

Mathematical Model of Predator-Prey  
System with Age Structure

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Submitted in Partial Fulfillment of the Requirements of the  
University Undergraduate Fellows Program

1983-1984

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A handwritten signature in cursive script, reading "William Rundell", is written above a horizontal line.

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April 1984

## ABSTRACT

This paper considers models of physical phenomena, in particular models from population dynamics. The main model of concern is a combination of two previously developed models: the model of non-linear age dependent population and the classic Lotka-Volterra model of interacting predator and prey populations. It is shown that this model has a unique solution for all time, and this solution is bounded for finite time. A particular case is studied by computer simulation, and the results show that indiscriminate eating leads to a stable periodic relation between the predator and the prey, while selective eating leads to nonstable behavior. It is suggested that age-selective predation can be a stabilizing agent in a predator-prey scheme.

## ACKNOWLEDGEMENTS

I would like to thank Dr. Rundell for his help and patience throughout this project, and Dr. Pilant for his help in developing the computer simulation.

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## 1. Introduction\*

This paper will consider the use of mathematical models in the study of natural events, in particular in the area of population dynamics.

### 1.1 Introduction to Modelling

The basic assumption behind all models is that there is some logical structure underlying natural happenings. Whether or not this assumption is valid is an important point, although we will not concern ourselves with it in this thesis. A model simplifies the study of natural events by isolating the event to be studied from its background. Let us define what it means to be an accurate model: a model is accurate if it retains many of the salient features of the situation, and if the conclusions of the model compare favorably with what is observed in nature. Modelling is not just an exercise in abstract mathematics, as it takes a thorough understanding of the real forces involved in an event.

Given the basic assumption that there is some logical structure, it is a fairly straightforward, although not necessarily easy, process to develop a model. The first step is to write down a system of relationships which describes everything that might influence the event. Then by translating these relationships into formulas, form a set of mathematical equations incorporating all, or as many as is possible, of these relationships. This part of the process is an art, as there is not usually a unique mathematical expression for each set of relationships. Some careful choices have to be made, since the different expressions may result in different conclusions. Another difficulty is that it may not be known how to translate some relationships accurately into mathematics. Also, when

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\*This paper conforms to the style of The American Mathematical Monthly.

developing a model it is sometimes hard to keep in mind that the model is supposed to represent a natural event. Thus a mathematical assumption could be made which would turn out to be a very poor assumption. This leads us to the major concern in the creation of a model.

With modern science and mathematics it would be possible, given enough time, to model everything that happens in the world. The problem, then, would be that while very accurate, the resulting expression would be totally unsolvable, and thus useless. To make this model useable some compromises would have to be made, but some accuracy would then be lost. Now consider the opposite case: a model of the world based on a simple relationship, like everything changing at a constant rate. This model is easily solved, even by a first year calculus student, but because it is so simple, it would not be at all accurate and, like the complex model above, would supply no useful information. This shows that the important part of modelling is not absolute accuracy, but a proper balance between accuracy and solvability. The best, meaning most successfully used, models are those that have maximum accuracy while remaining solvable.

## 1.2 Population Dynamics

The type of models which this paper will discuss come from the area of population dynamics. Population dynamics is concerned with the growth of one or more populations under various circumstances. Population growth is a popular subject of modelling, because the basic relationships are fairly simple (birth and death rates), there is data available to test the models, especially for human populations, and the results of the model have importance for future planning. Another advantage of population dynamics is that as a mathematical field, it is young enough to have some simple

unexplored areas left, and it is old enough to have developed a very good foundation. Also, the history of population dynamics is well documented, and reads like a lesson in model development.

### 1.2.1 Single Species

Although human population growth has been a topic of discussion among philosophers and politicians since before Christ, the first person to do any quantitative work in this area was the Reverend Thomas Malthus (1768-1834). Malthus was not a mathematician, but more of a social philosopher. In his paper "Population: The First Essay," [1] published in 1789, he discussed what he saw as the laws governing human population growth and the logical result of these laws. Malthus' assumption was that the growth of the human population is proportional to the total population. The mathematical translation of this assumption is that population grows geometrically. (See Appendix A.1 for the mathematical details.) Malthus also thought that food supplies would increase only arithmetically, implying that there was some upper limit of the population that could be supported. He realized that birth and death rates govern population growth, so for a stable population either the death rate had to increase or the birth rate had to decrease. Since Malthus believed "that the passion between the sexes is necessary and will remain nearly in its present state," he concluded that famine and starvation would be the only ways to limit population growth and, thus, are inevitable. This idea is not that strange in nature, as animals and plants reproduce as much as they can causing a population larger than the environment can support. Then part of the population will either starve to death or fall prey to other animals, reducing the population to a sustainable level. Fortunately for



us, Malthus' model is not accurate for human populations in general. However, it is usable for small populations with unlimited resources, like U. S. population before the 1840s. An important lesson is to be learned from this model: linear models are, in general, not accurate.

The next page in the history of population dynamics is related to the significance of the 1840s to U. S. history. In the 1840s the ever expanding U. S. population reached the West coast, thus limiting the room to grow. This oversimplification of history brings us to the idea presented by Verhulst in 1839. Verhulst used the basic assumption of the Malthusian model, but added the idea that the environment could only support a certain population. This population is the carrying capacity for the environment. So now instead of always growing geometrically, the Verhulst model predicts that the growth rate will depend on the total population times the room left in the environment. The major result of this is the population is always below the carrying capacity. (See Appendix A.2 for the mathematical details.) The Verhulst model was relatively unknown until Pearl and Reed [2] rediscovered it in 1920 while working with U. S. population predictions. Using data from the 1700s and 1800s the Verhulst model accurately predicts U. S. population until 1950. Today the Verhulst-Pearl equation is the standard of single species population dynamics as it combines good accuracy with explicit solvability.

As the Verhulst-Pearl equation was an improvement of the Malthus model, the Verhulst-Pearl equation can be improved. Some of the first modifications were to include another term to account for small discrepancies between the model and actual population growth. Since then others have used time dependent birth and death rates, and changing

carrying capacities. These are just a few of the many possible modifications, but in most cases when the final calculations are made, it will be found that these changes affect the accuracy very little. The loss in solvability, however, is often quite large, to the extreme of total unsolvability. These fine adjustments are not the answer to give new insight into human population growth.

