Mathematical Modelling of Populations

Barkley Education

Jason Liu

supervised by
Alexander Cameron

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1 Introduction

Mathematical models are used throughout science to describe the behaviour of various systems, examples include modelling the flow of fluids, the transfer of heat, and the spread of diseases. In this project we shall look at mathematical models which describe the change in population of various animals in different habitats.

Population models can generally be classified into discrete time models and continuous time models. In discrete time models, time is dicretized into fixed intervals, for example days or weeks. These models can be written as difference equations. However, in this project we shall look at continuous time models, written as differential equations, which describe the rate of change of a population as a function of the current size of the population and various other factors relating to their environment or competition between species.

In reality, animals in a population exhibit many variations such as their age and physiological charactersistics, whilst often living in a diverse environments. We hope to use a mathematical modelling approach to determine the role of density dependence in the behaviour of populations. We have to make many assumptions, often depend on the specific system we are looking at to simplify our problem. Using these simple models we hope to preserve the essential features of the ecological systems we look at.

2 Exponential Population Model

The most simple population model is known as the exponential model, in which the size of a population N, is dependent on the birth rate b and death rate d of the population. This is given by the differential equation

$$\frac{dN}{dt} = bN - dN. \tag{1}$$

We can simply solve this equation using integration to give

$$N = N_0 e^{(b-d)t}, \tag{2}$$

where N_0 is the initial size of the population. If $b > d$, that is, if the birth rate is greater than the death rate, the population will grow exponentialy. If $b < d$ such that the death rate is greater than the birth rate, the population will die out. In Figure 1 we show numerical simulations of these two cases, where initially $N = 20$.

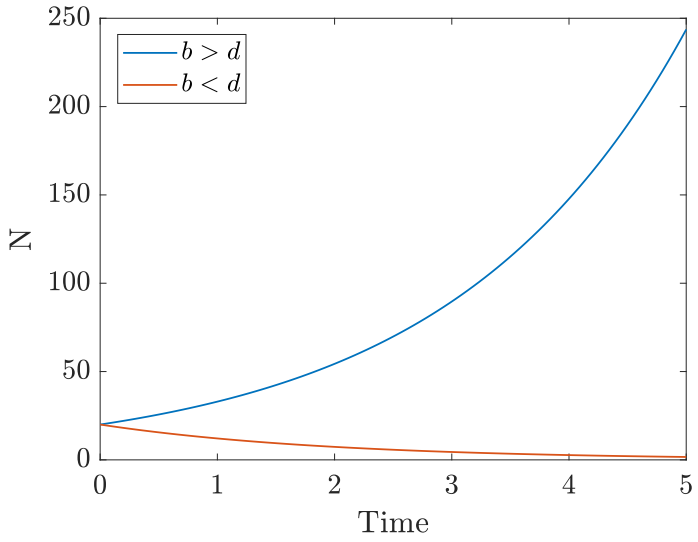


Figure 1: Solutions of (1) with different birth and death rate values.

3 Logistic Model

Model (1) though is not very realistic, as when the birth rate is greater than the death rate, it states that the population will grow exponentially without ever decreasing. In reality though, the are various factors which will mean that when a population reaches a certain size, the population will cease to grow. Commonly, this will be when the natural resources of an environment can no longer sustain population growth, for instance that there is now a scarcity of food or water. Hence, at this point the population should level off and reach an equilibrium.

A mathematical model which describes this scenario was proposed by Pierre-Franois Verhulst in 1838. This model is known as the logistic model, where the rate of reproduction is proportional to both the existing population and the amount of available resources. It can be described mathematically by the following differential equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{3}$$

where in this model we define r as the growth rate and K as the carrying capacity, which is the population size the environment can sustain [1].

The solution of this model is

$$N = \frac{KN_0e^{rt}}{K + N_0(e^{rt} - 1)}. \tag{4}$$

We note that the logistic differential equation (3) has to equilibrium solutions, that is

solutions where $dN/dt = 0$. These are given by $N = 0$, and $N = K$. The equilibrium solution $N = 0$ respresents the scenario when the population has died out. As there are no organisms left, they can no longer reproduce so the population will remain extict. The solution $N = K$ represents the case when the population has reached the carrying capacity of its environment.

