertility, the age-structure of the population, and the rate of increase of the population. This latter quantity is also mean fitness in evolutionary models.

The characteristic equation in its modern form was first derived by Alfred Lotka in the early part of the 20th century. Leonhard Euler, the 18th century Swiss mathematician, also derived a similar equation. As a result, the characteristic equation is often known as *The Euler-Lotka Equation*.

The fundamental assumption of the stable population model is that the age schedules of demographic rates, which we will denote  $l(a)$  for survival to exact age  $a$  and  $m(a)$  for the fertility of women age  $a$  ( $m$  for “maternity”; don’t ask about  $l$  for survivorship), have remained approximately constant for a long time. How long is “long”? It turns out that about 50 years, which also happens to be approximately the last age with non-zero fertility for women, is sufficient for a population to achieve stability.<sup>1</sup> It is also important to note that stability does not mean that the population remains constant (this is a common misunderstanding). In general, a stable population will grow at some intrinsic rate  $r > 0$ . If  $r = 0$ , the population size does not change and we refer to it as being *stationary*. A number of the relationships we investigate simplify considerably under stationarity. Note also that if  $r < 0$  for a long time, the population will go extinct. Thus, long-term negative growth rates are not terribly interesting.

The assumption of constant demographic rates may sound outlandish. The model turns out to be pretty robust, though it is always important to check assumptions, perform sensitivity analysis, etc.

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<sup>1</sup>The human life-cycle lends itself to remarkably rapid convergence to the stable population, a point noted by [Tuljapurkar \(1981\)](#), and subsequently not given the attention it deserves.

An important assumption in deriving the characteristic equation of Euler and Lotka is that we are working with a one-sex population. Now, humans are obviously not clonal. What this assumption translates to in a dioecious species like humans is what is known as *female demographic dominance*. This essentially means that the observed age-specific fertility rates (and therefore the observed births) are determined wholly by women. There are explicit two-sex extensions of the characteristic equation, but we won't trouble ourselves with them here, since Coale (1957), and the great majority of classical formal demography, assumes female demographic dominance.

Coale's paper is primarily concerned with explicating the effects on age structure of changes in fertility and mortality. He does this by analyzing the characteristic equation. It is useful for us to understand where the equation comes from, so we will look at two distinct ways to derive it.

## 1.1 Deriving the Characteristic Equation

See accompanying video [here](#).

Lotka's derivation of the characteristic equation is simply a model for the number of births at time  $t$ ,  $B(t)$ , as a function of the number of births prior to  $t$ .  $B(t)$ , is composed of two components (1) births to women already alive at time  $t = 0$  and (2) births to women born since  $t = 0$ . Write this as

$$B(t) = \int_0^t N(a, t)m(a)da + G(t) \quad (1)$$

where,  $N(a, t)$  is the number of women age  $a$  alive at time  $t$ ,  $m(a)$  is age-specific fertility rate of women age  $a$ ,  $G(t)$  are births from women alive at  $t = 0$ .

Equation 1 is the renewal equation. It shows how the present births were generated by previous births – that is, how the population renews itself.

Now the number of women age  $a$  at time  $t$  will be the number of the total born  $t - a$  years ago who survive. That is  $N(a, t)$  results from the survivors of the births  $B(t - a)$ :

$$N(a, t) = B(t - a)l(a),$$

where  $l(a)$  is the probability of surviving to exact age  $a$ .

Substitute back into equation 1 and assume  $t > 50$  (the assumed last age of reproduction for women in the population). Note that this is equivalent to integrating from the age of first reproduction,  $\alpha$ , to the age of last reproduction ( $\beta$ ):

$$B(t) = \int_{\alpha}^{\beta} B(t - a)l(a)m(a)da \quad (2)$$

where  $m(a)$  is the birth rate of women age  $a$ .

