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On a Simple Metapopulation Model with Delay

by

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In this thesis we shall examine two instances of a metapopulation model as introduced by Diekmann [6]. Doing so we encounter some well-known techniques often used in delay differential equations on a simpler level then is done in most existing literature. Clear examples of the usage of the method of steps, exponential scaling and the linearisation of a delay equation are given.

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Chapter 1

Delay Equations

1.1 Introduction

The field of differential equations has many applications. They arise naturally when one describes processes involving growth. For example calculating the growth of some bank saving in terms of interest and the costs of the bank account. The interest on the bank account depends on the size of the savings. So if we write this statement for time $t \in \mathbb{R}$ and size of the savings $x \in C(\mathbb{R}, \mathbb{R})$:

$$\frac{dx(t)}{dt} = rx(t) - c$$

where $r \in \mathbb{R}_{\geq 0}$ is the interest and $c \in \mathbb{R}_{\geq 0}$ the cost of the bank account, we find a differential equation.
Also when one does calculations on population growth in terms of birth- and death rates or on the speed of the flow of a liquid through a pipe in terms of the flow in and out of the pipe differential equations come into play.
Often in these differential equations there is some dependence on how the system evolved in the past. For example in a predator-pray system where the size of the populations influence the death rates and thereby the growth of the populations. If the way predators and prays participate in the system is dependent on the age of individual predators and prays, the history of the birth rates have an influence on the growth of both populations as well.
Another example would be a model for the stock market, where the difference between demand and supply determine in which direction the price will go. When one introduces to such a model investments with some penetration time for them to reach the market, the investments history influences future prices.

These types of differential equations give rise to a more complex field of study, namely Delay Differential Equations (DDE's, also called retarded differential equations).

1.2 Delay Differential Equations

A delay differential equation for function $x \in C(\mathbb{R}, \mathbb{R})$ of time $t \in \mathbb{R}$ can be described by the following set of equations:

$$\begin{aligned} \dot{x}(t) &= F(t, x(t), x_t) \\ x(t) &= \varphi(t) \quad \text{ for } \ t \in [-r, 0] \end{aligned} \tag{1.1}$$

where $x_t(\theta) = x(t+\theta)$ with $\theta \in [-r, 0]$ for some $r \in \mathbb{R}_+$ and some $F : \mathbb{R} \times C(\mathbb{R}, \mathbb{R}) \to \mathbb{R}$ and initial function $\varphi : [-r, 0] \to \mathbb{R}$.
An important difference between a DDE and an ODE is that the initial condition is not a value of the function in a point, but we have to define it for an interval of length r. Often one of the intervals $[-r, 0]$ or $[0, r]$ is chosen. One has to have an initial function of length r because for a $t_0 \in \mathbb{R}$ the derivative of $x(t)$ in t_0 depends on the past values of $x(t)$ over the interval $[t_0, t_0 - r]$.

To make the difference between an ODE and a DDE more clear we will look at a simple example of both. Even though this example has no relevance to a natural phenomena it does give a nice insight in some of the mathematics common to DDE's.

Example 1.2.1. Let $t \in \mathbb{R}$ and $x \in C(\mathbb{R}, \mathbb{R})$. In this example we look at the differential equation

$$\frac{dx(t)}{dt} = \frac{x(t)}{2} - \frac{3x(t-h)}{2}$$

for some $h \in \mathbb{R}_{\geq 0}$. For $h = 0$ we get an ODE. It is well-known that with initial condition $x(1) = 1$ we find:

$$x(t) = e^{1-t} \tag{1.2}$$

But any $h > 0$ we find a delay equation:

$$\frac{dx(t)}{dt} = \frac{x(t)}{2} - \frac{3x(t-h)}{2} \tag{1.3}$$

which is less straight forward to solve.
First we need an initial condition on $x(t)$. For this example we will take $x(t) = 1$ for $t \in [-h, 0]$.
To solve equation (1.3) one can use the method of steps. This method is very common in solving delay equations and will be explained in the next section. The solutions to the differential equation for $h = 0, \frac{1}{2}$ or 1 are plotted in figure 1.1. Notice that the solutions

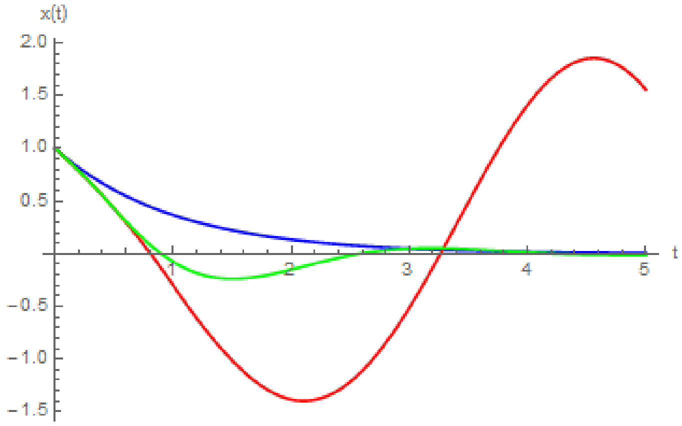

FIGURE 1.1: A plot of $x(t)$ for the ODE (equation (1.2), blue line) and the solution of the DDE (equation (1.3)) for $h = \frac{1}{2}$ (green line) and $h = 1$ (red line) in example 1.2.1

for the DDE's are vastly different from the solution to the ODE.
One typical difference is that the solutions to the delay equation are not monotonic, as is the case for real ODE's. The green line (for $h = \frac{1}{2}$) oscillates around the asymptote of equation (1.2), slowly approaching the same limit, while the red line (for $h = 1$) does not have a limit value.

The delay differential equation of example (1.2.1) is a simple one. When there is more then one delay involved solving the DDE gets more complicated. Nonetheless theory for this kind of equation is well-developed. See for example [5] chapter 3 or [15] chapters 2 & 5 for existence and stability theorems. Also for more general delay equations exists a lot of theory, see for example Hale, [14], Hale and Verduyn Lunel [15] or Diekmann Et. Al. [7] for extensive studies.

One can rewrite the DDE in equation (1.1) in an integral form:

$$x = k * x + f \tag{1.4}$$

where $*$ denotes the convolution product: $x*y = \int_0^t x(s)y(t-s)ds$ and k & $f \in C(\mathbb{R}, \mathbb{R})$. Equivalence of these equations is proved in appendix (.1). Equation (1.4) is an example of a Volterra equation of the second kind. Volterra introduced this, and other integral equations in his famous papers from 1928 [25] and 1931 [26]. Most literature on equations of the form of equation (1.4) deals with a continuous f and a normalised k of bounded variation. One can see in appendix (.1) that these conditions are needed for equations (1.1 & 1.4) to be equivalent.
For a DDE is presented in the form used in equation (1.4) it is tempting to look at less strict conditions to k. We can for example look at equations of the form

$$x = dk * x + f \tag{1.5}$$

where dk is a Borel measure and the Borel convolution product is given by $dx * y = \int_0^t dx(s)y(t-s)$. This type of equation is called a Volterra-Stieltjes equation. This differential equation is named after the Stieltjes-measure it uses. More information on the Stieltjes-measure can be found in for example Tao [24]. An extensive overview on theory on Volterra-Stieltjes equations can be found in Salamon [22] and Gripenberg Et Al. [12]. Discontinuous delay equations were studied more recently in d'Albis [1] and Frasson [8].
Examples of DDE's in economics can be found in for example Frisch and Holme [9] and Johansen [18]. Examples of DDE's in population dynamics can be found in Gyllenberg [13] and Chapter 11 of Arino [3].

1.3 The Method of Steps

The method of steps is a method often used to find a solution for or prove existence of solutions of delay equations, for example in [5] or [7]. The method of steps gives a recursive way of calculating the solution. However it is mostly just used for proving existence of solutions, because calculating the actual solution often gets quite cumbersome. The reason for this exhaustiveness will be explained later in this section. In below example of the method of steps a certain form of the delay equation is assumed, but it works for more general delay equations.