We would like to determine the stability of these two equilibrium solutions. An equilibrium solution is said to be stable if when perturbed by a small amount, the system returns to the equilibrium. We can determine the stability of an equilibrium solution by plotting dN/dt against N as done in Figure 2, where the parameter values used are $r = 1$ and $K = 80$. We see that at $N = 0$, dN/dt has a positive gradient, meaning that when N is just above 0, the population will grow, hence $N = 0$ is an unstable equilibrium solution. In the context of our population model, this is because when the population is very small (but not exactly zero), the environment has a surplus of resources so that the population can grow easily. Secondly, we see that dN/dt has a negative gradient when $N = 80$, the other equilibrium solutiom. This means that for N just smaller than 80, the population will increase, and for N just larger than 80, the population will decrease, hence $N = 80$ is a stable solution.

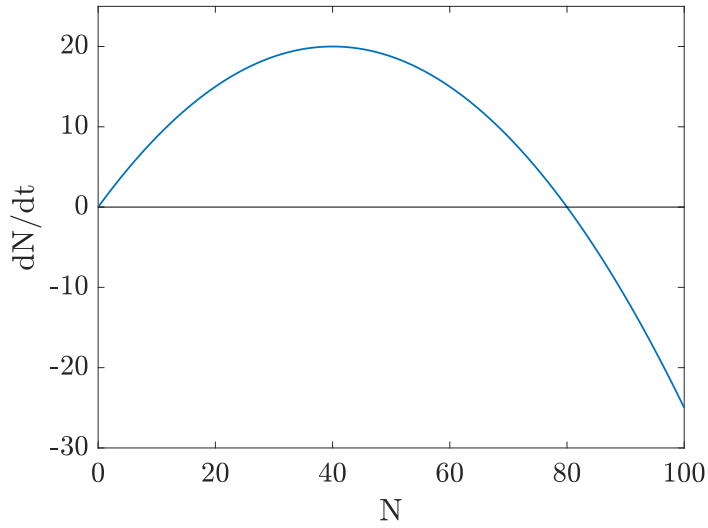


Figure 2: dN/dt plotted against N to determine stability of equilibrium solutions. Parameter values used are $r = 1$ and $K = 80$.

In Figure 3 we have plotted the numerical solution of (3), with different values of r. We observe that as r increases, the system reaches the equilibrium of $N = 80$ faster. In Figure 4 we have varied the value of K, the carrying capacity, and in Figure 5 we

have varied the initial population size N_0. We see that for $N_0 = 80$, the population decreases to the equilibrium of $N = 50$. When $N_0 = 50$, the population remains in equilibrium at $N = 50$ throughout, as the population started at its carrying capacity.

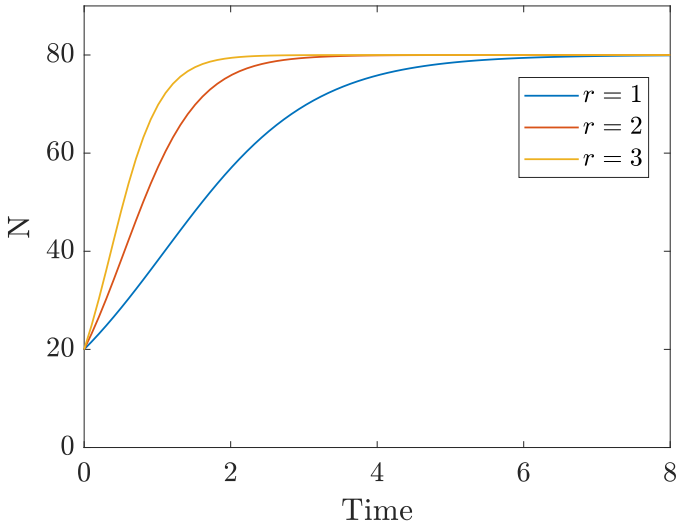


Figure 3: Numerical solution of (3) with different values of r, with $K = 80$ and $N_0 = 20$.