To take the next step in population dynamics a new direction is necessary. The improvement we are interested in is the addition of age structure to the birth and death rates. This is a radical departure from previous work, as now we can calculate the change in the age distribution of the population over time, rather than just the change in the total number. This will allow us to answer more important questions than just what the total population is, like how many people between ages 18 and 22 will there be in the year 2000, or how many people will there be over the age of 65 in 1990. Given an initial population distribution and the birth and death functions, we can construct a mathematical equation which would allow us to calculate the number of persons at each age for all time. (See Appendix A.5 for details) The application of this to planning for the future is almost unlimited. The resulting mathematical expression is, of course, more complex than the previous models, as the relationships are more complicated, but it is still solvable. The mathematical equation is known as the Sharpe-Lotka equation (1925) [3,4]. The Sharpe-Lotka model is linear, so in a sense it is like the Malthus model with age structure. Because it is linear, it is unstable, so it does not give too much useful information, unless the initial population is small and the resources large in comparison. The next logical step would be to improve the Sharpe-Lotka

model, like the Malthus model was improved into the Verhulst-Pearl model. This has been done recently by Gurtin [5], in a paper on non-linear age structure. He assumes that the birth and death rates are dependent on age, but also on the total population. This makes for a fairly complex model, but it is still solvable, and as he shows, it is stable, given the proper restraints.

Again more improvements could be made. Other possibilities are using time dependent birth rates, age and sex structure, or some other modification. But again we have reached the optimization point between solvability and accuracy. To realize a small increase in accuracy, we must lose a large amount of solvability. So we must approach the problem from another viewpoint.

### 1.2.2 Multiple Species

Now we will leave human population dynamics for awhile, and discuss animal populations. All of the previous models work just as well for animal populations, as for human populations. However, there are factors that affect animals that do not affect humans, primarily interaction with other animals. Consider a case where two groups of animals are competing for a common food source. Each group would have its own birth and death rates (as complex as we want them to be, from above), but the death rate should depend on the population of the other species. In this case of competitive hunters, using a linear model, the birth rate for one species would increase as the population increases, but would decrease as the population of the other animal increased. The same would be true for the other animal group. So we will have two equations which are interdependent.

Now we will use the same considerations to look at the situation where one species eats the other. This is the predator-prey model. In this case the interaction between the two species increases the predator and decreases the prey population. Taking the linear model, we have the predator population decreasing with more predators, as there would be more competition, and increasing with more prey. The prey population increases proportionally to the number of prey, like the Malthusian model, but decreases with and increase in the predator population. This model is easily solved and, while apparently complete, is very unstable. The choice of the constant for the birth rate of the prey is so critical, that a small change could change the growth from geometrically increasing to geometrically decreasing. (See Appendix A.3 for the details.) This result reaffirms what we learned before: linear models are unstable. We need to improve the accuracy of the model.

The improvement that will solve our problem is based on the work of Lotka and Volterra [6,9]. Their assumption is that the change should be dependent not just on the other population but on the interaction between the two populations. With this assumption even if there is an enormous number of predators, the change in the number prey will be small, if the number of prey is small. The model which results from this assumption is called the Lotka-Volterra model, and is usually associated with a predator-prey relationship. The advantage of this model is this model is no longer linear. Unfortunately, one disadvantage is it is not solvable in a closed form. Some qualitative results can be calculated. (See Appendix A.4 for the details.) The important result is that the model predicts a periodic relationship between the predator and the prey, which is

comparable to what is seen in nature. Lotka-Volterra is like the Verhulst-Pearl equation, in that it is highly successful, because of its combination of simplicity with good accuracy and solvability.

No model is perfect, some are just better than others. In the above case, the linear model was highly unstable, and thus useless, while the Lotka-Volterra model predicts stable oscillatory behavior, similar to what is found in nature. It seems that the Lotka-Volterra model could also be improved. For instance, one could add higher order interaction terms, or make the birth and death rates time dependent, but as before, these improvements (whether they would actually improve the results or not is highly questionable) come at the expense of solvability while adding little accuracy [7]. One possibly profitable change would be to add age structure to the interactions. Just adding age structure to the birth and death rates would not make much difference, but if the interaction is also based on age then some interesting and useful results may be found. If one looks at the typical predator-prey relationship in nature, you have a small number of predators eating on a comparatively large number of prey, but the prey are eaten selectively, by age. For example, lions in the plains of Africa eat only those they can easily catch, usually the young, the old, and the sick. If a model of interaction could reflect this relationship it would be more accurate than previous models. Also, questions about the effects certain discriminatory eating habits would have on the age distribution of the prey could be answered. This thesis will develop such a model. It combines the interaction from the Lotka-Volterra model with the age structure for a single species placed upon the prey. The groundwork for this idea has been established by Gurtin [5,8].

The rest of this paper is divided into three sections. In Section 2 we develop our model formally, state and prove the existence and uniqueness of a solution for all time, and discuss some of the consequences of this mathematical study. Section 3 contains the development and results of the computer simulation of our problem. And finally, in Section 4 we state our conclusions.

## 2. Development and Solution of Model

We will use the following notation throughout:

$$\mathbb{R} = (-\infty, \infty)$$

$$\mathbb{R}^+ = [0, \infty)$$

$$C(A:B) = \{f: A \rightarrow B \mid f \text{ is continuous}\}$$

$$C(A) = C(A:\mathbb{R})$$

$$C^+(A:B) = \{f \in C(A:B) \mid f \geq 0\}$$

$L_1, L_\infty$  are sets of continuous functions whose integrals are finite.

