The McKendrick-von Foerster Equation

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1 Introduction

In this paper, we discuss a partial differential equation that models the evolution over time of an age-structured population. Our equation is useful for age-structured models, demographic models where the population at time t has an age distribution superimposed on it. In other words, at a given time t, the ages of the individuals in a population are also considered. Age-structured models are related to general physiologically-structured models, where any other variable (such as size or weight) can replace the age variable. For example, De Roos and Persson use a physiologically structured population model to model a "size-structured consumer population feeding on a non-structured prey population," studying the qualitative and quantitative population dynamics of a planktivorous fish population [1]. Consequently, the ideas we discuss in this paper, though focused on age, can also be extended to other physiological structures.

Anderson Gray McKendrick (A.G. McKendrick) was a Scottish physician and epidemiologist. In 1926, McKendrick published a paper titled *Applications of mathematics to medical problems*. He aimed to study the transfer of disease caused by interactions between people and apply mathematical modeling to epidemiology; his paper introduced a version of the McKendrick-von Foerster equation [2]. McKendrick's paper went relatively unseen; independently, in 1959, biophysicist Heinz von Foerster discovered the same equation when studying cell divisions [3]. The equation itself was later named in recognition of their independent work, as what we now know as the **McKendrick–von Foerster equation**, a form of the advection equation that incorporates the mortality rate to study the population density at a given age and time.

In our project, we will derive the general age-structured model arising from the McKendrick-von Foerster equation [4]. We will then discuss the stable age structure to see what happens after a long period of time. Finally, after detailing various extensions of the McKendrick-von Foerster equation, we will close by highlighting its importance in helping scientists understand population models.

2 The McKendrick-von Foerster Equation

2.1 Context

Consider a population of female organisms with age structure at time $t = 0$ given by $f(a)$. Equivalently, $f(a)da$ is the number of females between age a and age $a + da$ in the population.

Though age should technically be finite, let the domain for a be $[0, \infty)$. The goal of the McKendrick-von Foerster equation is to model the age structure $u = u(a, t)$ for the population for any time $t > 0$. By definition, $u(a, t)da$ represents the number of females at time t between ages a and $a+da$. The total female population at time t can consequently be represented as

$$N(t) = \int_0^\infty u(a, t)da.$$

Note that the quantity $u(0,t)$, the number of newborns at time t, is not known; this quantity depends on the reproduction rate of females and the mortality rate. We define $m(a)$ to be the *per capita mortality rate*, which will be given to us in any initial statement of the problem, and $b(a,t)$ to be the *fecundity rate* (also known as the *maternity function*), the average number of offspring per female at time t.

2.2 Formula

The general form of the **McKendrick–von Foerster equation**, which models the population dynamics described above, is

$$u_t = -u_a - m(a)u.$$

This equation is a form of the advection equation where $m(a)$ is the per capita mortality rate defined above. Similarly, $u = u(a,t)$ represents the density of a population of age a and time t, for nonnegative a and positive t (where a and t are measured in the same units). More precisely, the McKendrick–von Foerster equation is the advection equation with speed one and sink term given by the mortality rate; notice that the flux is $\phi = u$, or the density of the population at that age. This means we can use a certain age, a, and a time, t, and then compute the density of the population of that particular age at that time.

We can now derive the initial conditions and boundary values for the population dynamics of the given equation.

Note that we have an initial condition

$$u(a,0) = f(a), \quad a \geq 0.$$

where, as stated before, $f(a)$ represents the initial population of female organisms of age a at time $t = 0$.

Recall that $u(a,t)$ represents the number of females at time t at age a, and $b(a,t)$ is the average reproduction rate of females of age a at time t. Summing over all possible ages, from 0 to infinity, we derive the boundary condition $u(0,t) = B(t)$ where $B(t)$ represents the total amount of offspring produced by females of all ages at time t. Our work tells us that

$$u(0,t) = \int_0^\infty b(a,t)u(a,t)\,da, \quad t > 0.$$

Here, we see that u is part of our boundary condition. This is known as a *nonlocal boundary condition*, where the unknown solution is a part of the condition.

We have now derived the general age-structured model

$$u_t = -u_a - m(a)u, \quad a > 0,\, t > 0$$

$$u(0,t) = \int_0^\infty b(a,t)u(a,t)\,da, \quad t > 0$$

$$u(a,0) = f(a), \quad a \geq 0$$

extending from the McKendrick-von Foerster Equation.

3 Deriving the Stable Age Structure

A common technique used to study demographic models is to determine the solution over a long-time period. Consequently, we will derive the **stable age structure** of the above general age-structured model system.