Suppose we have a delay equation for time $t \in [0, \infty)$ and function $x \in C([-h, \infty), \mathbb{R})$ with the following form:

$$\begin{aligned} \frac{dx(t)}{dt} &= Ax(t) + Bx(t-h) \\ x(t) &= \varphi(t) \text{ for } t \in [-h, 0] \end{aligned} \tag{1.6}$$

where $\varphi : [-h, 0] \to \mathbb{R}$ and for some $h \in \mathbb{R}_+$. Note that the delay equation from example (1.2.1) is such a delay equation.
The function $x(t)$ is known for $t \in [-h, 0]$. So for $t \in [0, h]$ above delay equation can be written as:

$$\frac{dx(t)}{dt} = Ax(t) + B\varphi(t-h)$$

which is a inhomogeneous ordinary differential equation. This ODE is not to hard to solve. We are going to do this a little more general than needed for this example, because we're going to need this later in this thesis:

Let $x : \mathbb{C} \to \mathbb{C}^n$, $a : \mathbb{C} \to \mathbb{C}$ and $d : \mathbb{C} \to \mathbb{C}^n$ such that the following holds:

$$\begin{aligned} \frac{d}{dt}x(t) &= a(t)x(t) + d(t) \\ x(t_0) &= x_0 \end{aligned} \tag{1.7}$$

where $t_0 \in \mathbb{C}^n$ and $x_0 \in \mathbb{C}^n$. Equation (1.7) is called a first order linear inhomogeneous differential equation. The inhomogeneous term $d(t)$ is called the driving function.
We will construct a general solution to differential equation (1.7). Define $A : \mathbb{C} \to \mathbb{C}$ as:

$$A(t) := e^{-\int_{t_0}^{t} a(s)ds}$$

By multiplying (1.7) with $A(t)$ it can be rewritten to:

$$\frac{dA(t)x(t)}{dt} = A(t)d(t)$$

By integrating this equation from t to t_0 we find:

$$A(t)x(t) - x_0 = \int_{t_0}^{t} A(s)d(s)ds$$

where we used that $A(t_0) = 1$. If we divide this by $A(t)$ we find:

$$\begin{aligned} x(t) &= e^{\int_{t_0}^{t} a(s)ds}x_0 + e^{\int_{t_0}^{t} a(s)ds} \int_{t_0}^{t} e^{-\int_{t_0}^{s} a(u)du} d(s)ds \\ &= e^{\int_{t_0}^{t} a(s)ds}x_0 + \int_{t_0}^{t} e^{\int_{s}^{t} a(u)du} d(s)ds \end{aligned} \tag{1.8}$$

Which is an explicit formula for $x(t)$ and thus the desired result. This formula is often called the variation of constants formula.

We now have to prove that $x(t)$ is unique. Suppose there is an other function $y : \mathbb{C} \to \mathbb{C}^n$ such that equations (1.7) hold. We then find:

$$\begin{aligned} \frac{d}{dt}(x(t) - y(t)) &= a(t)(x(t) - y(t) \\ x(t_0) - y(t_0) &= 0 \end{aligned} \tag{1.9}$$

The only solution of this differential equation is $x(t) - y(t) = 0$, so $x(t) = y(t)$. Therefore we have that equation (1.8) is the unique solution of equation (1.7).

With this formula we found a solution for $x(t)$ with $t \in [0, h]$. Now we can proceed in the same way for $t \in [h, 2h]$ and so on. Hereby existence of a solution is proved and a recursive way of calculating $x(t)$ is given as well. This recursiveness is the reason that it's often hard to calculate $x(t)$ in general. Even calculating $x(t)$ for high t can cost a lot of time, since you have to do a new calculation for every step of length h.

Another typicality for delay equations is that $x(t)$ often can not be calculated for t smaller than the initial interval. This can also be explained with the method of steps. If one looks at the general delay equation

$$\begin{aligned}\frac{dx(t)}{dt} &= Ax(t) + Bx(t-h)\\ x(t) &= \varphi(t) \text{ for } t \in [-h, 0]\end{aligned}$$

We see that if $\varphi(t)$ is continuous, $x(t)$ will be differentiable for $t \in [0, h]$, is of class C^2 for $t \in [h, 2h]$ and so on. With this in mind, if a solution of this equation for $t \in [-2h, h]$ existed, $\varphi(t)$ would have to be differentiable. Since this is not in general the case, we find that $x(t)$ for $t \in [-2h, h]$ does not exist.

1.4 More Difference Delay Equations

Next to DDE's there are some other types of differential equations worth mentioning. In this section some of these equations will be summed up and compared to the definition of a DDE in equation (1.1).

When one looks at definition (1.1) it is natural to wonder about differential equations with a future dependence instead of a past one. These equations are less common in models of reality. One can think of models involving the prediction of the effect of an investment. Differential equations with both past and future dependence are called Mixed Difference Differential Equations (MFDE's). A MFDE can be described by:

$$\begin{aligned}\dot{x}(t) &= F(t, x(t), x(t+\theta), x(t+\gamma))\\ x(t) &= \varphi(t) \quad \text{ for } \; t \in [-r, 0]\end{aligned} \tag{1.10}$$

Where $t, x(t), \varphi(t)$ and F are defined as in equation (1.1), $\theta \in [-r, 0]$ and $\gamma \in [0, r]$. MFDE's are quite complicated differential equations, therefore not that many results on MFDE are known, but they are studied in for example Mallet-Paret and Verduyn Lunel [21] or d'Albis Et. Al. [2].

A type of differential equation that is sightly more general than a DDE is the NDDE. A NDDE can be described by:

$$\begin{aligned}\dot{x}(t) &= F(t, x(t), x_t, \dot{x}_t)\\ x(t) &= \varphi(t) \quad \forall\, t \in [-r, 0]\end{aligned} \tag{1.11}$$

Where again $t, x(t), \varphi(t)$ and F are defined as in equation (1.1). The most important difference between a DDE and a NDDE is that the history of the derivative of $x(t)$ influences the future of $x(t)$ as well. Theory on NDDE's is less developed than that on DDE's, but results can be found in Salamon [22] and also Hale and Verduyn Lunel [15].

Chapter 2

A Stuctured Metapopulation Model

2.1 Introduction to the model

2.1.1 The McKendrick-von Foerster Model

A well-known population model is the McKendrick-von Foerster model introduced first by McKendrick in 1925 [19] and then studied by von Foerster in 1959 [10]. This model can be described by the following equation for a population distribution $n : \mathbb{R}^2 \to \mathbb{R}$:

$$\frac{\partial}{\partial t}n(t,x) + \frac{\partial}{\partial x}n(t,x) = -\mu(x)n(t,x), \quad t \geq 0,\ 0 \leq x \leq \omega \tag{2.1}$$

where $t \in \mathbb{R}$ is time, $x \in \mathbb{R}$ is the structure parameter with a maximum value of ω and $\mu : \mathbb{R} \to \mathbb{R}$ is the death rate. We add equation (2.2a) as a boundary condition and equation (2.2b) as an initial condition:

$$n(t,0) = \int_0^\omega \beta(x)n(t,x)dx, \qquad t > 0 \tag{2.2a}$$

$$n(0,x) = \phi(x) \qquad x \geq 0 \tag{2.2b}$$

Where $\beta : \mathbb{R} \to \mathbb{R}$ is the birth rate and $\phi(x)$ is an initial function defining the structure-distribution at $t = 0$.

The structure parameter of the McKendrick-von Foerster model is a parameter adding structure to the distribution. For example in Dutch population the total number of people does not give you that much information. If one adds a structure through age or

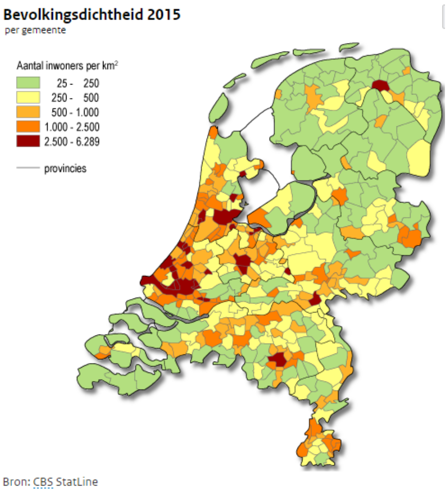

FIGURE 2.1: The population density of the Netherlands

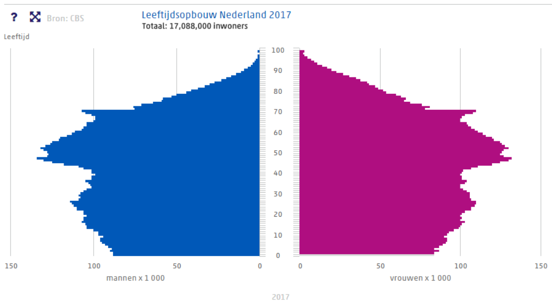

FIGURE 2.2: The population pyramide of the Netherlands.

the location of their house (as done in figures (2.1) & (2.2)) more can be said about the Dutch population.

In the McKendrick-von Foerster model the structure parameter can still represent different things. Often x is age, but the model also applies to for example length, population size or diameter.