### 2.1 Introduction of Problem

To create the model of a predator-prey system with age structure, we need to combine two models. For the prey population we will use the formation of the Sharpe-Lotka model (see Appendix A.5) with a few changes. The birth function will remain the same, but the death function  $\mu(a)$  is replaced with  $\mu(a,t;Q)$ , i.e. it depends on the predator population. The death function will now be:

$$\pi(\alpha, \beta, t; Q) = \exp\left(-\int_{\alpha}^{\beta} \mu(a, a+t-\beta; Q) da\right)$$

$$\pi(\alpha, t; Q) = \pi(0, \alpha, t; Q)$$

For the predator population,  $Q(t)$ , we will use the relationship from the Lotka-Volterra model of predator-prey interaction. So, we have:

$$\frac{d}{dt} Q(t) = -cQ(t) + dQ(t)P(t),$$

where  $c, d > 0$  constants. To complete our problem we need initial conditions. For the prey population we have  $\phi(a) = \rho(a, 0)$ , the initial population distribution, and for the predator population we have  $Q_0 = Q(0)$ , the initial population.

Before we start we need to lay down some basic hypotheses, which we will assume are always satisfied. Some of these are of a technical nature, while some are inherent to the problem, like  $\mu, \beta, \phi > 0$ .

(H1)  $\phi \in L_1(\mathbb{R}^+)$  is piecewise continuous

(H2)  $\mu \in C(\mathbb{R}^+ \times \mathbb{R}^+)$ ,  $\beta \in C(\mathbb{R}^+)$ ;  $\frac{d}{dQ} \mu(a,t;Q)$  exists for all  $a \geq 0$ ,  $t \geq 0$ ;  $\mu(a,t;Q)$  and  $\frac{d}{dQ} \mu(a,t;Q)$  as functions of  $Q$  belong to  $C(\mathbb{R}^+; L_\infty(\mathbb{R}^+))$ .

(H3)  $\phi \geq 0$ ,  $\mu \geq 0$ ,  $\beta \geq 0$ ,  $Q_0 \geq 0$ .

It is important to note that the formula for  $B(t)$  will not necessarily hold for  $t = 0$ , because of the arbitrary initial conditions. It will hold at  $t = 0$  if and only if the following restrictions are placed on  $\phi(a)$ :

$$\phi(0) = \int_0^\infty \beta(a)\phi(a)da$$

Since the initial conditions will be, in most cases, totally arbitrary, we will not require that  $\phi(a)$  satisfy this restriction (Gurtin [5]).

Now we have the following:

$$(2.1) \quad B(t) = \int_0^t \beta(t-a)\pi(t-a,t;Q)B(a)da + \int_0^\infty \beta(a+t)\pi(a,a+t,t;Q)\phi(a)da$$

$$(2.2) \quad P(t) = \int_0^t \pi(t-a,t;Q)B(a)da + \int_0^\infty \pi(a,a+t,t;Q)\phi(a)da$$

$$(2.3) \quad Q(t) = Q_0 \exp\left(\int_0^t -c + dP(a)da\right)$$

where

$$\pi(t-a,t;Q) = \exp\left(-\int_a^t \mu(\tau-a,\tau;Q)d\tau\right)$$



$$\pi(a, a+t, t; Q) = \exp\left(- \int_0^t \mu(\tau+a, \tau; Q) d\tau\right)$$

This is our predator-prey model with age structure. Now to solve it.

## 2.2 Existence and Uniqueness of Solution

The basic outline of our method for finding a solution is to first show we have a unique solution up to time  $T > 0$  for some sufficiently small  $T$  (Theorem 1). Then with another assumption, show that the populations grow at an exponential rate at worst (Theorem 2), and from this we show that a solution exists for all time (Theorem 3). First we need to establish some basic lemmas.

### Lemma 1 (Gronwall's Inequality)

If  $f(t)$ ,  $\phi(t)$ , and  $k(a, t)$  are continuous functions, and

$$\phi(t) \leq f(t) + \int_0^t k(s, t)\phi(s)ds$$

then

$$|\phi(t)| \leq C|f(t)|$$

where

$$C = \exp\left(\int_0^t |k(s, t)| ds\right)$$

Proof (see Brauer and Nohel [11])

### Lemma 2 (Banach's Fixed Point Theorem)

Consider a metric space  $X = (X, d)$ ,  $x \neq \emptyset$ . Suppose  $X$  is complete and  $M: X \rightarrow X$  is a contraction on  $X$ , i.e. for some  $\alpha < 1$ ,  $d(Mx, My) \leq \alpha d(x, y)$  for all  $x, y \in X$ . Then  $M$  has exactly one fixed point, i.e. there exists a unique  $x \in X$  such that  $Mx = x$ .

Proof (see Kreysig [10])

Theorem 1

There exists a  $T > 0$  such that the problem has a unique solution up to time  $T$ .

Proof

Consider the equation for  $Q(t)$  (2.3), for fixed  $P(t) \in C^+[0, T]$ , this equation has an exact solution, call it  $Q_T(P)(t)$ . For this fixed value of  $Q$ , the equation for  $B(t)$  (2.1) is a linear Volterra integral for  $B(t)$ . This means that it can be solved using Laplace transforms for a unique  $B(t)$ . Call this solution  $B_T(P)(t)$ . Now, substituting the two solutions  $Q_T(P)$  and  $B_T(P)$  into the equation for  $P(t)$  (2.2), we can define an operator  $P_T(P)$  on  $C^+[0, T]$ . The formula for  $P_T(P)$  is:

$$P_T(P(t)) = \int_0^t \pi(t-a, t; Q_T(P)) B_T(P)(a) da + \int_0^\infty \pi(a, a+t, t; Q_T(P)) \phi(a) da .$$

From our hypothesis,  $\pi$ ,  $B_T(P)$ , and  $\phi$  are all continuous and non-negative on  $\mathbb{R}^+$  so  $P_T$  maps  $C^+[0, T]$  into  $C^+[0, T]$ .

Now all that needs to be done is to show that there is some  $P(t) \in C^+([0, T])$ , such that  $P_T(P) = P$ . The next lemma will show that such a  $P(t)$  exists (using Lemma 2). If we have such a  $P(t)$  then it will be unique, and thus the corresponding  $Q(t)$  will be unique, and finally  $B(t)$  will be unique. The set of equations  $P(t)$ ,  $Q(t)$ , and  $B(t)$  will be the unique solution to our problem up to time  $T > 0$ .

The advantage of this next lemma is that it is constructive, that means it will tell us how to find the fixed point  $P(t)$ , rather than just stating that it exists.

