Age-Structured Populations with Continuous Age Distributions

Simple models often give good information about simple populations or useful ”big picture” information about large, complicated populations. However, in many cases the structure of the population significantly affects its dynamics. For example, removing all women between the ages of 15 to 40 from a human population would reduce the population size by 20–30% but would reduce the birth rate almost to zero. Many animals cannot reproduce until individuals reach a certain size (eg fish) or level of maturity (mammals and birds). Further, predation might fall most heavily on certain age groups. Often this is the youngest individuals (the larvae of fish or marine molluscs for example have a very low survival rate for example) but in other species mature individuals may come under the heaviest pressure. African elephants, for example are only attractive to ivory poachers when they are old enough to have grown tusks.

In populations where reproduction is not seasonal a model with continous age distributions can be constructed.

For the continuous case the number in the population at time t between the ages of a and $a + da$ is given by

$$\int_a^{a+da} n(a', t)da' , \tag{1}$$

where $n(a, t)$ is the age distribution of the population at time t. As in the discrete case, individuals in the population die and reproduce. We shall assume here that the birth and death rates are functions of age only and do not vary over time. Let $\mu(a)$ be the death rate and $b(a)$ be the birth rate where here a is the maternal/parental age. Births only contribute to the population at $a = 0$ and so for all other values of a we have

$$\frac{dn}{dt} = -\mu(a)n(a, t). \tag{2}$$

That is, for $a \neq 0$, population numbers change only through death. In equation (2) n is a function not only of time t but also age a and age itself is a function of time $a = a(t)$. Using the chain rule, we rewrite the total derivative as follows:

$$\frac{dn}{dt} = \frac{\partial n}{\partial t} + \frac{\partial n}{\partial a}\frac{da}{dt} = \frac{\partial n}{\partial t} + \frac{\partial n}{\partial a}$$

since $da/dt = 1$. (You grow old at the same rate as time passes!) Hence the differential equation for the evolution of the population is

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)n(a, t) \quad \text{for } a \neq 0. \tag{3}$$

Equation (3) is known as the *Von Foerster equation*. It states that the population of a particular age changes because of loss through death and because the population grows older. If $\mu(a) = 0$ in (3) then the population is simply changing by the rate at which it is getting older.

The number of individuals born at any time is related to the birthrate at any particular age a multiplied by the number of individuals of age a and then integrated over all age classes. In other words:

$$n(0, t) = \int_0^\infty b(a)n(a, t)da, \quad \text{for}\, t > 0. \tag{4}$$

Of course, the upper limit really is finite, the oldest age to which an individual can survive, but it is mathematically convenient to take it as infinity. Finally, equation (3) needs a condition for $t = 0$ for it to be solved. (Because it is a first order partial differential equation in two variables it requires two boundary conditions/initial conditions.) This condition is

$$n(a, 0) = f(a) \tag{5}$$

where $f(a)$ is the age distribution of the population at $t = 0$.

Equation (3) together with conditions (4) and (5) can be solved. They constitute a linear first order hyperbolic partial differential equation with boundary condition(4) and initial condition (5). The problem is solved by the method of characteristics.

Let us assume that the solution to (3), $n(a, t)$ is known. The characteristic curves of equation (3) are the lines $a = t + c$ where c is a constant. You will note that when $t = 0$, $a = c$. We define w_c, the *cohort function* corresponding to age c as:

$$w_c(t) = n(t + c, t), \quad \text{for } t \geq t_c \tag{6}$$

where t_c is defined by $t_c = \max(0, -c)$. The cohort function $w_c(t)$ tracks through time those individuals whose age is c when $t = 0$. If we subsititute $w_c(t)$ into equation (3) we get

$$\frac{dw_c}{dt} = -\mu(t + c)w_c(t), \quad \text{for } t \geq t_c. \tag{7}$$

This is a first order linear equation and can be solved by applying an integrating factor, to give

$$w_c(t) = w_c(t_c) \exp\left(-\int_{t_c}^{t} \mu(s + c)ds\right), \quad t \geq t_c. \tag{8}$$

To convert this equation back into the original variables we need to consider two different cases: one where $a > 0$ at $t = 0$ and so c is positive and $t_c = 0$; the other where $a = 0$ at some time $t > 0$ and so c is negative and $t_c = -c$

For the first case we set $c = a - t$ where $a \geq t$, and get

$$w_c(t) = w_c(0) \exp\left(-\int_{0}^{t} \mu(s + c)ds\right), \quad t \geq 0. \tag{9}$$

If we then substitute $n(a, t)$ for $w_c(t)$ we have

$$n(a, t) = n(c, 0) \exp\left(-\int_{0}^{t} \mu(s + (a - t))ds\right), \quad a \geq t. \tag{10}$$

In the second case we set $c = a - t$, where $a < t$, and so we get

$$w_c(t) = w_c(-c) \exp\left(-\int_{-c}^{t} \mu(s + c)ds\right), \quad t \geq -c. \tag{11}$$