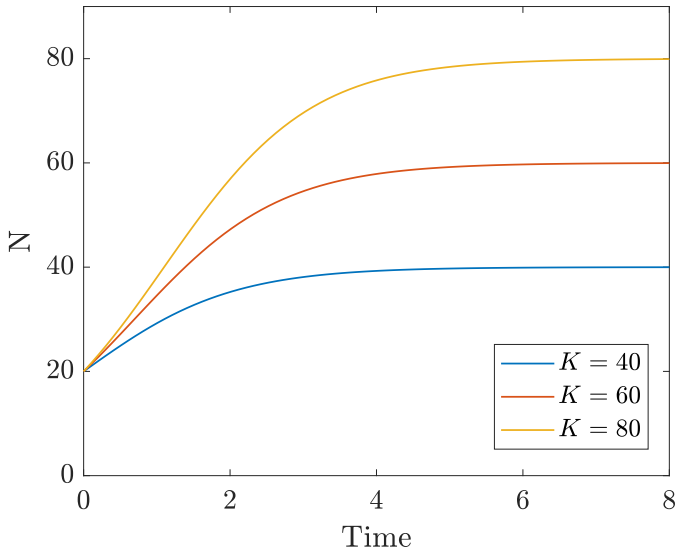


Figure 4: Numerical solution of (3) with different values of r, with $r = 1$ and $N_0 = 20$.

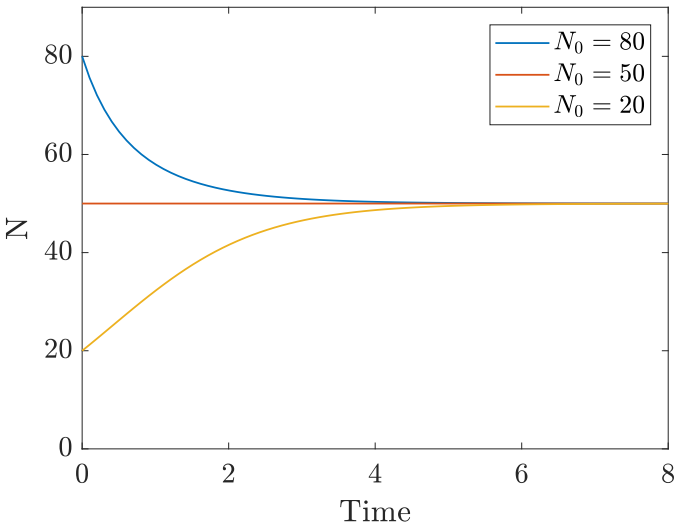
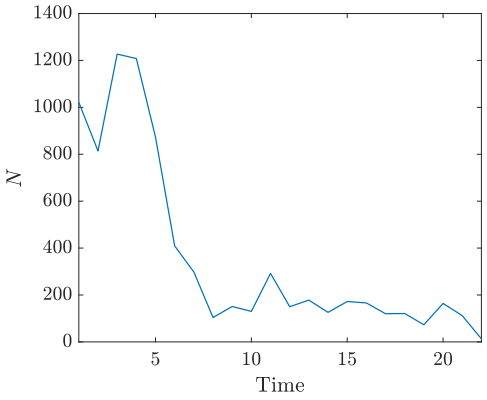


Figure 5: Numerical solution of (3) with different values of N_0, with $r = 1$ and $K = 50$.

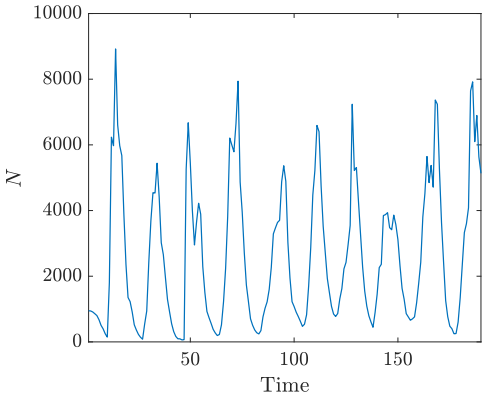
4 Data

We now consider population data of five different organisms; bears, blowflies, bruchids, delias flies, and drosophila. In Figure 6 we plot the data for each species. We observe in Figure 6 that the bear population initially starts high but then falls rapidly. The blowfly population oscillated periodically, reaching a similar approximate high and low popeulation size in each cycle. The bruchid population seems to fluctuate without much pattern, and the delia population remains fairly steady apart from one large peak. Finally, the dropsphila popululation appears to oscillate, but without any clear trend.