Lemma 3

There exists  $T > 0$  such that the operator  $P_T(P)$  defined in the previous lemma has a unique fixed point.

Proof (see Appendix B)

It is important to note that nothing has been said about the size of  $T$ , except that  $T > 0$ . This is just a statement of local existence; a statement of global existence is desired, but it is seemingly unobtainable by this present approach. We need the added assumption that the birth rate is bounded. This, along with the hypothesis concerning  $\mu$ , will give us a bound on the growth of the population. The next result is important because it shows that  $P(t)$  and  $B(t)$  grow at most like a Malthusian population.

Theorem 2

If  $P(t)$ ,  $Q(t)$ , and  $B(t)$  are solutions to the problem for  $0 \leq t \leq T$ , and

$$\beta_0 = \sup_{0 \leq t \leq T} (\beta(a)) < +\infty, \text{ then}$$

$$P(t) < P_0 e^{\delta t}$$

$$B(t) < P_0 \beta_0 e^{\delta t}$$

where

$$P_0 = \int_0^{\infty} \phi(a) da$$

$$\mu_0 = \inf_{\substack{0 \leq t \leq T \\ a > 0}} \mu(a, t; Q)$$

$$\delta = \beta_0 - \mu_0$$

Proof (see Appendix B)

Now with this result we can show global existence.

### Theorem 3

If  $\beta_0$  (from previous Theorem)  $< +\infty$  then the problem has a unique solution for all time.

Proof (see Appendix B).

### 2.3 Discussion of Results and Conclusion

So we have a solution for our given problem. That is, we have a mathematical solution. Unfortunately the existence and uniqueness of the solution tells us nothing of the properties of the solution. As it stands now, there are many unanswered questions. Like, is the solution bounded for all time, or better yet, does it exhibit periodic behavior? Even a simple question like what the solution looks like, is unanswerable from the work done so far. However, before we attempt to answer any of these questions, let us look at exactly what the mathematics tells us.

First, by construction, the solution equations for  $P(t)$ ,  $B(t)$ , and  $Q(t)$  are non-negative and continuous. This means that the age distribution for the prey,  $\rho(a,t)$ , has at most one discontinuity (at  $a = t$ , from compatibility requirements). Second, the prey population and the prey birth rate each grows at most geometrically (Theorem 2). The final result, is that a necessary condition for global existence is that the birth rate be bounded. Although the mathematics tells us little about the properties, it is useful because of its generality. Since the birth and death functions are used in a most ambiguous form, these results would be true for any set of birth and death functions.

The next step in looking for more answers would be to either try some sample problems or delve deeper into the mathematics and try to determine the existence and stability of some equilibrium populations. The second option would be best, but it is beyond the scope of this paper. In Gurtin's study of non-linear age structure [5], he examines the properties of an equilibrium solution, but since he is only considering one population, his results are not applicable here. Our approach then, is to take a sample problem and write a computer program to arrive at a numerical solution. The assumption in doing this is that the model is complex enough, so that a common-sense problem would give fairly typical results. The details of this work are in the next section. Of course, it is not the intent of this thesis to imply that a successful computer simulation of the problem constitutes a rigorous proof, however, the results from this work show that the addition of age structure and age-dependent predation does not change the general relationship between the two species from what was found from the Lotka-Volterra model, for a constant eating rate. Figure 2.1 is a graph of a typical solution to the Lotka-Volterra model, and Figure 2.2 is a typical result of the computer simulation. The similarity between the two curves is remarkable, but this is to be expected (see Gurtin [8]). Now comes the surprising result. If we use a polarized prey selection process, where the predator eats only the young and the old, the resulting curve is not stable, but spirals into an equilibrium point (see Figures 2.3 - 2.5). There is nothing in the model that would predict that such an eating process would stabilize the relationship, and as a matter of fact, Gurtin [8] considered a similar situation and found that the results were totally unbounded.