Solve the homogeneous integral equation (2). Use  $B(t) = Be^{rt}$  as a trial solution.

$$Be^{rt} = \int_{\alpha}^{\beta} Be^{r(t-a)}l(a)m(a)da = \int_{\alpha}^{\beta} Be^{rt}e^{-ra}l(a)m(a)da \quad (3)$$

Now divide both sides by  $Be^{rt}$  to get:

$$1 = \int_{\alpha}^{\beta} e^{-ra} l(a) m(a) da \quad (4)$$

This is *the Characteristic Equation* of Euler and Lotka. The unique value of  $r$  that equates the two sides of 4 is known as the *intrinsic rate of increase*.

### 1.1.1 Deriving the Renewal Equation from Considerations of Age Structure

Lotka (1907) actually used a different approach to derive the characteristic equation. Assume we have a birth series:  $B(t) = Be^{rt}$ . The number of women age  $a$  alive at time  $t$  is again

$$N(a, t) = B(t - a)l(a).$$

Substitute the birth series into the age interval size

$$\begin{aligned} N(a, t) &= Be^{r(t-a)}l(a) = Be^{rt}e^{-ra}l(a) \\ &= B(t)e^{-ra}l(a) \end{aligned}$$

Rearrange and integrate both size:

$$\int_0^{\beta} N(a, t) da = B(t) \int_0^{\omega} e^{-ra} l(a) da \quad (5)$$

Rearranging a bit, we get an expression for the crude birth rate of the population,

$$\frac{B(t)}{\int_0^{\omega} N(a, t) da} = \frac{B(t)}{N(t)} = b(t) = \frac{1}{\int_0^{\omega} e^{-ra} l(a) da} = b. \quad (6)$$

Divide the numbers in each age by the total population size to get the proportionate age structure:

$$c(a, t) = \frac{N(a, t)}{N(t)} = \frac{B(t)}{N(t)} e^{-ra} l(a) \quad (7)$$

$$= be^{-ra} l(a) = c(a) \quad (8)$$

Multiply both sides by  $m(a)$  and integrate across all child-bearing ages:

$$\int_{\alpha}^{\omega} be^{-ra} l(a) m(a) da = \int_{\alpha}^{\omega} c(a) m(a) da \quad (9)$$

The right-hand side is the crude birth rate of the population.

$$\int_{\alpha}^{\omega} e^{-ra} l(a) m(a) da = 1. \quad (10)$$

Once again, we have the characteristic equation, this time derived from considerations of age structure.

## 1.2 Three Equations Characterize a Stable Population

Coale' (1957) paper is really an explication of the properties of a stable population described by the characteristic equation. You can find a video deriving these equations [here](#). In addition to this video on the derivation of the stable-population relationships, you can find [this one](#) on the relationships under population stationarity (i.e.,  $r = 0$ ).

A stable population has an exponential birth series  $B(t) = Be^{rt}$ . The number of age  $a$  people alive at time  $t$ ,  $N(a, t)$ , is simply the number of births  $a$  years ago times the probability of surviving to age  $a$ :  $N(a, t) = B(t - a)l(a)$ . Substitute this birth series into the equation for  $N(a)$

$$N(a, t) = Be^{r(t-a)}l(a) = Be^{rt}e^{-ra}l(a) = B(t)e^{-ra}l(a) \quad (11)$$

Integrate this across all ages and rearrange

$$\begin{aligned} \int_0^\infty N(a, t)da &= B(t) \int_0^\infty e^{-ra}l(a)da \\ \frac{B(t)}{\int_0^\infty N(a, t)da} &= \frac{B(t)}{N(t)} = \frac{1}{\int_0^\infty e^{-ra}l(a)da} = b \end{aligned} \quad (12)$$

Return to (11), divide both sides by the total population size  $N(t)$  to get an expression for the proportionate age structure  $c(a, t)$

$$\begin{aligned} c(a, t) &= \frac{N(a, t)}{N(t)} = \frac{B(t)}{N(t)}e^{-ra}l(a) \\ c(a, t) &= be^{-ra}l(a) = c(a) \end{aligned} \quad (13)$$

That's two, what's the third equation?

$$1 = \int_0^\beta e^{-ra}l(a)m(a)da$$

The Euler-Lotka characteristic equation. Note that for all ages at which  $m(a) = 0$ , the integral is irrelevant: it doesn't matter if you integrate from age zero or age  $\alpha$  and you can, of course, integrate to arbitrarily high ages above the age of last reproduction,  $\beta$ .