First, note that the initial condition $u(a,0) = f(a)$ represents the initial population of females at age a. When looking for a long-term solution, we ignore this condition as these individuals and their offspring will die after a finite time period; said differently, we know births from the initial population will not affect our long-term solution.

When deriving the solution, we consider the case where the maternity function $b = b(a,t)$ is independent of time and thus, $b = b(a)$, a function of just the age. Now, we are ready to solve for u as a stable age structure.

We start by assuming the solution takes on the form

$$u(a,t) = U(a)e^{rt}$$

where $U(a)$ is some unknown age structure and r represents the growth rate of the population for large t.

For our above solution form, we get that

$$u_a = U'(a)e^{rt} \text{ and } u_t = rU(a)e^{rt}.$$

Substituting these results and the solution form for $u(a,t)$ into the McKendrick-von Foerster equation $u_t = -u_a - m(a)u$ we get that

$$rU(a)e^{rt} = -U'(a)e^{rt} - m(a)U(a)e^{rt}.$$

Simplifying by dividing both sides by e^{rt} and grouping terms, we get an ODE for $U(a)$:

$$U'(a) = -(m(a) + r)U(a).$$

Applying separation of variables (dividing both sides by $U(a)$ and integrating), we get the solution

$$U(a) = Ce^{-ra}e^{-\int_0^a m(s)\,ds}$$

for some constant C.

Let us define $S(a) = e^{-\int_0^a m(s)\,ds}$ to be the *survivorship function*, the probability of surviving at age a. Substituting this into our age structure function, we get that

$$U(a) = Ce^{-ra}S(a)$$

With this, we can rewrite our long-term solution $u(a,t) = U(a)e^{rt}$ as

$$\begin{aligned} u(a,t) &= \left(Ce^{-ra}S(a)\right)e^{rt} \\ &= Ce^{r(t-a)}S(a). \end{aligned}$$

To determine the growth constant r, we can substitute our long-term solution $u(a,t) = Ce^{r(t-a)}S(a)$ into our nonlocal boundary condition

$$u(0,t) = \int_0^\infty b(a,t)u(a,t)\,da.$$

And since we assumed our maternity function is independent of time, we can update this boundary condition to be

$$u(0,t) = \int_0^\infty b(a)u(a,t)\,da.$$

Since $u(0,t) = Ce^{rt}S(0) = Ce^{rt}$, we get that

$$Ce^{rt} = \int_0^\infty b(a)Ce^{r(t-a)}S(a)\,da$$

or equivalently, after dividing both sides by Ce^{rt},

$$1 = \int_0^\infty b(a)e^{-ra}S(a)da.$$

The above equation is a form of the **Euler–Lotka equation**, one of the most important equations in age-structured population growth models [5]. One can solve for r from the Euler-Lotka Equation using numerical methods [5].

Consequently, from the McKendrick-von Foerster equation and its associated general age-structured model, we have derived the long-time age structure of the population

$$u(a,t) = Ce^{r(t-a)}S(a)$$

where C is a constant and $S(a)$ represents the survivorship function

$$S(a) = e^{-\int_0^a m(s)}ds$$

and the Euler-Lotka Equation

$$1 = \int_0^\infty b(a)e^{-ra}S(a)da,$$

which can be used to solve for the growth rate r.

4 Discussion and Conclusions

In this paper, we introduce the McKendrick-von Foerster equation, which is used in age-structured models to study the population density at a given age and time. We derive the general age-structured model from the equation and then derive the stable age structure/long-term solution to the general age-structured model.

Further studies of specific cases of the McKendrick-von Foerster equation and the general age-structured model lead to different behaviors in the age structure for the population. For example, when the maternity rate m is constant, one can study what is known as a renewal equation (see [4] for more details).

While the context of our paper is for age-structured models, for which the McKendrick-von Foerster equation can be used to study areas in epistemology [3] and biology [6], the McKendrick-von Foerster equation can also be used more broadly to study other general physiologically-structured models, such as size-structured models as in [1].

The McKendrick-von Foerster equation allows researchers to work with the complexities of population growth and structure. The equation accounts for the fact that mortality rates and fertility rates usually vary with age, and it allows for the study of populations with different age structures. However, the equation comes with a few limitations. The equation assumes homogeneous populations with no migration and that all individuals have the same mortality and fertility rates. This may not be a reasonable assumption for some populations.

In conclusion, the McKendrick-von Foerster equation and the systems it models make it a useful tool to study population dynamics and general demography, and we hope this paper gave a glimpse into its power and flexibility.

References

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