Figure 2.1 Typical Curve from Lotka-Volterra Model

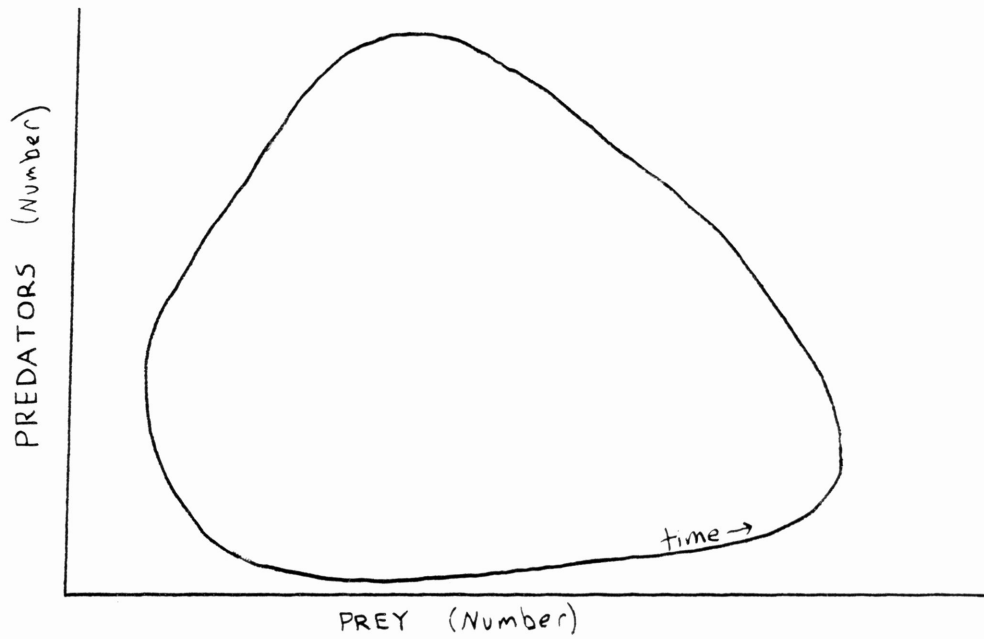


Figure 2.2 Result of Problem with Constant Eating Rates

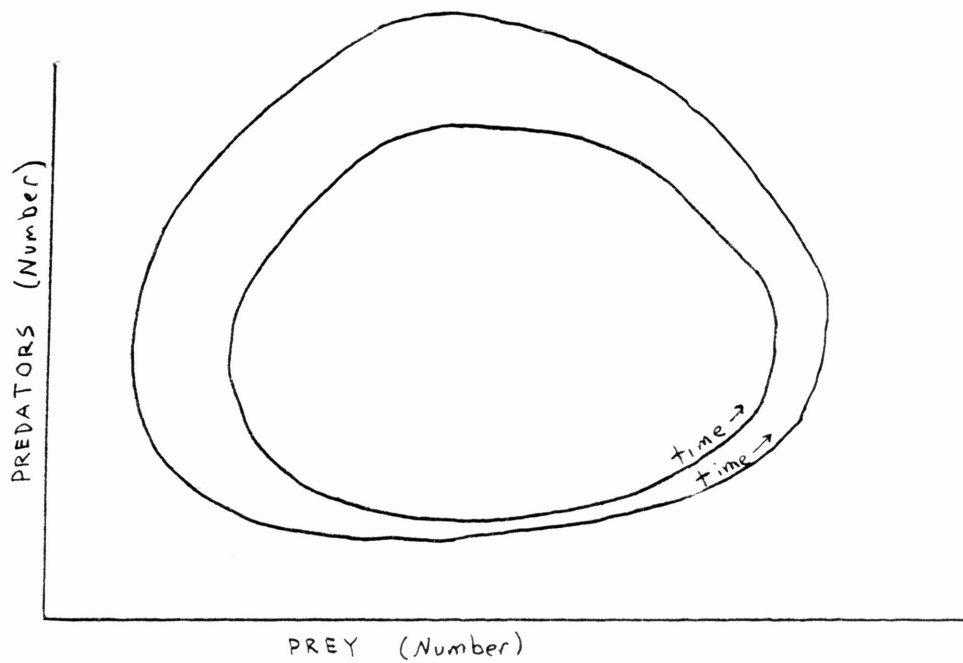


Figure 2.3 Result of Problem with Varied Eating Rate I

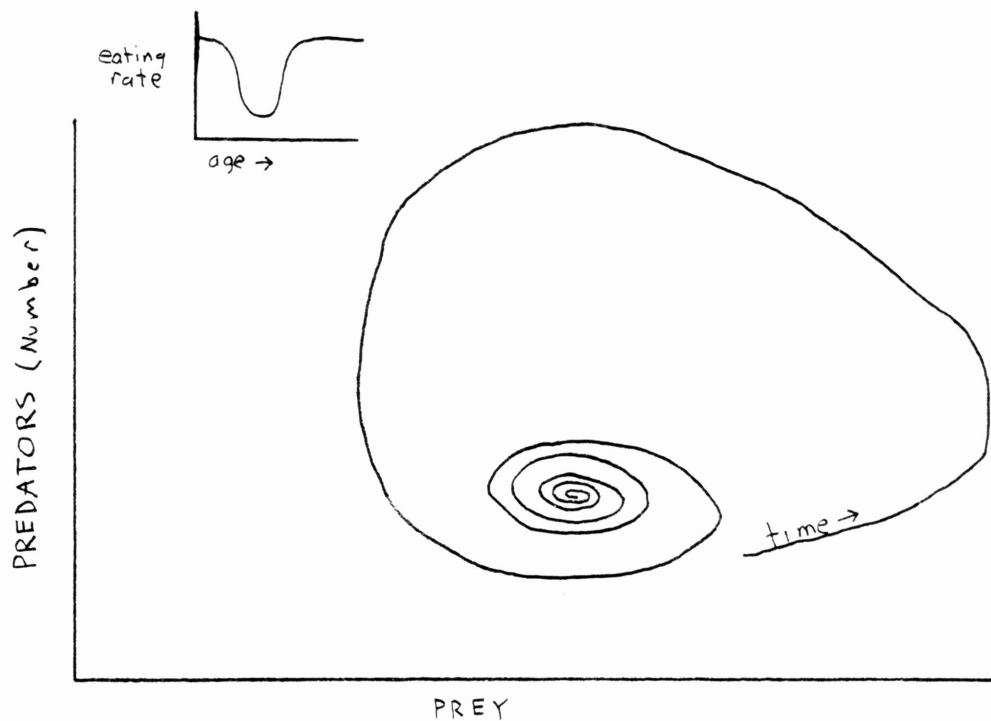


Figure 2.4 Result of Problem with Varied Eating Rate II

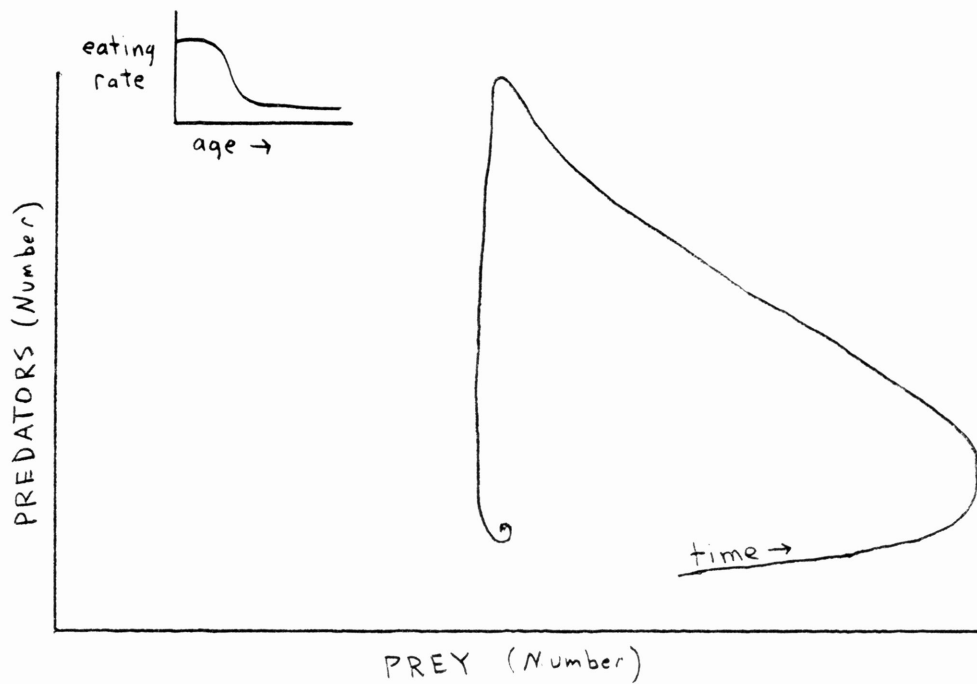
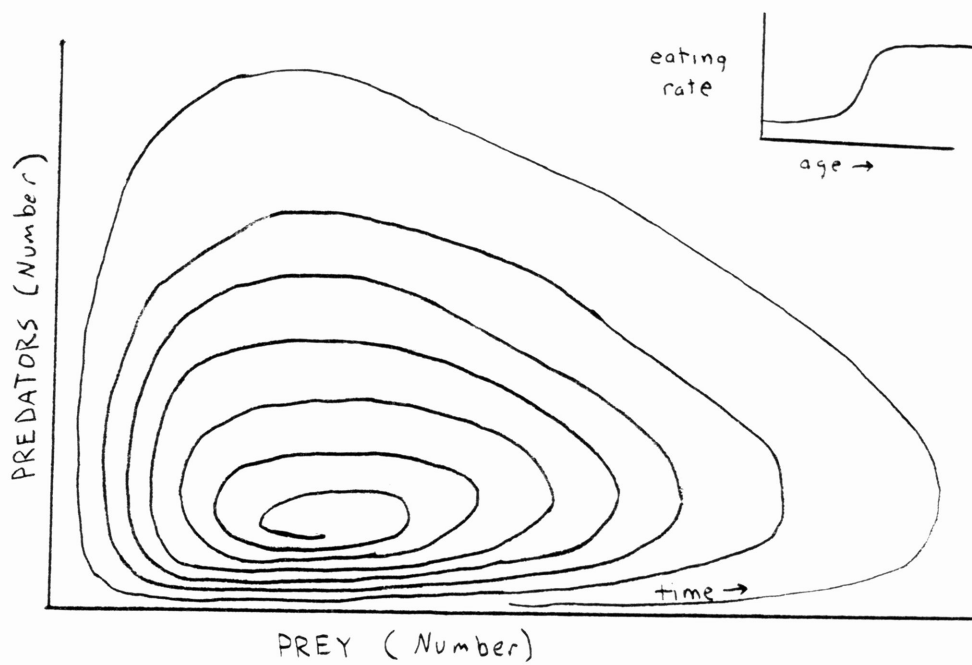


Figure 2.5 Result of Problem with Varied Eating Rate III





This model could be improved. Making the birth and death functions dependent upon the prey population, as well as the age and the predator population, would be a logical change. This would make the equations for the prey population highly non-linear and probably very stable. Another reasonable improvement would be to add the physical limitations of the environment, by considering the density of the population. Beyond these two, any other improvements to this model would be purely pedantic, since this model has almost exceeded the bounds of solvability, as is.

### 3. Computer Simulation of Sample Problem

The assumption made at the beginning of this computer simulation of this problem, is that the solutions are fairly stable. From this assumption, which we will soon see is not that unreasonable, we chose to approach the problem by approximating the functions  $P(t)$ ,  $B(t)$ , and  $Q(t)$  by piecewise linear functions. Using the Finite Element Method, we were able to create a computer program which could give us some of the answers we needed. The first thing to consider is that there are many constants and known functions involved in the expression of our problem. For most of these common sense values were taken. Of course, it would have been best to use values from a real situation, but there are three problems with this. First, we did not have the time to search for data for our problem, second, even if we had some real data, the values needed in the model are not always well-defined, so it would still require some approximation, and third, the object of this computer simulation is to test the general theory of the model, not some particular case. So some trial and error was used to find some numbers that seemed reasonable. For the birth function we used the standard function, which starts out equal to zero at  $t = 0$  and then increases to the maximum birth rate at some optimal age and then decreases asymptotically to zero after that. We assumed that the death function was of the form:

$$\mu(a,t;Q) = \mu_0 + f(a)Q(t),$$