## 2 What Coale Was All On About

Coale's questions:

1. How does the stable age distribution change with mortality?
2. How does the stable age distribution change with fertility?

Coale's brief paper is surprisingly sparse on analysis and is mostly heuristic.

## 2.1 Change of Stable Age Distribution with Mortality

Briefly, changing mortality does not have a large impact on the stable age structure. This is perhaps a surprising result. One might easily imagine that a population characterized by lower overall mortality would be older on average, since a larger fraction of the population would survive to old age. However, in the absence of effective contraception (and parity-specific control), lower mortality also means more opportunities for women to have children. Coale shows that, in fact, populations with lower overall mortality, but the same fertility as some comparison population, will, in fact, have a *lower average age*. Turns out that the overall age structure of a population is more sensitive to the number of births and juvenile survival than it is to the death rates of adults.

What really matters is the age pattern of mortality.<sup>2</sup> If the mortality reduction is for women over age 50 then, yes, the population will be older on average. Note that selection will be very low on over-50 mortality. If the mortality reduction applies to reproductive-age or pre-reproductive women, then there will be little difference in average age of the population.

We tend to think in terms of cohorts: if a greater fraction of a cohort survives to old age, then the average age of the population will indeed be greater. However, populations are, in fact, *renewal* processes. More reproductive-age adults means more infants and the fate of the infants can swamp out any changes in later ages.

In a famous paper outlining a theory for the evolution of senescence, written in the same year as Coale’s essay, the evolutionary biologist George Williams laid out a series of nine predictions, including a hypothesis that has gone on to be broadly accepted by evolutionary anthropologists (Williams 1957). Namely, Williams suggested that high “external” mortality on adults should select for more rapid senescence and shorter lifespan. He further suggested that juvenile mortality should have no impact on senescence. The analytical result in the next section (2.1.1) shows that changing the mortality rate by a constant amount across the board has no effect whatsoever on the average age of death or age structure of the population more generally.

It is remarkable that this idea has had so much traction in the evolutionary sciences, when the contemporaneous analysis of Coale shows it to be simply not true. This is one of the many reasons why it is critical that evolutionary scientists interested in the evolution of life histories should study formal demography.

### 2.1.1 A Uniform Increase in Mortality Does Not Change Age Structure

Coale used heuristic arguments. We can add a bit of analysis for a simple case. Assume that mortality is reduced uniformly at all ages by an amount  $k$ :

$$\mu'(a) = \mu(a) - k.$$

This changes the survivorship function

$$l'(a) = \int_0^a -[\mu(x) - k]dx = l(a)e^{ka}$$

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<sup>2</sup>Pay attention to this. It will be a theme in subsequent work on life history theory proper.

$r$  will increase by  $k$ . Why? By definition, the characteristic equations from before and after the mortality change will be equal

$$\int_0^\omega e^{-ra} l(a) m(a) da = \int_0^\omega e^{-(r+k)a} l(a) m(a) da.$$

And now for the stable age distribution (from equation 13):

$$c'(a) = \frac{e^{-r'a} l'(a)}{\int_0^\infty e^{r'x} l'(x) dx} = \frac{e^{-(r+k)a} l(a) e^{ka}}{\int_0^\infty e^{-(r+k)x} l(x) e^{kx} dx} = c(a)$$

We can see that the age stable structure remains unchanged. Same result would apply if we added a value  $k$ . So much for Williams's conjecture.

## 2.2 Change of Stable Age Distribution with Fertility

### 2.2.1 Quick Calculus Aside

It turns out that many of the key results in formal demography depend on an identity from calculus that you may have missed. This identity involves the derivative of the logarithm of a function, namely,

$$\frac{d \log[f(r)]}{dr} = \frac{df(r)}{dr} \frac{1}{f(r)}. \quad (14)$$

Why is this? It follows directly from the properties of logarithms and application of the chain rule for differentiation. Write  $u = f(r)$ . Applying the chain rule, we get:

$$\frac{d}{dr} \log[f(r)] = \frac{d \log[u]}{du} \frac{du}{dr}.$$

Now, by definition

$$\frac{d \log[u]}{du} = \frac{1}{u},$$

so, substituting back  $f(r)$  for  $u$ , we see that

$$\frac{d \log[f(r)]}{dr} = \frac{df(r)}{dr} \frac{1}{f(r)}.$$

We apply this identity to derive many of key results of stable population theory. It is also very important for understanding the concept of elasticities, which we will discuss later in the course.