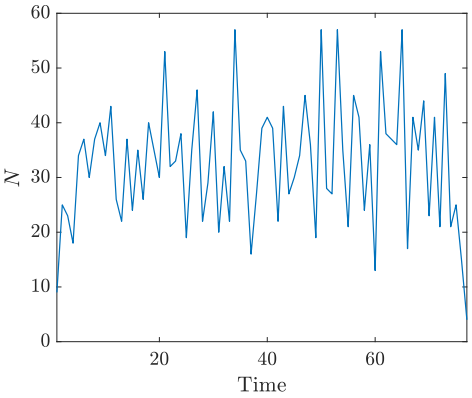
We conjecture that the the population dynamics of each species is density dependent, that is the rate of population growth or decline depends on the density of the population at any given time. This is due to intraspecific competition where members of the same species compete for limited resources. There are two types of competition, firstly scramble competition where a finite resource is shared equally amongst the competitors. Food per individual declines with increasing population density and often results in periodic or chaotic population dynamics. Secondly there is contest competition where one individual emerges victorious. This allows monopolization of resources so that offspring will be produced and survive until adulthood independent of population size and in general results in stable population dynamics.



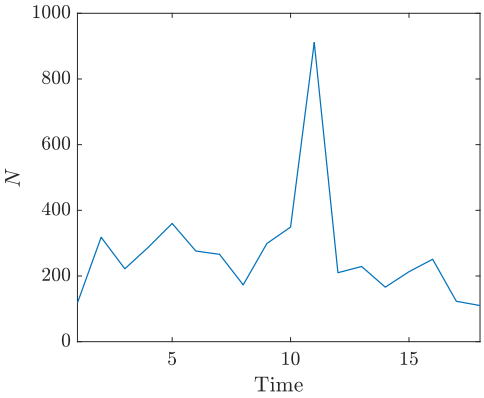
(a) Bear



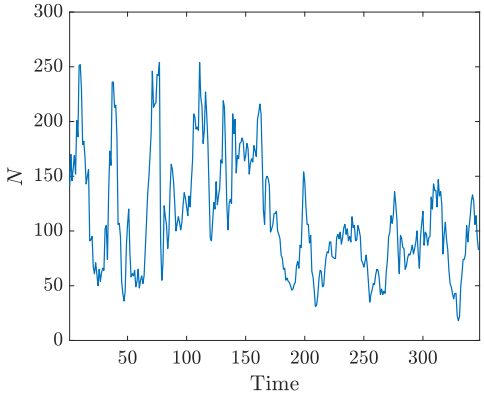
(b) Blowfly



(c) Bruchid



(d) Delia



(e) Drosophila

Figure 6: Population data for five different organisms.

Data Analysis

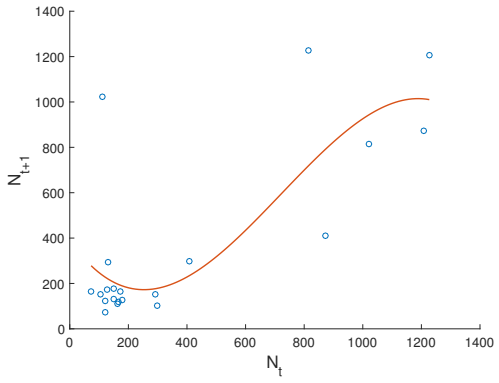
We shall analyse the data to determine firstly whether there is evidence of density dependence, and secondly whether the data suggests contest or scramble competition. We can use the technique of plotting the number of survivors, S against the initial egg density ,N, of an organism. We though just have data on the size of populations but we can still plot N_{t+1} against N_t where N_{t+1} is the number of organisms which have survived until the next time step. It is important to note though that our data includes births so this method will not tell us how the birth and death rate are density dependent separately, but it will give us an insight into the role of density dependence in general. A density independent population would yield a straight line through the origin, so any large deviation from that would be indicative of a density dependent population. A monotonic curve (constantly increasing) would suggest contest competition while a humped curve with a turning point would suggest scramble competition.