where  $\mu_0$  is the natural death rate, and  $f(a)$  is the selective eating function for the prey. This function was chosen because it is similar to the factor in the Lotka-Volterra predator-prey model, and it is fairly easy

to work with. The initial conditions were chosen to be consistent with other constants.

The process for calculating the approximate solution is to start with an initial guess at  $t = 0$ , and iterate using the equations for  $P(t)$ ,  $B(t)$ , and  $Q(t)$  to get the value at time  $= t + dt$ . The idea is very similar to the method used in the proof of Lemma 3. The advantage to this process is that by iterating many times the error can be kept very small, and that results can be produced at any time.

The results of this computer simulation can be seen in Figures 2.2 - 2.5 of Section 2. The only difference between the 4 graphs is the function chosen for the selective eating process. In Figure 2.2 both curves represent constant eating rates, with the outside one being a low rate and the inside one being a high rate. When this graph was originally done it was thought that any selective eating process with values between the high and low rate would result in a graph which lies between these two curves. Figures 2.3 - 2.5 show that this is not the case. Selective eating causes a spiralling effect, where the populations approach the equilibrium point asymptotically. As we said before, this was not at all expected.

#### 4. Conclusion

This model is more accurate than the Lotka-Volterra predator-prey model, since the age structure gives us more information about the prey, and allows us to have age-structured predation. However, too much has been lost in solvability. At this point, the only results come from a computer simulation, and most of those results cannot be explained. So for any situation where information about the age distribution of the prey is not needed, the Lotka-Volterra model is adequate. The predator-prey model with age-structure could be made better, if more work is done to try and explain some of the behavior seen in the computer simulations. We suspect that it will not be at all easy to show the spiralling effect as a result of a selective eating process.

The future of population dynamics will probably be like its past. Many people will work at making modifications to existing models, until a new idea comes along for a completely different type of model. However, the Verhulst-Pearl equation and the Lotka-Volterra model will still be the standards of population dynamics, because of their fine balance between accuracy and solvability.