A second calculus fact that we frequently bring to bear in the analysis of the characteristic equation is that the derivative of the Euler-Lotka equation with respect to  $r$  is minus the average age of the population. Let

$$f(r) = \int_0^\beta e^{-ra} l(a) m(a) da$$

Then

$$f'(r) = - \int_0^\beta a e^{-ra} l(a) m(a) da.$$

This follows from the fact that the only thing in the characteristic equation that is a function of  $r$  is the exponential term. Remember that

$$\frac{d}{dr} e^u = e^u \frac{du}{dr},$$

so the derivative of  $e^{-ra}$  is thus  $-ae^{-ra}$ .

To get some intuition on this, I find it useful to recall that an integral is really just a sum in continuous time (i.e., where the bins that we're summing across are infinitesimally small). Suppose you have two age classes,  $a_1$  and  $a_2$ , and let  $\psi(a) = l(a)m(a)$ , so that

$$f(r) = e^{-ra_1} \psi(a_1) + e^{-ra_2} \psi(a_2)$$

The derivative of this with respect to  $r$  is clearly

$$f'(r) = -a_1 e^{-ra_1} \psi(a_1) + -a_2 e^{-ra_2} \psi(a_2).$$

The integral of the Euler-Lotka equation just has (a lot) more bins.

I also just made the claim that the average age of the population, which we can denote as  $A_P$  is

$$A_P = \int_0^\beta a e^{-ra} l(a) m(a) da.$$

How is that? Note that another important interpretation of the characteristic equation is that it is a probability distribution of the ages of individuals in the population. That is, the probability that a woman is age  $x$ , assuming population stability, is

$$p(x) = e^{-rx} l(x) m(x)$$

When we integrate the product of this and the ages  $a$ , we are calculating an expected value of the ages in the population.

### 2.2.2 Increased Fertility (Usually) Leads to a Lower Death Rate

Consider the case where a change in fertility increases  $r$ . Express the gross death rate of the population as:

$$\begin{aligned} d &= \int_0^\infty c(a) \mu(a) da = \int_0^\infty b e^{-ra} l(a) \mu(a) da \\ &= b \int_0^\infty e^{-ra} l(a) \mu(a) da. \end{aligned}$$

Take logarithms of both sides and differentiate with respect to  $r$ :

$$\frac{d \log(d)}{dr} = \frac{d \log(b)}{dr} + \frac{\frac{d}{dr} \int_0^\infty e^{-ra} l(a) \mu(a) da}{\int_0^\infty e^{-ra} l(a) \mu(a) da}$$

Compute the derivatives and simplify. Note that the first term is again the mean age of the stable population (which follows from equation 14) and the second term in the expression is the mean age of death in the stable population:

$$A_D = \frac{\int_0^\infty a e^{-ra} l(a) \mu(a) da}{\int_0^\infty e^{-ra} l(a) \mu(a) da}$$

This yields:

$$\frac{d \log(d)}{dr} = A_P - A_D$$

The effects on mortality of a fertility change: (1) A reduction in overall mortality if the mean age of the population is less than the mean age of death, (2) An increase in mortality if the mean age of the population is greater than the mean age of death. When is this likely to happen? It can actually happen when there is very high infant/childhood mortality. So in environments that are bad for juvenile mortality, increasing fertility can actually increase the overall death rate.

## References

- Tuljapurkar, S. (1981). Primitivity and convergence to stability. *Journal of Mathematical Biology* 13(2), 241–246.
- Williams, G. C. (1957). [Pleiotropy, natural selection, and the evolution of senescence](#). *Evolution* 11, 398–411.