The McKendrick-von Foester model is widely studied. One can check for example Webb [27] or Hoppensteadt [17] for a theoretical analysis of the McKendrick-von Foerster model or Keyfitz [20] for future population estimates based on the McKendrick-von Foerster model. A nonlinear version of this model can be found in Webb [27]

2.1.2 The Structured Metapopulation Model

The model we're going to look at a model that is quite similar to the McKendrick-von Foerster model introduced in the last subsection. In Gyllenberg [13] a more general model is proposed which adds the influence of immigration and emigration to the existing model. The extended model was studied by Hanski [16] and Diekmann, Getto & Gylenberg ([6], p. 1058). We will walk through the calculations that were done on this model in [6], because it helps to get understanding on delay equations.
Where the McKendrick-von Foerster model deals with a general structure parameter x, the model described in [6] is size-structured. This means we have a model existing of identical patches which support local populations and $x \in \mathbb{R}_{\geq 0}$ is the size of a local population. Catastrophes can happen on a patch which wipe out the local population, but the patches are immediately recolonised by immigrants.
The model on distribution $n : \mathbb{R} \times \mathbb{R}_{\geq 0} \to \mathbb{R}_{\geq 0}$ of populations at time $t \in \mathbb{R}$ with size x

is described by these equations:

$$\frac{\partial}{\partial t}n(t,x) + \frac{\partial}{\partial x}(f(x,D(t))n(t,x)) = -\mu(x)n(t,x) \quad t>0,\ x>0 \tag{2.3a}$$

$$f(0,D(t))n(t,0) = \int_{\mathbb{R}_+} \mu(x)n(t,x)dx, \quad t>0 \tag{2.3b}$$

$$\frac{d}{dt}D(t) = -(\alpha+\nu)D(t) + \int_{\mathbb{R}_+} \gamma(x)n(t,x)dx, \quad t>0 \tag{2.3c}$$

Equation (2.3b) is the boundary condition equivalent to equation (2.2a) in the McKendrick-von Foerster model. In these equations $D : \mathbb{R} \to \mathbb{R}_{\geq 0}$ the density of dispersers at time t, $\gamma : \mathbb{R}_{\geq 0} \to \mathbb{R}_{\geq 0}$ is the emigration rate defined by $\gamma(x) = k(x)x$ ($k : \mathbb{R}_{\geq 0} \to [0,1]$ is the per capita emigration rate), $\mu : \mathbb{R}_{\geq 0} \to [0,1]$ is the size-specific catastrophe rate of local populations, $\alpha \in \mathbb{R}_{\geq 0}$ is the rate at which dispersers immigrate into a patch and $\nu \in \mathbb{R}_{\geq 0}$ is the death rate during dispersal. $f : \mathbb{R}_{\geq 0} \times \mathbb{R}_{\geq 0} \to \mathbb{R}$ is the growth rate of a local population of size x when the density of dispersers is D. In this thesis we assume that $f(x,D)$ is given by:

$$f(x,D) := (r(x) - k(x))x + \alpha D \tag{2.4}$$

where $r : \mathbb{R}_{\geq 0} \to [-1,1]$ is the difference between the per capita birth and death rates when the population is of size x. The age $a \in \mathbb{R}_{\geq 0}$ of a local population is the time since the last catastrophe, so populations have size zero at time $t-a$. If we then write the size of a local population as a function of time $\tau \in [0,a]$ we find that equation (2.4) can be written as:

$$\begin{aligned} \frac{d}{d\tau}x(\tau) &= (r(x(\tau)) - k(x(\tau)))x(\tau) + \alpha D_t(\tau - a) \\ x(0) &= 0 \end{aligned} \tag{2.5}$$

where $D_t(\tau - a) := D(t+\tau-a)$ is written in this form, equivalent to the x_t notation of last chapter, for notational comfort. The following observation will be useful later on:

$$\frac{d}{d\tau}x(\tau) = f(x,D) \tag{2.6}$$

To complete the model we also need initial conditions for $n(t,x)$ and $D(t)$. We will assume the following general initial conditions:

$$D(t) := D_0(t) \qquad \text{for } t<0 \tag{2.7a}$$

$$n(t,x(\tau,a,D(t)) := n_0(t,x(\tau,a,D(t)) \qquad \text{for } t<0 \tag{2.7b}$$

where $D_0 : \mathbb{R} \to \mathbb{R}_{\geq 0}$ and $n_0 : \mathbb{R} \times \mathbb{R}_{\geq 0} \to \mathbb{R}_{\geq 0}$ are given functions. The second of these equations is equivalent to equation (2.2b) in the McKendrick-von Foerster model.

We can see that for $f(x, D) = 1$ equations ((2.3a) & (2.3b)) simplify to the McKendrick-von Foerster model. It should not come as a surprise that there are a lot of similarities between the techniques used for our model and the ones used for the McKendrick-von Foerster model. For example in section 1.2 of [27] one also encounters delay equations and the birth rate, which will be introduced in subsection 2.1.3.
This finishes the introduction to the model. The delay component of these equations can be found in the integrals in equations ((2.3b) & (2.3c)). That the delay component is contained in these terms, will become more transparent after manipulations postponed till section 2.1.3.

Throughout this chapter we will show several techniques used in [6]. To keep focus on the techniques and less on complicated calculations, we will make the assumptions that both r and k are constants (so $\gamma(x) = kx$).

Assumption 1: *The simplification we use is the assumption that r and k are constants.*

With this assumption we find that equation (2.5) can be written as:

$$\begin{aligned} \frac{d}{d\tau}x(\tau) &= (r-k)x(\tau) + \alpha D_t(\tau - a), \quad 0 \leq \tau \leq a \\ x(0) &= 0 \end{aligned} \tag{2.8}$$

This equation is a first order linear inhomogeneous differential equation. This type of differential equation can be solved via the method seen in section 1.3. If we use equation (1.8) for differential equation (2.8) we find an expression for $x(\tau, a, D_t)$:

$$x(\tau, a, D_t) = \alpha \int_0^\tau e^{(k-r)(\sigma-\tau)} D_t(\sigma - a) d\sigma \tag{2.9}$$

Even though equation (2.8) is a differential equation for x as a function of τ our solution for x depends on a and D_t as well. This because, as one can see in the solution of $x(\tau, a, D_t)$ implicitly is a function of these variables. Equation (2.9) is equivalent to equation (5.13) in [6].

We are going to work a lot with $x(a, a, D_t)$. This can be written into a more elegant form:

$$\begin{aligned} x(a, a, D_t) &= \alpha \int_0^a e^{(k-r)(\sigma-a)} D_t(\sigma - a) d\sigma \\ &= \alpha \int_0^a e^{-(k-r)\sigma} D(t - \sigma) d\sigma \end{aligned} \tag{2.10}$$

2.1.3 Introducing the Birth Rate $b(t)$

Now we got an explicit form for $x(\tau, a, D_t)$ we can continue solving equations (2.3a - 2.3c). We are going to rewrite them in a form to make our calculations easier. For this purpose we introduce the birth rate, $b(t)$.

As we can see from equation (5.14) from [6] the probability that a local population survives to age a is given by:

$$F(a) = e^{-\int_0^a \mu(x(\tau,a,D(t)))d\tau} \tag{2.11}$$

We introduce the birth rate:

$$b(t) := f(0, D(t))n(t, 0) \tag{2.12}$$

The initial condition for $b(t)$ follows from equations (2.6, 2.7 & 2.12):

$$b(t) = \alpha D(t)n(t, 0) \quad t < 0 \tag{2.13}$$

we will denote this with $b_0(t) := \alpha D_0(t)n_0(t, 0)$ for $t < 0$ to stress that this function is given. We can now express the size-distribution of the population in terms of D and $b(t)$ as follows:

$$f(x, D(t))\, n(t, x) = F(a)b(t - a) = e^{-\int_0^a \mu(x(\tau,a,D(t)))d\tau} b_t(-a), \quad 0 \leq t,\, 0 \leq a$$

where $b_t(-a) = b(t - a)$.

Using equation (2.6) we obtain the following expression for $n(t, x)dx$:

$$n(t, x)dx = e^{-\int_0^a \mu(x(\tau,a,D(t)))d\tau} b_t(-a)da \tag{2.14}$$

Rewriting equation (2.3a) & (2.3c) using (2.12) & (2.14), yields the following equations:

$$b(t) = \int_0^\infty \mu(x(a, a, D(t)))e^{-\int_0^a \mu(x(\tau,a,D(t)))d\tau} b_t(-a)da, \tag{2.15a}$$

$$\frac{d}{dt}D(t) = -(\alpha + \nu)D(t) + k \int_0^\infty x(a, a, D_t)e^{-\int_0^a \mu(x(\tau,a,D(t)))d\tau} b_t(-a)da, \tag{2.15b}$$

The above expressions are similar to equations (5.20) & (5.21) in [6]. These equations are now written as integral equations. We can see the delay in these equations in the $b_t(-a)$ $(= b(t - a))$ term as well as in the term $D(t)$, which picks up a delay in equation

(2.9). We will analyse the stability of solutions for constant μ (section 2.2) and for linear μ (section 2.3).