## Appendix A

1. Malthusian Model

The assumption of the Malthusian model is that the rate of change of the population is proportional to the population, that is:

$$\frac{d}{dt} P(t) = aP(t),$$

where  $P(t)$  is the total population at time  $t$ , and  $a$  is the growth factor. Solving this we arrive at the following equation:

$$P(t) = P_0 e^{at}, \quad P_0 \text{ is the initial population}$$

Thus for  $a > 0$ ,  $P(t)$  grows without bound. See Figure A.1.

2. Verhulst-Pearl Equation [2]

The Verhulst-Pearl equation is:

$$\frac{d}{dt} P(t) = aP(t)(b - P(t)),$$

where  $a$ ,  $P(t)$  are as defined above, and  $b$  is the carrying capacity.

Solving this equation we get:

$$P(t) = \frac{b}{1 + \left(\frac{b}{P_0} - 1\right)e^{-at}}$$

If  $P_0 < b$  then  $P(t)$  approaches  $b$  asymptotically. See Figure A.2.

3. Linear Predator-Prey Model

The system of equations associated with the linear predator-prey model, where  $Q$  is the predator, and  $P$  the prey, is:

Figure A.1 Malthusian Model Applied to U.S. Population

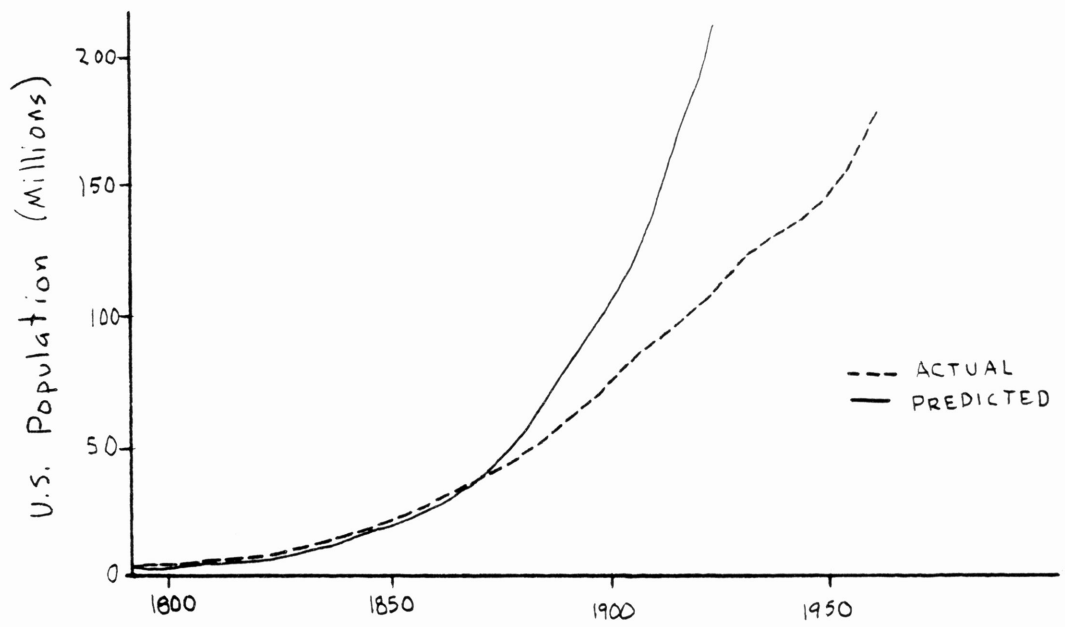
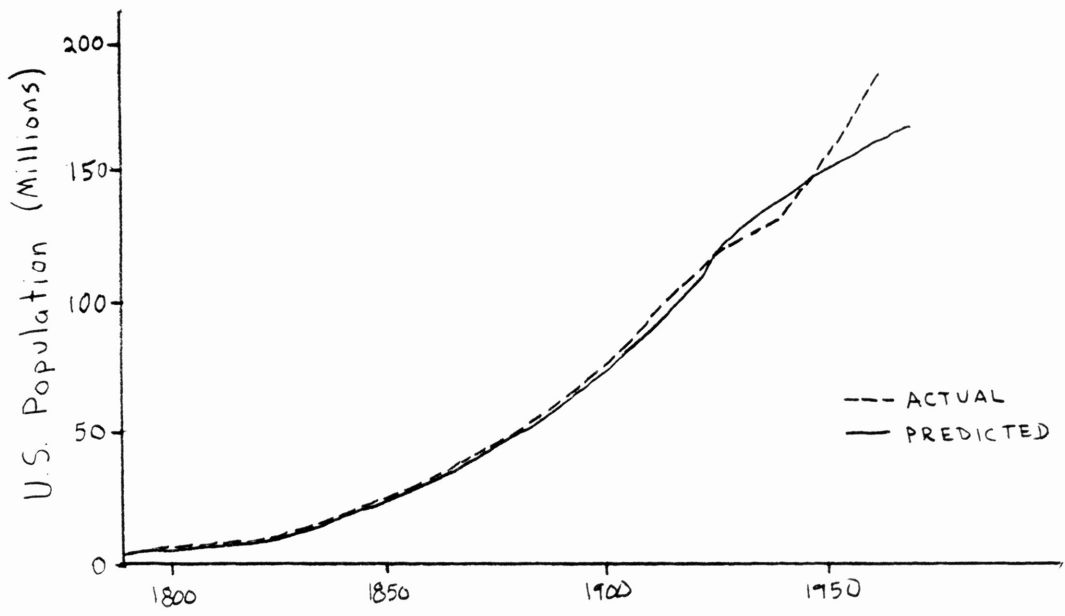


Figure A.2 Verhulst - Pearl Equation Applied to U.S. Population



$$\frac{d}{dt} P(t) = aP(t) - bQ(t)$$

$$\frac{d}{dt} Q(t) = -cQ(t) + dP(t).$$

Written in matrix form, we have:

$$\frac{d}{dt} U(t) = AU$$

where  $a, b, c, d$  are constants  $> 0$ ,  $U = (P, Q)$ ,  $A = (a, b, c, d)$ . This matrix differential equation is solvable, and is dependent on the eigenvalues of the coefficient matrix  $A$ . If the eigenvalues are  $\lambda_1, \lambda_2$ ,  $\lambda_1 \neq \lambda_2$ , then the solution is  $(P_0 e^{\lambda_1 t}, Q_0 e^{\lambda_2 t})$ . If, for instance,  $\lambda_1$  is near zero, the solution for  $P(t)$  would be increasing, constant, or decreasing, depending on whether  $\lambda_1$  was  $> 0, = 0, < 0$ , respectively.