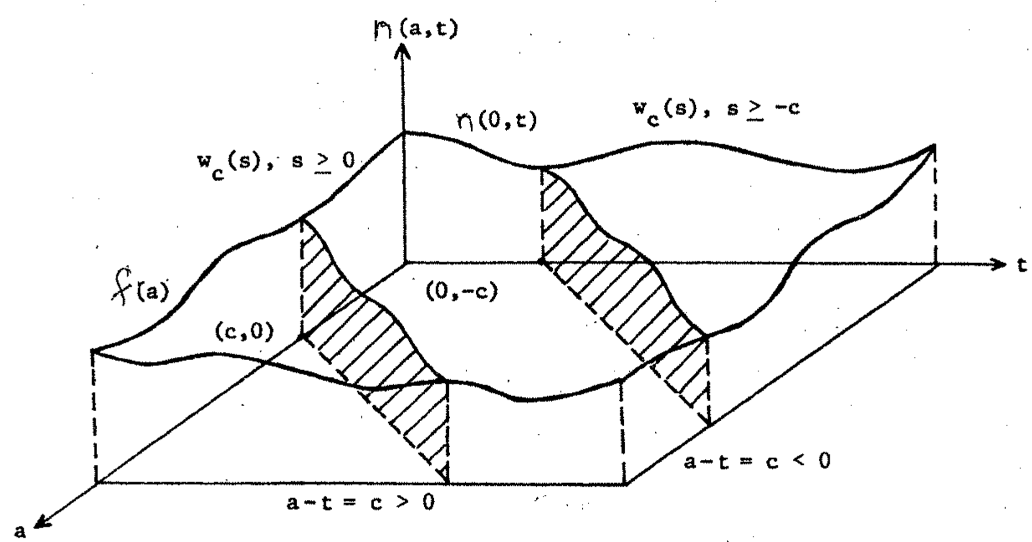
(Remember in this case the cohort is born at $t = -c$ and $-c > 0$.) Substituting to get the equation in terms of $n(a, t)$ gives us:

$$n(a, t) = n(0, t - a) \exp\left(-\int_{t-a}^{t} \mu(s + (a - t))ds\right), \quad a < t. \tag{12}$$

The complete solution for (3) with boundary condition (4) and initial condition (5) is therefore

$$n(a,t) = \begin{cases} n(0, t-a)\exp\left(-\int_0^a \mu(s)ds\right) & \text{for } a < t \\ f(a-t)\exp\left(-\int_{a-t}^a \mu(s)ds\right) & \text{for } a \geq t \end{cases} \tag{13}$$

since $n(a-t, 0) = f(a-t)$. You can see from equation (13) that the solution is divided into two parts: the first gives the evolution for cohorts that were born after $t = 0$, the second part (corresponding to the first case above) gives the evolution of cohorts which were already alive at $t = 0$. A diagrammatic representation of the different co-ordinates used in this solution is given below. It is very helpful in understanding the above analysis to be able to understand and interpret this diagram. (Diagram from G.F. Webb, *The Theory of Nonlinear Age-Dependent Population Dynamics*)



An equilibrium solution of the equation (3) is defined to be a solution independent of time so that $n(a,t) = \nu(a)$, a function of a only. Substituting $\nu(a)$ into equation (3) we get

$$\frac{d\nu}{da} = -\mu(a)\nu(a) \tag{14}$$

and the boundary condition (5) becomes

$$\nu(0) = \int_0^\infty b(a)\nu(a)da. \tag{15}$$

Equation (14) can be solved using the same method as for equation (7) to give

$$\nu(a) = \nu(0)\exp\left(-\int_0^a \mu(s)ds\right), \quad a \geq 0. \tag{16}$$

This must also satisfy the boundary condition (15). If we substitute (16) into (15) and assume that $\nu(0) \neq 0$ we get

$$1 = \int_0^\infty b(a)\exp\left(-\int_0^a \mu(s)ds\right)da. \tag{17}$$

This equation imposes a condition on $b(a)$ and $\mu(a)$; they must satisfy the relation of equation (17). If they do not then the only equilibrium condition which exists is the one with $\nu(0) = 0$. If the zeroth age cohort has no members then $\nu(a) = 0$ for all $a > 0$ also. Hence the population is zero.

Because of the unlikelihood of satisfying equation (17), another special class of solution has been defined. These are *stable age distributions*. For these solutions the total size of the population can change in size but the proportion in any age backet $[a_1, a_2]$ remains constant. That is,

$$\frac{\int_{a_1}^{a_2} n(a,t)da}{\int_0^\infty n(a,t)da} \tag{18}$$

is independent of time. These solutions have the form

$$n(a,t) = A(a)T(t). \tag{19}$$

Substituting this into equation (3) gives

$$A(a)\frac{dT}{dt} + T(t)\frac{dA}{da} = -\mu(a)A(a)T(t) \tag{20}$$

which can be separated to give

$$\frac{\frac{dT}{dt}}{T(t)} = -\frac{\left(\frac{dA}{da} + \mu(a)A(a)\right)}{A(a)} = \lambda \tag{21}$$

where λ is a constant. Solving for $T(t)$ gives

$$T(t) \propto e^{\lambda t} \tag{22}$$

and for $A(a)$ we get

$$A(a) = A(0)\exp\left(-\lambda a - \int_0^a \mu(s)ds\right). \tag{23}$$

When we combine these we have

$$n(a,t) = A(0)\exp\left(\lambda(t-a) - \int_0^a \mu(s)ds\right). \tag{24}$$

For the boundary condition (4) to hold, λ must satisfy

$$1 = \int_0^\infty b(a)\exp\left(-\lambda a - \int_0^a \mu(s)ds\right)da. \tag{25}$$

This is called the *characteristic equation* and relates b, μ and λ to each other.

The material in these notes has been adapted from G.F. Webb, *Theory of Nonlinear Age-Dependent Population Dynamics* and from J.D. Murray *Mathematical Biology*