2.2 Case 1: Constant $\mu(x)$

2.2.1 Model for constant $\mu(x)$

In this section we simplify equations (2.15a & 2.15b) by taking μ to be a constant function. In this case we find an explicit formula for $b(t)$. For $D(t)$ it is possible to prove the existence and uniqueness of a solution, to formulate conditions for a steady state to exist and conditions for these conditions to be stable.

We simplify further by taking μ to be a constant function.

With these assumptions equations (2.15a & 2.15b) simplify to:

$$b(t) = \int_0^\infty \mu e^{-\mu a} b_t(-a)da, \tag{2.16a}$$

$$\frac{d}{dt}D(t) = -(\alpha+\nu)D(t) + k\int_0^\infty x(a,a,D_t)e^{-\mu a}b_t(-a)da, \tag{2.16b}$$

With this assumption on μ not every initial condition on $b(t)$ and $D(t)$ is allowed. We can see in equation (2.16a) that $b_0(-t)$ should grow slower than $e^{\mu t}$ for the integral to be smaller than infinity. From equation (2.16b) we find that $D(-t)$ should grow slower than $e^{(\mu+r-k)}O(b(-t))$. We will assume both $b_0(t)$ and $D_0(t)$ obey these conditions.
In practice these conditions are often satisfied since populations never have an infinity history. So for many application there exists a t' such that $b(t) = 0$ for $t < t'$ and $D(t) = 0$ for $t < t'$.

2.2.2 Find an expression for $b(t)$

Equation (2.16a) is autonomous and linear in $b(t)$. Therefore we can solve this delay differential equations by taking the Laplace transform. This solution will then be used in the analysis of equation (2.16b).

To be able to calculate the Laplace transform we first need to rewrite this equation. When we write:

$$b(t) = \mu\int_0^t e^{-\mu a}b(t-a)da + \mu\int_t^\infty e^{-\mu a}b(t-a)da \tag{2.17}$$

we can recognise a convolution in the first term on the right. It is well-known that the Laplace transform of this is the product of the Laplace transforms of both convoluted terms.
The second term is dependent on $b(t)$ for $t < 0$, so we use $b_0(t)$ defined in equation (2.13). By plugging this into equation (2.17) we get:

$$\begin{aligned} b(t) &= \mu e^{-\mu t} * b(t) + \mu \int_t^{\infty} e^{-\mu a} b_0(t-a)da \\ &= \mu e^{-\mu t} * b(t) + \mu \int_0^{\infty} e^{-\mu(t+a)} b_0(-a)da \\ &= \mu e^{-\mu t} * b(t) + \mu m_b e^{-\mu t} \end{aligned} \tag{2.18}$$

Here we defined the constant m_b as:

$$m_b := \int_0^{\infty} e^{-\mu a} b_0(-a)da \tag{2.19}$$

By applying the Laplace transformation to equation (2.18) we can find an expression for $b(t)$:

$$\hat{b}(\lambda) = \frac{\mu}{\mu+\lambda}\hat{b}(\lambda) + \frac{\mu m_b}{\mu+\lambda}$$

or, simplified:

$$\hat{b}(\lambda) = \frac{\mu m_b}{\lambda} \tag{2.20}$$

So we obtain:

$$b(t) = \mu m_b$$

We have found the following formula for $b(t)$:

$$b(t) = \begin{cases} \mu \int_0^{\infty} e^{-\mu a} b_0(-a)da & \text{if } t \geq 0 \\ b_0(t) & \text{if } t < 0 \end{cases} \tag{2.21}$$

We see that $b(t)$ is independent of t for $t \geq 0$.

2.2.3 Existence and Uniqueness of $D(t)$ in equation (2.16b)

We can now use this formula for $b(t)$ to take on equation (2.16b), which can now be written as:

$$\frac{d}{dt}D(t) = -(\alpha+\nu)D(t) + k\int_0^{\infty} x(a,a,D_t)e^{-\mu a} b(t-a)da \tag{2.22}$$

This delay differential equation is non-autonomous, due to the term $b(t-a)$ which depends on t for $t \in [-a, 0]$. Because of this dependency equation (2.22) is not solvable with the Laplace transformation method we used for equation (2.16a).

We can however prove existence and uniqueness of a solution of equation (2.22) via a contraction mapping theorem. This is done for more general delay equations in [15] (Ch. 2). We will prove it ourselves here, since the prove is insightful in delay equations. We will use the theorem stated in Arnold ([4], corollary of section 31.8):

Theorem 1. (Contraction Mapping Theorem)
Suppose $t \in \mathbb{R}$, $x \in C(\mathbb{R}, \mathbb{R}^n)$ and $v : C(\mathbb{R}, \mathbb{R}^n) \times \mathbb{R} \to C(\mathbb{R}, \mathbb{R}^n)$, where $v(x,t)$ is a contraction on the domain $[x_0, x(t_0+\epsilon)] \times [t_0, t_0+\epsilon]$ near the point (x_0, t_0) and for a $\epsilon > 0$. Then the differential equation:

$$\frac{dx(t)}{dt} = v(x(t), t)$$

has a unique solution $\phi(t)$ passing through (x_0, t_0) for $t \in [t_0, t_0+\epsilon)$.

If we prove that $F(D(t), t)$ is a contraction for

$$F(D(t),t) = -(\alpha+\nu)D(t) + k\int_0^\infty x(a,a,D_t)e^{-\mu a}b(t-a)da \tag{2.23}$$

we have that equation (2.22) has a solution for $t \in (-\infty, \epsilon)$ for some $\epsilon > 0$. To prove that $F(D(t), t)$ defined by equation (2.23) is in fact a contraction we have to show that $\|F(D_1(t), t) - F(D_2(t), t)\| \leq k\|D_1(t) - D_2(t)\|$ for some $0 \leq k < 1$.

First we write:

$$\begin{aligned}
F(D(t),t) &= -(\alpha+\nu)D(t) + \alpha k\int_0^\infty e^{-\mu a}b(t-a)\int_0^a e^{-(k-r)\sigma}D(t-\sigma)d\sigma da \\
&= -(\alpha+\nu)D(t) + \alpha k b'\int_0^t e^{-\mu a}\int_0^a e^{-(k-r)\sigma}D(t-\sigma)d\sigma da \\
&+ \alpha k\int_0^\infty e^{-\mu(a+t)}b_0(-a)\int_0^{a+t} e^{-(k-r)\sigma}D(t-\sigma)d\sigma da \\
&= -(\alpha+\nu)D(t) + \alpha k b'\int_0^t e^{-\mu a}\int_0^a e^{-(k-r)\sigma}D(t-\sigma)d\sigma da \\
&+ \alpha k\int_0^\infty e^{-\mu(a+t)}b_0(-a)\int_0^t e^{-(k-r)\sigma}D(t-\sigma)d\sigma da \\
&+ \alpha k\int_0^\infty e^{-\mu(a+t)}b_0(-a)\int_0^a e^{-(k-r)(\sigma+t)}D_0(-\sigma)d\sigma da
\end{aligned}$$

where we defined $\overline{b}' = \mu\int_0^\infty e^{-\mu a}b_0(-a)da$ for the constant solution of $b(t)$ for $t > 0$ and used equation (2.22) for $x(a, a, D_t)$. If we now write the constant m_b as in (2.19) and the constant $m_{D'}$ as:

$$m_{D'} = \int_0^\infty e^{-\mu a}b_0(-a)\int_0^a e^{-(k-r)\sigma}D_0(-\sigma)d\sigma da$$

we obtain the form:

$$F(D(t),t) = -(\alpha+\nu)D(t) + \alpha k b' \int_0^t e^{-\mu a} \int_0^a e^{-(k-r)\sigma} D(t-\sigma) d\sigma da$$
$$+ \alpha k m_b e^{-\mu t} b_0(-a) \int_0^t e^{-(k-r)\sigma} D(t-\sigma) d\sigma + \alpha k m_{D'} e^{-(\mu+k-r)t}$$

Notice that the fourth term is a constant. Therefore we can write:

$$F(D_1(t),t) - F(D_2(t),t) = \alpha k b' \int_0^t e^{-\mu a} \int_0^a e^{-(k-r)\sigma} (D_1(t-\sigma) - D_2(t-\sigma)) d\sigma da$$
$$+ \alpha k m_b e^{-\mu t} b_0(-a) \int_0^t e^{-(k-r)\sigma} (D_1(t-\sigma) - D_2(t-\sigma)) d\sigma - (\alpha+\nu)(D_1(t) - D_2(t)) \tag{2.24}$$