Looking at Figure 7 we can see that the scatter plots (a), (c) and (d) are relatively uncorrelated and it has to be said their lines of best fit are somewhat crude. The fact that in each of these plots we have many varying values of N_{t+1} for similar N_t makes it hard to decipher any trend. We can though state that (c) and (d) suggest that density dependent processes are at play. With (a) it is difficult to draw any conclusions and so we cannot say with any confidence whether the data is density dependent or not.

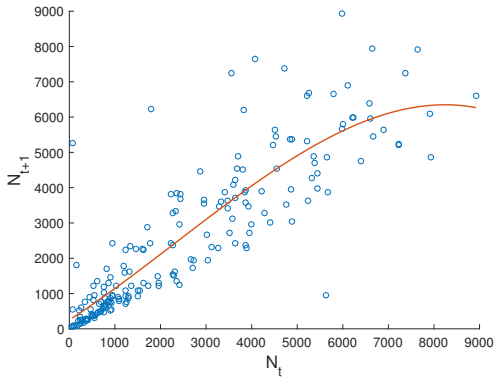
It seems that (b) and (e) show traits of density independence. While plotting N_{t+1} against N_t is does shed some light on this matter, it may be more useful to plot N_{t+n} against N_t for some $n > 1$. This is because it may take more than one time-step for the current population density to have an affect on the future population density. Looking at Figure 8 where we have plot N_{t+8} against N_t we see see a negative correlative for the blowfly data and essentially no correlation in the drosophila data in contrast to (b) and (e) in Figure 7. This suggests there may be a time lag between the current density and it's effects on the future population, thus motivating using delay differential equations to model the system.

5 Delay Differential Equations

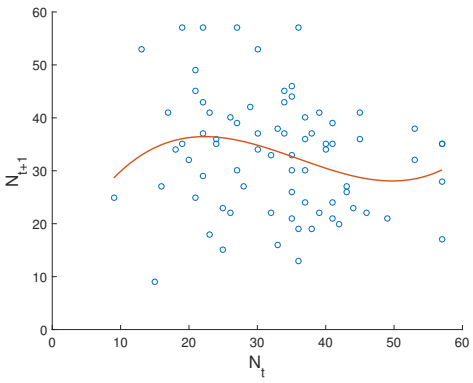
Delay differential equations are a type of differential equation in which the rate of change of a given quantity is given in terms of the values of the quantity at previous