To be able to prove that $F(D(t),t)$ is in fact a contraction for all $t > 0$ we will use a trick called exponential scaling. We are going to need a norm to use theorem (1). We haven't chosen a norm for the state space of $D(t)$ yet, so we can allow ourselves some freedom by introducing the following norm:

$$\|x\|_\lambda = \sup_{t\in\mathbb{R}} |e^{-\lambda t} x(t)|$$

where we can still choose a λ. If there exists a λ such that $F(D(t),t)$ is a contraction with respect to the norm $\|x\|_\lambda$ we can use theorem (1) to prove existence and uniqueness of the solution of equation (2.22).
Note that this norm is only well-defined if for some $t' < 0$ we have that $x(t) = 0$ for $t < t'$. We define $C_0 := \{x(t) \in C(\mathbb{R},\mathbb{R}) : \exists t' : D(t) = 0 \text{ for } t < t'\}$. As noted at the end of subsection 2.2.1 this is in practice a very reasonable restriction. For example in population dynamics this would mean that populations can't have been around for an infinite amount of time.
By applying this norm to equation (2.24) we get:

$$\|F(D_1(t),t) - F(D_2(t),t)\|_\lambda = \sup_{t\in\mathbb{R}} |e^{-\lambda t}(\alpha k b' \int_0^t e^{-\mu a} \int_0^a e^{-(k-r)\sigma} (D_1(t-\sigma) - D_2(t-\sigma)) d\sigma da$$
$$+ \alpha k m_b e^{-\mu t} b_0(-a) \int_0^t e^{-(k-r)\sigma} (D_1(t-\sigma) - D_2(t-\sigma)) d\sigma - (\alpha+\nu)(D_1(t) - D_2(t)))|$$
$$\leq \sup_{t\in\mathbb{R}} |\alpha k b' \int_0^t e^{-\mu a} \int_0^a e^{-\lambda\sigma} e^{-(k-r)\sigma} e^{-\lambda(t-\sigma)} (D_1(t-\sigma) - D_2(t-\sigma)) d\sigma da|$$
$$+ \sup_{t\in\mathbb{R}} |\alpha k m_b e^{-\mu t} b_0(-a) \int_0^t e^{-\lambda\sigma} e^{-(k-r)\sigma} e^{-\lambda(t-\sigma)} (D_1(t-\sigma) - D_2(t-\sigma)) d\sigma|$$
$$\leq \sup_{t\in\mathbb{R}} |\alpha k b' \int_0^t e^{-\mu a} \int_0^a e^{-\lambda\sigma} e^{-(k-r)\sigma} d\sigma da| \sup_{t\in\mathbb{R}} |e^{-\lambda(t-\sigma)} (D_1(t-\sigma) - D_2(t-\sigma))|$$
$$+ \sup_{t\in\mathbb{R}} |\alpha k m_b e^{-\mu t} b_0(-a) \int_0^t e^{-\lambda\sigma} e^{-(k-r)\sigma} d\sigma| \sup_{t\in\mathbb{R}} |e^{-\lambda(t-\sigma)} (D_1(t-\sigma) - D_2(t-\sigma))|$$

We obtain:

$$\|F(D_1(t),t)-F(D_2(t),t)\| \leq (\sup_{t\in\mathbb{R}}|\alpha k b'\int_0^t e^{-\mu a}\int_0^a e^{-\lambda\sigma}e^{-(k-r)\sigma}d\sigma da| \\ +\sup_{t\in\mathbb{R}}|\alpha k m_b e^{-\mu t}b_0(-a)\int_0^t e^{-\lambda\sigma}e^{-(k-r)\sigma}d\sigma|)\|D_1(t)-D_2(t)\| \tag{2.25}$$

Both terms in front of $\|D_1(t)-D_2(t)\|$ can be made arbitrarily small by choosing big λ. So $F(D(t),t)$ is a contraction on $C_0 \times \mathbb{R}$.

Using theorem (1) we conclude that equation (2.22) has a solution if the initial disperser density does not have an infinite history.

2.2.4 Existence of a Steady State Solutions for (2.22)

Even though we are not able to solve equation (2.16b) in general, we can say some things about its solutions and their stability. It is possible to formulate a condition for the existence of a steady state for (2.16b). We can also find criteria for that steady state solution to be stable. In this subsection we will find the steady state condition, the criteria for stability can be found in subsection 2.2.6.

For our steady state solution we also have to find a steady state for $b(t)$, due to the coupling of equations (2.16a) & (2.16b). We will call such a stead state $\bar{b}$ and equivalently the steady state of $D(t)$ will be called $\overline{D}$. To find $\bar{b}$ we revisit equation (2.21). If we fill in any constant $\bar{b}$ equation (2.21) becomes an identity. This implies that we can always find a steady state for $b(t)$ and thus we can choose a value for $\bar{b}$. It is a natural choice to take:

$$\bar{b} = \mu \tag{2.26}$$

Using this in equation (2.22) to find a steady state condition we obtain:

$$\alpha + \nu = \frac{\alpha k}{\mu + k - r} \tag{2.27}$$

As we can see this is no restriction on $\overline{D}$. Again we are free to choose our steady state. However, since the choice we make here does not influence the outcome of our stability analysis, we will keep working with $\overline{D}$.
So we can always find a steady state for $b(t)$. If we choose this te be $\bar{b} = \mu$ and we then find that $\alpha + \nu = \frac{\alpha k}{\mu+k-r}$ holds, there exist a steady state for $D(t)$ as well..

2.2.5 The Fréchet Derivative

Now that we found conditions for the existence of the steady state for equation (2.22) we want to say something about the stability of this steady state. To discuss the stability of the steady states we have to linearise it around the steady state and solve the linearised formula. To do so we are going to determine the derivative of $x(a, a, \psi)$ with respect to ψ at D_t; $\frac{\partial x(a,a,D_t)}{\partial \psi} \circ \psi$. This will not be a function, but an operator acting on the state space of $x(\tau, a, D_t)$. We expect our result to match equation (5.27) in [6].

Since $x(\tau, a, D_t)$ is not a function of one variable we need to use the more general notion of the Fréchet derivative instead of the ordinary derivative. The Fréchet derivative is a generalisation of the usual derivative. When we are working with real-valued, one variable functions the derivative of a function at a point is usually interpreted as a slope. Since we are working with operators instead of one-variable functions, we need a more general understanding of the derivative. We will use the definition as it can be found in Lebedev and Vorovich ([23], p. 177).

Definition 1. (The Fréchet Derivative) Let X & Y be Banach spaces and $F : X \to Y$ be an operator. $F(x)$ is Fréchet differentiable at $x_0 \in X$ if there is a bounded operator $A \in L(X, L(X, Y))$, such that:

$$F(x_0 + h) - F(x_0) = A(x_0) \circ h + \omega(x_0, h) \quad \forall ||h|| < \epsilon$$

for some $\epsilon > 0$, where $h \in X$ and $\frac{||\omega(x_0,h)||}{||h||} \to 0$ as $h \to 0$. We call $A(x_0)$ the Fréchet derivative of F at x_0, which we denote by $DF(x_0)$.

Note that $DF(x_0)$ is an operator working on X. To take the derivative in x_0 in the direction of h one calculates $DF(x_0) \circ h$, which is a function in Y. It is clear that the Fréchet derivative of a continuous linear operator T is the operator T itself, or in notation of the definition of the Fréchet derivative: $DF(x_0) \circ h = F(h)$.

To get more familiar with the Fréchet derivative, we will continue with an example:

Example 2.2.1. Let $x \in \mathbb{C}^n$, $u \in X := C(\mathbb{C}^n, \mathbb{C}^n)$ and $T : X \to \mathbb{R}_{\geq 0}$ be defined by

$$(Tu)(x) = \|u(x)\|^2$$

Than we have for any $h \in X$:

$$(Tu)(x + h) - (Tu)(x) = u(x) \cdot h^T(x) + h(x) \cdot u^T(x) + \|h(x)\|^2$$

where $u(x)v(x)$ denotes the dot-product. Since we have $\frac{||h(x)||^2}{||h(x)||} \to 0$ as $h \to 0$, we can identify this term with $\omega(x_0, h)$ from Definition 1. The other terms on the right side of above equation are linear in $h(x)$ and are thereby no part of $\omega(x_0, h)$. From this we can conclude that:

$$DT(u(x)) \circ h(x) = u(x) \cdot h^T(x) + h(x) \cdot u^T(x)$$

So this is the Fréchet derivative of T at u in direction $h(x)$.

A more complicated example of the Frechet derivative can be found in subsection 2.3.3.

We can interpret $x(\tau, a, D_t)$ from in equation (2.9) as an operator. Then the Fréchet derivative of $x(\tau, a, \psi)$ with respect to ψ is found to be:

$$\frac{\partial x(\tau, a, \psi)}{\partial \psi} \circ h(t) = \alpha \int_0^\tau e^{-(k-r)\sigma} h(t-\sigma) d\sigma \tag{2.28}$$

When we apply our simplifications to (5.27) in [6], we find the same results.

2.2.6 Stability of the Steady States

Now we are ready to linearise equation (2.16b). If we assume our steady state conditions, equations (2.26) & (2.27), hold and use (2.28) we can linearise around $\overline{D}$. Defining $\psi : \mathbb{R} \to \mathbb{R}_{\geq 0}$ as:

$$\psi(t) = \overline{D} - D(t) \tag{2.29}$$

with $|\psi(t)| \ll 1$ we find:

$$\begin{aligned} \frac{d}{dt}\psi(t) = -(\alpha+\nu)\psi(t) + k \int_0^\infty x(a, a, \overline{D}) e^{-\mu a} b(t-a) da \\ + \alpha k \mu \int_0^\infty e^{-\mu a} \int_0^a e^{-(k-r)a} \psi(t-a) da \end{aligned}$$

If we take the Laplace transform of this equations we get:

$$\begin{aligned} \lambda \hat{\psi}(\lambda) - \psi(0) = -(\alpha+\nu)\hat{\psi}(\lambda) + \frac{\alpha k \overline{D}(\hat{b}(\lambda) + m_{b'})}{\lambda + \mu + k - r} \\ + \frac{\alpha k \mu (\hat{\psi}(\lambda) + m_D)}{\lambda + \mu + k - r} \end{aligned}$$

Here we defined the constants:

$$\begin{aligned} m_{b'} &:= \int_0^\infty e^{-(\mu+k-r)a} b_0(-a) da \\ m_D &:= \int_0^\infty e^{-(\mu+k-r)a} D_0(-a) da \end{aligned}$$

took $\lambda \in \mathbb{C}$ and we assumed $\mathrm{Re}(\lambda) > -(\mu + k - r)$. We know from equation (2.20) that $\hat{b}(\lambda) = \frac{\mu m_b}{\lambda}$. So we find the characteristic equation:

$$(\lambda + \mu + k - r)(\lambda + \alpha + \nu) - \alpha k \mu = 0$$

Or, when we apply our steady state condition (2.27):

$$\lambda^2 + (\alpha + \nu + \mu + k - r)\lambda + \alpha k(1 - \mu) = 0 \tag{2.30}$$

We can solve this equation explicitly for λ, but since we're only interested in the stability of the solutions of equations (2.16a) & (2.16b) there are more efficient methods. We can find criteria sufficient for stability from the quadratic formula. But to give a method that works for polynomals of higher grade I will use the Routh-Hurwitz stability criterion. I will only state the Routh-Hurwitz stability criterion for polynomial of degrees two and three. The general theorem can be found in Gantmacher ([11], Vol 2, page 194).

Theorem 1. (Routh-Hurwitz Stability Criterion for Polynomial of Degree Two)
Given the polynomial $P(x) = a_2x^2 + a_1x + a_0$ where $a_i \in \mathbb{R}\,\forall\, i$ and $a_2 > 0$. Then the roots of polynomial $P(x)$ have negative real part if $a_n > 0\,\forall\, n$.

(Routh-Hurwitz Stability Criterion for Polynomial of Degree Three)
Given the polynomial $P(x) = a_3x^3 + a_2x^2 + a_1x + a_0$ where $a_i \in \mathbb{R}\,\forall\, i$ and $a_3 > 0$. Then the roots of polynomial $P(x)$ have negative real part if $a_n > 0\,\forall\, n$ and $a_2a_1 > a_3a_0$.

We see that the Routh-Hurwitz stability criterion applied to equation (2.30) gives us the following inequalities to guarantee a stable solution to equations (2.16a) & (2.16b):

$$\alpha + \nu + \mu + k > r$$
$$\alpha k(1 - \mu) > 0$$

Earlier we also had to make some assumptions to get to these criteria. We're going to sum up all our assumptions before we're going to see which ones aren't redundant. First we have the criterion which guarantees a steady state for $D(t)$ exists: $(\alpha+\nu)(\mu+k-r) = \alpha k$. Next we also assumed that $\mathrm{Re}(\lambda) > -(\mu + k - r)$.

If use this last assumption and our steady state condition it becomes equivalent to $\mu > 0$, which is per definition true. We also have that $\alpha > 0$ and $k > 0$, so our second Routh-Hurwitz stability criterion simplifies to $1 > \mu$, which also is per definition true. Since $(\alpha + \nu) > 0$ and $\alpha k > 0$ our steady state condition implies that $\mu + k - r > 0$. So our first Routh-Hurwitz stability criterion can be simplified as well.

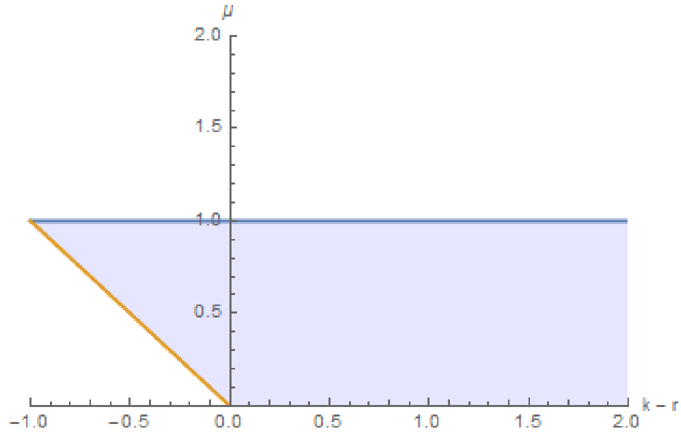

FIGURE 2.3: $(k-r)$ and μ in one plot. The filled area is the stable area for our model

We can see that in the model described by equations (2.3a - 2.3c) with the assumptions that $r(x)$, $k(x)$ and $\mu(x)$ are constants has a steady state solution if $(\alpha+\nu)(\mu+k-r) = \alpha k$ with $n(t,x)$ still undetermined. If we then choose $\bar{b} = \mu$ and $\mu > -(k-r)$ holds, then this solution is stable. For $k > r$ the conditions on μ are per definition satisfied, since $0 < \mu < 1$. This can be seen graphically in figure 2.3.

To interpret the inequalities we reminisce the definition of the variables in them. We have that r is the difference between the per capita birth and death rates, which can be called the net. birth rate, k is the per capita emigration rate and μ is the size-specific catastrophe rate of local populations.
So we find that if the net. birth rate is smaller than the emigration rate, we have a stable steady state. If the net. birth rate is bigger then the emigration rate, but smaller than the emigration rate summed with the catastrophe rate, then the steady state is also stable, but in other cases the steady state is not. Apparently the growth of the local populations has to be bounded by phenomena like emigration and catastrophes for the populations to be stable.

A remarkable thing about these relatively simple criterion's is that they are independent of the initial conditions.

In this section we've seen some ways to analyse the delay equation we started with. We've explicitly solved the equation for the birth rate $b(t)$ and analysed the existence and stability of the steady state of the disperser density.

2.3 Case 2: Linear $\mu(x)$

2.3.1 Model for linear $\mu(x)$

We've seen several techniques in solving and analysing delay equations in our analysis with constant μ. To be able to show some more of the techniques used in [6] we're now going to look at the same equations, but with the assumption that $\mu(x)$ is linear in x. With these assumptions our system of equations isn't linear in $b(t)$ and $D(t)$ anymore. This will give us room to explore the techniques discussed in [6] in more depth. So:

We will simplify by assuming that $\mu(x)$ is linear in x, so $\mu(x) = \mu x$.

To be clear, we will still work with constant r and k. As seen in [6] (5.16) equation (2.11) now becomes:

$$F(a) = e^{-\int_0^a \mu x(\tau,a,D(t))d\tau} \tag{2.32}$$

Using this, definition (2.12) and equation (2.14), we find that equations (2.3b - 2.3c) simplify to:

$$b(t) = \mu \int_0^\infty x(a,a,D_t)\, e^{-\int_0^a \mu x(\tau,a,D(t))d\tau}\, b(t-a)da, \tag{2.33a}$$

$$\frac{d}{dt}D(t) = -(\alpha+\nu)D(t) + k\int_0^\infty x(a,a,D_t)\, e^{-\int_0^a \mu x(\tau,a,D(t))d\tau}\, b(t-a)da, \tag{2.33b}$$

It is easy to see that our calculations for the explicit formula for $x(\tau, a, D_t)$ still hold, so we can still use equation (2.9). We will again use the initial conditions introduced in equation (2.7).

To analyse the differential equations (2.33a - 2.33b) we are going to use the same technique as we did in the case where $\mu(x)$ was a constant. First we're going to find conditions for a steady state solution of equations (2.33a - 2.33b). Then, to prove stability we linearise the differential equations around steady state solutions for $b(t)$ and $D(t)$ and solve the resulting equations. To linearise equations (2.33a - 2.33b) we first need to find the steady states $\overline{b}$ and $\overline{D}$ (or conditions for these to exist) and the derivatives $\frac{dx(a,a,\overline{D})}{d\psi}\psi$ and $\frac{de^{-\int_0^a x(\tau,a,\overline{D})d\tau}}{d\psi}\psi$.