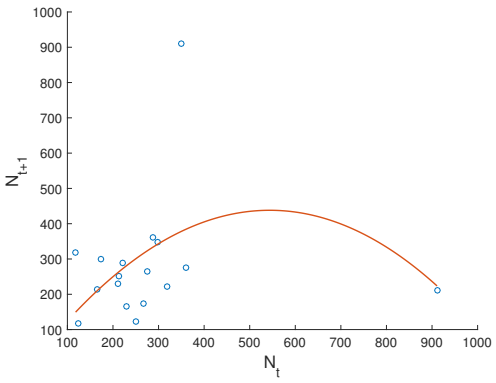
(a) Bear



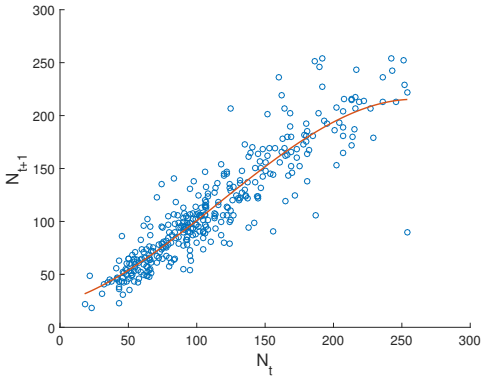
(b) Blowfly



(c) Bruchid

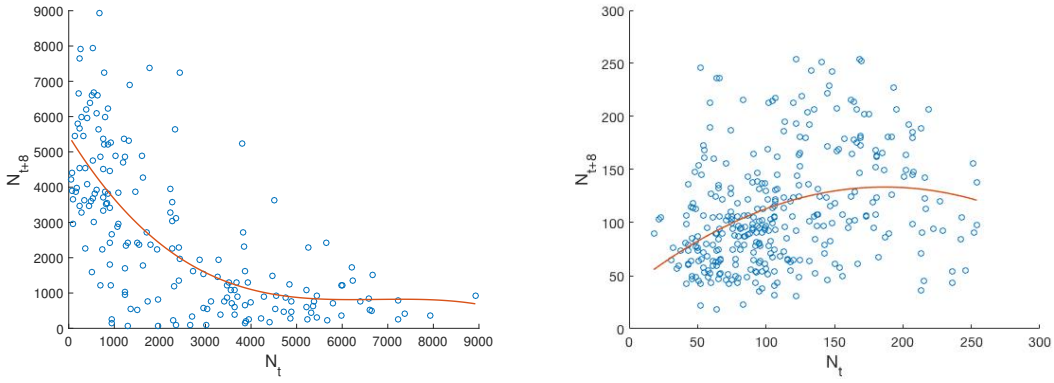


(d) Delia



(e) Drosophila

Figure 7: N_{t+1} against N_t



(a) Blowfly (b) Drosophila

Figure 8: N_{t+8} against N_t

times. They are commmonly used to model the evolution of populations, as often the rate of change of the size of a population is dependent on the population size at an earlier time. For instance these time delays may represent represent resource regeneration times, maturation periods or feeding times, reaction times [2]. In general, delay differential equations exhibit much more complicated behaviour than ordinary differential equations since a time delay could cause a stable equilibrium to become unstable and cause the populations to fluctuate. Following [3], we shall use delay differential equations to model the population of blowflies.

Delayed Logistic Model

In the models we have looked at thus far we have assumed that the growth rate of a population was dependent on the instantaneous population density. In reality though many biological processes are not instantaneous. For example, the rate of reproduction is more likely to be determined by the number of organisms at a previous time-step. Thus [4] proposed the following time-delayed logistic equation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N(t-\tau)}{K}\right) \tag{5}$$

where r, is the intrinsic growth rate, K is the carrying capacity and $\tau > 0$ is the time lag. We note that the blowfly data is from a laboratory, where the number of adult blowflies was counted and the food supply was renewed every 2 days. Therefore the carrying capacity K of the population is determined by the amount of food available and the time-delay is based on the time it takes for the blowfly larva to mature into an adult.

We wish to fit the delayed logistic model (5) to the blowfly data. This involves finding the values of the parameters in the model which minimise the error between the model solution and the data. We find that the parameter values $\tau = 3$, $K = 1083$, and $r = 0.88$ are the best fit values. In Figure 9 we plot the solutions of the model against the data showing a reasonable agreement, although we note that our model solutions give that the blowfly density is approximately zero for long periods of time between its peak values.

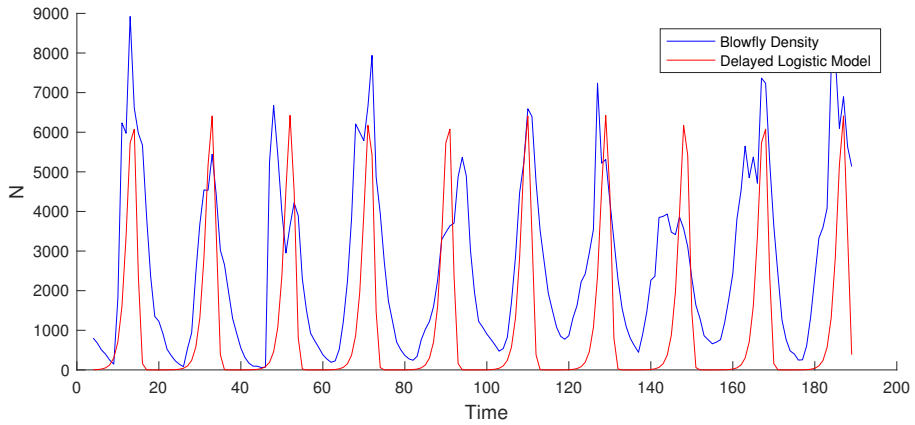


Figure 9: Delayed logistic model fitted to blowfly population data with $\tau = 3$, $k = 1083$ and $r = 0.88$