2.3.2 Existence of Steady States for equations (2.33a) and (2.33b)

We want to find the steady state conditions for equations (2.33a) & (2.33b). As we can see in [6] (5.22) for constant $b(t)$ and $D(t)$ equation (2.33a) becomes an identity:

$$\mu \int_0^\infty x(a,a,\overline{D})\, e^{-\int_0^a \mu x(\tau,a,\overline{D})d\tau} da = 1 \tag{2.34}$$

This identity reflects the conservation of local populations: After a catastrophe, the patch is immediately recolonised. Over the whole collection of patches there is no net immigration. If we choose to normalise the amount of patches to 1, the only contribution to the size of our system is the birth- and death rates. We then get an explicit expression for our steady state:

$$\bar{b} = \frac{1}{\int_0^\infty e^{-\int_0^a \mu x(\tau,a,\overline{D})d\tau} da} \tag{2.35}$$

We can use equation (2.9) to explicitly calculate $\bar{b}$:

$$\begin{aligned}
\bar{b}^{-1} &= \int_0^\infty e^{-\int_0^a \mu\alpha \int_0^\tau e^{(k-r)(\sigma-\tau)}\overline{D}d\sigma d\tau} da \\
&= \int_0^\infty e^{\frac{\mu\alpha\overline{D}}{r-k}\int_0^a 1-e^{(r-k)\sigma}d\tau} da \\
&= \int_0^\infty e^{\frac{\mu\alpha\overline{D}}{r-k}(a-\frac{e^{(r-k)a}-1}{r-k})} da
\end{aligned}$$

This integral can with the help of Mathematica be written into the following explicit form:

$$\bar{b}^{-1} = (r-k)^{-1}(\frac{(r-k)^2}{-\mu\alpha\overline{D}e})^{\frac{\mu\alpha\overline{D}}{(r-k)^2}} \int_{\frac{-\mu\alpha\overline{D}}{(r-k)^2}}^0 t^{\frac{\mu\alpha\overline{D}}{(r-k)^2}-1} e^{-t} dt \tag{2.36}$$

For $k > r$ and $\mu\alpha\overline{D} > 0$. The latter is true as long as all the variables involved are non-zero. As one can see equation (2.36) isn't the nicest formula, but we can determine it's value with the help of Mathematica. In the rest of this section we're going to keep writing $\bar{b}$. The conditions needed for equation (2.36) to hold aren't relevant for the rest of our calculations, since we could always choose a different value for $\bar{b}$ then we did in equation (2.35). Nevertheless it is nice to have an expression for this $\bar{b}$ since the normalisation we did to get this expression is quite a common one.

The steady state condition for $\overline{D}$ is:

$$\overline{D} = \frac{\mu k \bar{b}}{\alpha+\nu} \int_0^\infty x(a,a,\overline{D}) e^{-\int_0^a \mu x(\tau,a,\overline{D})d\tau} da$$

This gets simplified a lot if we use (2.34):

$$\overline{D} = \frac{k\bar{b}}{\alpha + \nu} \tag{2.37}$$

2.3.3 The Fréchet Derivative

For our linearisation we need to find the derivatives $\frac{dx(a,a,\overline{D})}{d\psi}\psi$ and $\frac{de^{-\int_0^a x(\tau,a,\overline{D})d\tau}}{d\psi}\psi$. It is obvious that the change in the assumption on $\mu(x)$ has no influence on $\frac{dx(a,a,\overline{D})}{d\psi}\psi$, so this derivative is still given in equation (2.28) It is different however that we now also have to find $\frac{de^{-\int_0^a x(\tau,a,\overline{D})d\tau}}{d\psi}\psi$. We're going to find this derivative by using definition 1, which can be found in subsection 2.2.5.

Define

$$F(D_t) := e^{-\int_0^a \mu x(\tau,a,D_t)d\tau}$$

Then:

$$\begin{aligned}
F(\overline{D}+\psi) - F(\overline{D}) &= e^{-\int_0^a \mu x(\tau,a,\overline{D}+\psi)d\tau} - e^{-\int_0^a \mu x(\tau,a,\overline{D})d\tau} \\
&= \sum_{i=0}^{\infty} \frac{(-\int_0^a \mu x(\tau,a,\overline{D}+\psi)d\tau)^i}{i!} - \sum_{i=0}^{\infty} \frac{(-\int_0^a \mu x(\tau,a,\overline{D})d\tau)^i}{i!} \\
&= \sum_{i=0}^{\infty} \frac{(-\mu\int_0^a x(\tau,a,\overline{D})d\tau - \mu\int_0^a x(\tau,a,\psi)d\tau)^i}{i!} \\
&- \sum_{i=0}^{\infty} \frac{(-\int_0^a \mu x(\tau,a,\overline{D})d\tau)^i}{i!} \\
&= \sum_{i=0}^{\infty} \frac{-\mu i(\int_0^a x(\tau,a,\psi)d\tau)(-\mu\int_0^a x(\tau,a,\overline{D})d\tau)^{i-1}}{i!} + O(\psi^2) \\
&= -\mu e^{-\int_0^a \mu x(\tau,a,\overline{D})d\tau} \int_0^a x(\tau,a,\psi)d\tau + O(\psi^2)
\end{aligned}$$

And as we can see in definition (1) this implies that:

$$\frac{de^{-\int_0^a x(\tau,a,\overline{D})d\tau}}{d\psi}\psi = -\mu e^{-\int_0^a \mu x(\tau,a,\overline{D})d\tau} \int_0^a x(\tau,a,\psi)d\tau \tag{2.38}$$

Now that we have found $\frac{de^{-\int_0^a x(\tau,a,\overline{D})d\tau}}{d\psi}\psi$ there is still one issue to address with respect to the Fréchet derivative. We should mention one property of the Fr échet derivative that we will use without prove: The Fréchet derivative obeys the Leibniz rule for derivatives.

2.3.4 Stability of the Steady States

Now that we've got our steady states (2.35 & 2.37) and both derivatives (2.28 & 2.38) we can linearise equations (2.33a & 2.33b). If we define $\psi(t)$ as in equation (2.29) and also define $\varphi : \mathbb{R} \to \mathbb{R}_{\geq 0}$ as:

$$\varphi(t) = \bar{b} - b(t)$$

with $|\varphi(t)| \ll 1$ we find:

$$\varphi(t) = \mu \int_0^\infty x(a, a, \overline{D})\, e^{-\int_0^a \mu x(\tau, a, \overline{D}) d\tau}\, \varphi(t-a) da, \tag{2.39}$$

$$\begin{aligned} \frac{d}{dt}\psi(t) = &-(\alpha+\nu)\psi(t) + k \int_0^\infty x(a, a, \overline{D})\, e^{-\int_0^a \mu x(\tau, a, \overline{D}) d\tau}\, \varphi(t-a) da \\ &+ k\bar{b}\alpha \int_0^\infty e^{-\int_0^a \mu x(\tau, a, \overline{D}) d\tau} \int_0^a e^{-(k-r)\sigma} \psi(t-\sigma) d\sigma\, da \\ &- \alpha\mu k\bar{b} \int_0^\infty x(a, a, \overline{D})\, e^{-\int_0^a \mu x(\tau, a, \overline{D}) d\tau} \int_0^a \int_0^\tau e^{-(k-r)\sigma} \psi(t-\sigma) d\sigma d\tau da \end{aligned} \tag{2.40}$$

When taking the Laplace transform of these equations one will find the following equations for $\hat{b}(\lambda)$ and $\hat{D}(\lambda)$.

$$\hat{\varphi}(\lambda) = \frac{\mu\hat{\beta}(\lambda)}{1 - \mu\alpha(a)}, \tag{2.41a}$$

$$\begin{aligned} \lambda\hat{\psi}(\lambda) - \psi(0) = &-(\alpha+\nu)\hat{\psi}(\lambda) + k(\alpha(a)\hat{\psi}(\lambda) + \hat{\beta}(\lambda) + \alpha k\bar{b}(\frac{\hat{\gamma}(\lambda)\hat{\psi}(\lambda)}{\lambda+k-r} + \hat{A}(\lambda, \hat{\psi}(\lambda)) + \hat{\delta}(\lambda)) \\ &- \alpha\mu k\bar{b}(\frac{\alpha(a)\hat{\psi}(\lambda)}{\lambda(\lambda+k-r)} + \hat{B}(\lambda, \hat{\psi}(\lambda)) + \hat{C}(\lambda, \hat{\psi}(\lambda)) + \hat{\epsilon}(\lambda)) \end{aligned} \tag{2.41b}$$

where to simplify notation we define:

$$\alpha(a) = x(a, a, \overline{D})\, e^{-\int_0^a \mu x(\tau, a, \overline{D}) d\tau} \tag{2.42a}$$

$$\beta(t) = \int_0^\infty x(a+t, a, \overline{D})\, e^{-\int_0^{a+t} \mu x(\tau, a, \overline{D}) d\tau}\, b_0(-a) da \tag{2.42b}$$

$$\gamma(t) = e^{-\int_0^t \mu x(\tau, t, \overline{D}) d\tau} \tag{2.42c}$$

$$\delta(t) = \int_0^\infty e^{-\int_0^{a+t} \mu x(\tau, a, \overline{D}) d\tau} \int_0^a e^{-(k-r)(\sigma+t)} D_0(-\sigma) d\sigma da \tag{2.42d}$$

$$\epsilon(t) = \int_0^\infty x(a+t, a, \overline{D})\, e^{-\int_0^{a+t} \mu x(\tau, a, \overline{D}) d\tau} \int_0^a \int_0^\tau e^{-(k-r)\sigma+t} D_0(-\sigma) d\sigma d\tau da \tag{2.42e}$$

and

$$A(t,\psi(t)) = \int_0^t e^{-(k-r)\sigma}\psi(t-\sigma)d\sigma \int_0^\infty e^{-\int_0^a \mu x(\tau,a,\overline{D})d\tau} da \tag{2.43a}$$

$$B(t,\psi(t)) = \int_0^t \int_0^\tau e^{-(k-r)\sigma}\psi(t-\sigma)d\sigma d\tau \int_0^\infty x(a+t,a,\overline{D}) e^{-\int_0^{a+t} \mu x(\tau,a,\overline{D})d\tau} da \tag{2.43b}$$

$$C(t,\psi(t)) = \int_0^\infty a x(a+t,a,\overline{D}) e^{-\int_0^{a+t} \mu x(\tau,a,\overline{D})d\tau} \int_0^t e^{-(k-r)\sigma}\psi(t-\sigma)d\sigma da \tag{2.43c}$$

To continue our calculations we need to find the characteristic equation of differential equations (2.41a) and (2.41b). To do so we need to find the Laplace transform of all factors defined in equations (2.42a) to (2.42e) and (2.43a) to (2.43c), apart from $\alpha(a)$, which is no function of t. Unfortunately the only one of these factors which has a solvable Laplace transform is $\gamma(t)$:

$$\hat{\gamma}(\lambda) = \frac{e^{\frac{\alpha\mu\overline{D}}{(k-r)^2}}}{k-r} \int_1^\infty e^{-\frac{\alpha\mu\overline{D}}{(k-r)^2}t} t^{\frac{\alpha\mu\overline{D}+(k-r)\lambda}{(k-r)^2}-1} dt$$

It is also worth mentioning that $\alpha(a)$ is explicitly solvable with the help of Mathematica:

$$\alpha(a) = \frac{e^{\frac{\alpha\mu\overline{D}}{(k-r)^2}}}{k-r} \left(\int_1^\infty e^{-\frac{\alpha\mu\overline{D}}{(k-r)^2}t} t^{\frac{\alpha\mu\overline{D}}{(k-r)^2}} dt - \frac{\alpha\mu\overline{D}}{(k-r)^2}^{\frac{-\alpha\mu\overline{D}}{(k-r)^2}} \int_0^\infty t^{\frac{\alpha\mu\overline{D}}{(k-r)^2}-1} e^{-t} dt\right)$$

It is no longer possible to do the computations explicitly and we can no longer continue our explicit computations. Solving these equations numerically is beyond the scope of this thesis. It should be clear that delay equations can get very complicated quite quickly.

In [6] the same model is studied as we studied in these last three sections. In that paper they look into the assumptions that k and μ are stable, but $r(x)$ is of the form $r(x) = \frac{\beta x}{H+x}$ for some constants $H, \beta \in \mathbb{R}_+$. Similar to our last analysis they do not get explicit results, but end up with an expression (5.41) with an integral that is not explicitly computable (5.36).

We've now seen some of the techniques common to analysis of DDE's. The strategy used in this chapter, to analyse the steady states and their stability, is one used in many papers on DDE's. A lot of theory on DDE's is finding conditions on the specific type of DDE's such that existence or stability of solutions can be proved. Examples of such theorems can be found in the literature referenced to in chapter 1 of this thesis.

.1 Rewriting a DDE to a Volterra equation of the Second Kind

As seen in Chapter 1 a DDE for time $t \in \mathbb{R}$ and variable $x : \mathbb{R} \to \mathbb{R}$ can be described by the following set of equations:

$$\begin{aligned} \dot{x}(t) &= Fx_t \\ x_0 &= \varphi \end{aligned} \tag{44}$$

where $x_t(\theta) = x(t+\theta)$ with $\theta \in [-r, 0]$ for some $r \in \mathbb{R}_+$, some operator $F : C(\mathbb{R}, \mathbb{R}) \to \mathbb{R}$ and some initial function $\varphi : [-r, 0] \to \mathbb{R}$. We will now see how such an equation can be written into the form:

$$x = k * x + f \tag{45}$$

where $k \in C(\mathbb{R}, \mathbb{R}$ is a normalised function of bounded variation (which we will denote $k \in NBV$. For a definition of NBV functions see [7] p. 13), $f \in C(\mathbb{R}, \mathbb{R}$ and $*$ denotes the convolution product: $x * y = \int_0^t x(s)y(t-s)ds$. This transition between the two descriptions is done equivalent to Diekmann Et. Al. [7]. We start by stating a version of the the Riesz Representation Theorem.

Theorem 1. (Riesz Representation Theorem)
Let $F : C(\mathbb{C}^n, \mathbb{C}^n) \to \mathbb{C}^n$ be linear and continuous. Then there exists a $k \in \mathbb{R}$ and a unique function, $k : [0, r] \to \mathbb{C}^n$ and $k \in NBV([0, r])$, such that for all $\psi : [-r, 0] \to \mathbb{C}^n$:

$$F\psi = \int_0^r \mathrm{d}k(\theta)\psi(-\theta) \tag{46}$$

Where, since $F\psi$ is a n-dimensional vector, we have:

$$(F\psi)_i = (\int_0^r \mathrm{d}k(\theta)\psi(-\theta))_i = \sum_{j=1}^n \int_0^r \mathrm{d}k_i j(\theta)\psi_j(-\theta)$$

By equation (46) it is clear that every $k \in NBV([0, r], \mathbb{C}^n)$ gives rise to a linear and continuous functional $F : C \to \mathbb{C}^n$.

We can use this theorem to rewrite (44) as:

$$\begin{aligned} \dot{x}(t) = Fx_t &= \int_0^r \mathrm{d}k(\theta)x(t-\theta) \\ &= \int_0^t \mathrm{d}k(\theta)x(t-\theta) + \int_t^r \mathrm{d}k(\theta)x(t-\theta) \end{aligned}$$

Using integration by parts and recalling that $k(0) = 0$ we get:

$$\dot{x}(t) = k(t)x(0) + \int_0^t k(\theta)\dot{x}(t-\theta)d\theta + \int_t^r \mathrm{d}k(\theta)x(t-\theta)$$

So that we now have the following equation for $\dot{x}(t)$:

$$\dot{x} = k * \dot{x} + g \tag{47a}$$

$$g(t) = k(t)x(0) + \int_t^r \mathrm{d}k(\theta)x(t-\theta) \tag{47b}$$

$$x(0) = \varphi(0) \tag{47c}$$

We now get by integrating (47a):

$$\begin{aligned}
x(t) - \varphi(0) &= \int_0^t \int_0^s k(\theta)\dot{x}(s-\theta)d\theta ds + \int_0^t g(s)ds \\
&= \int_0^t k(\theta) \int_\theta^t \dot{x}(s-\theta)ds d\theta + \int_0^t g(s)ds \\
&= \int_0^t k(\theta)(x(t-\theta) - \varphi(0))d\theta + \int_0^t g(s)ds \\
&= \int_0^t k(\theta)x(t-\theta)d\theta + \int_0^t (\int_s^r \mathrm{d}k(\theta)x(s-\theta))ds
\end{aligned}$$

Therefore we can write:

$$x = k * x + f \tag{48a}$$

$$f(t) = \varphi(0) + \int_0^t \int_s^r \mathrm{d}k(\theta)x(s-\theta)ds \tag{48b}$$

which is a Volterra equation of the second kind for x. Hence, we proved that equations of the form (44) can be written as a delay equation.

Notice that the reverse implication can be proved by reversing the arguments used here combined with equation (46): Given $\varphi : [-r, 0] \to \mathbb{R}$ and a NBV function $k : [0, r] \to \mathbb{C}^n$, if $x \in C$ satisfies equations (48a) & (48b), then there exists a functional $F : c \to \mathbb{C}^n$ for which $x(t)$ satisfies equations (44), given by equation (46).

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