Nicholson Model

The authors in [3] suggested a new recruitment model incorporating time delays to model laboratory blowfly populations. The rate of change of the population is the instantaneous rate of recruitment to the adult population $R(t)$ minus the instantaneous total death rate $D(t)$. That is:

$$\frac{dN(t)}{dt} = R(t) - D(t) \tag{6}$$

To determine $R(t)$ certain assumptions have to be made about the life-cycle of the blowflies. Namely that all eggs take τ time units to develop into mature adults, the rate at which the adult population produces eggs depends only the on the current density of the population. This suggests that R can be expressed as

$$R = R(N(t - \tau)) \tag{7}$$

so that the rate of change of density can be expressed as

$$\frac{dN}{dt} = R(N(t-\tau)) - D(t). \tag{8}$$

In the experiment in which the blowfly data was obtained from, the only limiting resource was food for the adult population (the larvae were provided with ample food to survive). Thus it is reasonable to suggest that at high densities, intraspecific competition will reduce the per capita fecundity of the population. When scramble competition is occurring it may be that the population requires all the food available to survive and so produces no offspring at all. Evidence for this is the sharp decline in the population density after it reaches its peak at each cycle. Therefore the recruitment rate $R(N)$ should tend to zero as N gets very large and it is reasonable to suggest it should attain a maximum at an intermediate non-zero population size. The function suggested which displays these properties is

$$R = PN\exp(-N/N_0). \tag{9}$$

It was assumed in [3] that the per capita death rate was density independent so that $D = -\delta N$. Hence we arrive at a new model, which we shall call the Nicholson model, given by the equation

$$\frac{dN}{dt} = PN\exp(-N(t-\tau)/N_0) - \delta N. \tag{10}$$

In Figure 10 we show the best fit Nicholson model, which is fitted to the data using the paramaters $\tau = 8$, $P = 202$, $d = 84$ and $N_0 = 0.7$. We see that this model fits the data more accurately than the logistic model shown in Figure 9, suggesting that the Nicholson model does indeed better describe the population dynamics of blowflies.

6 Conclusion

In this project we have described the behaviour of the basic exponential population model and the logistic model. We looked at the equilibrium solutions of the logistic model and determined their stability. We considered population data from five different sources, and by ploting the data in a certain manner determined whether the population dynamics of each species was density dependent or not. We looked at the data of the blowfly population in more detail, and fitted two different delay differential equation models to the data, showing that the Nicholson model described the blowfly population most accurately.

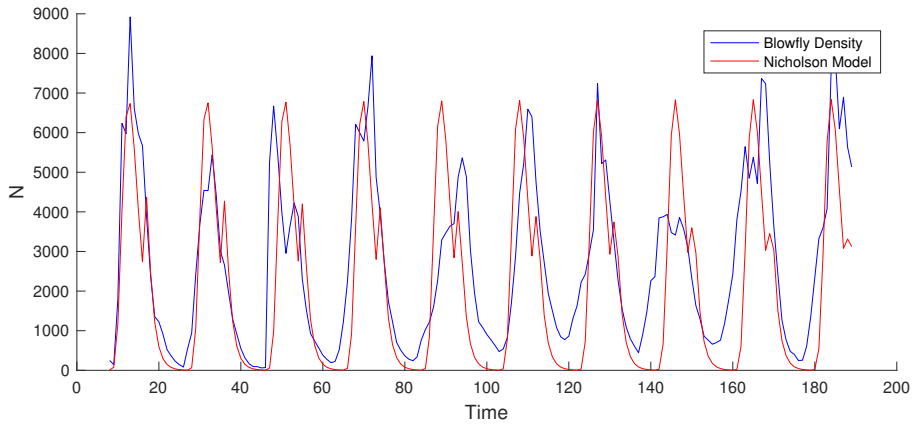


Figure 10: Nicholson model fitted to blowfly population data with $\tau = 8$, $P = 202$, $d = 84$ and $N_0 = 0.7$

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