#### 4. Lotka-Volterra Predator-Prey Model [9]

The system of equations for this model are:

$$\frac{d}{dt} P(t) = aP(t) - bP(t)Q(t)$$

$$\frac{d}{dt} Q(t) = -cQ(t) + dP(t)Q(t),$$

where  $P, Q$  are as defined above, and  $a, b, c, d$  are constants  $> 0$ . As mentioned in the text, this problem cannot be solved in closed form, that is there is no equation which gives the solution exactly. One can, however, notice that  $Q(t) = a/b$  and  $P(t) = c/d$  is an equilibrium point. Writing the Taylor series expansion of these two equations about the point  $(c/d, a/b)$ , and ignoring higher order terms, we can arrive at:

$$\frac{d}{dt} \left( P(t) - \frac{c}{d} \right) = - \frac{bc}{d} \left( Q(t) - \frac{a}{b} \right)$$

$$\frac{d}{dt} \left( Q(t) - \frac{a}{b} \right) = \frac{ad}{b} \left( P(t) - \frac{c}{d} \right) .$$

The curve in the P-Q plane, resulting from these equations, is shown in Figure 2.1. This curve is typical of the Lotka-Volterra model. The important result is that if the initial populations are not at the equilibrium point, then the solution tends toward a limit cycle which does not pass through the equilibrium point. We shall see that this is not the case in the predator-prey problem with age structure of Section 2.

#### 5. Sharpe-Lotka Model [3,4]

For this model we need to define some functions first.

$$P(t) = \int_0^{\infty} \rho(a,t) da$$

is the total population, where  $\rho(a,t)$  is the population distribution function.  $\rho(a,t)$  is the number of individuals of age  $a$  alive at time  $t$ .

$$B(t) = \rho(0,t),$$

is the birth rate. It is assumed that the birth rate is governed by a birth law of the form:

$$B(t) = \int_0^{\infty} \beta(a)\rho(a,t) da$$

where  $\beta(a)$ , the birth function, is the average number of offspring (per unit time) produced by an individual of age  $a$ . We also have the death function,  $\mu(a)$ , which is the death rate at age  $a$  per unit population of age  $a$ . From this we can construct the life table  $\pi(a)$ .  $\pi(a)$  is the



probability of living to age  $a$ , and  $\pi(a,b)$  is the probability of living to age  $b$  if presently age  $a$ . Formally this is:

$$\pi(a,b) = e\left(-\int_a^b \mu(t)dt\right)$$

$$\pi(a) = \pi(0,a)$$

With the birth rate, the life table, and the initial age distribution,  $\phi(a) = \rho(a,0)$ , we can determine  $\rho(a,t)$  for all time  $t > 0$ . First, for  $a \geq t$  we have  $\rho(a,t)$  equal to the initial number of age  $a-t$  times the probability of living from age  $a-t$  to age  $a$ . Formally:

$$\rho(a,t) = \pi(a-t,a)\phi(a-t) \quad a \geq t$$

Similarly, for  $a < t$ ,  $\rho(a,t)$  equals the number born at time  $t-a$  times the probability of living to age  $a$ . Formally:

$$\rho(a,t) = \pi(a)B(t-a) \quad 0 \leq a < t$$

Substituting these into the formulas for  $P(t)$  and  $B(t)$  we have:

$$P(t) = \int_0^t \pi(t-a)B(a)da + \int_0^\infty \pi(a,a+t)\phi(a)da$$

$$B(t) = \int_0^t \beta(t-a)\pi(t-a)B(a)da + \int_0^\infty \beta(a+t)\pi(a,a+t)\phi(a)da$$

The equation for  $B(t)$  is the Sharpe-Lotka equation, and is a linear Volterra integral equation for  $B(t)$ . This can be solved using Laplace transforms.

## Appendix B

Some notational conventions which will be used in this Appendix:

$$\mu_1(P) = \mu(\tau-a, \tau; Q_T(P))$$

$$\mu_2(P) = \mu(\tau+a, \tau; Q_T(P))$$

$$\pi_1(P) = \exp\left(-\int_a^t \mu_1(P) d\tau\right)$$

$$\pi_2(P) = \exp\left(-\int_0^t \mu_2(P) d\tau\right)$$

Proof of Lemma 3.

Let

$$P_0 = \int_0^\infty \phi(a) da, \quad r > 0.$$

Let

$$\Omega = \{(a, P) \mid a \geq 0, \quad P \geq 0, \quad |P - P_0| \leq r\}$$

Define the following:

$$\bar{\mu} = \sup_{\substack{(a, P) \in \Omega \\ t \in [0, T]}} \mu(a, t; Q_T(P))$$

$$\bar{\mu}_Q = \sup_{\substack{(a, P) \in \Omega \\ t \in [0, T]}} \frac{d}{dQ} \mu(a, t; Q_T(P))$$

$$\beta_0 = \sup_{a \geq 0} \beta(a)$$

Since  $\beta$ ,  $\mu$ , and  $\frac{d}{dQ} \mu$  are all continuous by (H2), the values  $\bar{\mu}$ ,  $\bar{\mu}_Q$ , and  $\beta_0$  are well-defined and finite. Now consider the complete Banach space  $C[0, T]$  with the sup norm:

$$\|X(t)\|_T = \max_{t \in [0, T]} |x(t)|,$$

Let  $D_T = \{f \mid f \in C^+[0, T], \|f - P_0\|_T \leq r\}$ . Since  $C[0, T]$  is complete and  $D_T$  is a closed subset of  $C[0, T]$ ,  $D_T$  is complete. So to use Lemma 2 (Banach's Fixed Point Theorem) all we need to show is that  $P_T$  maps  $D_T$  into itself and is contractive, i.e.  $\|P_T(P_1) - P_T(P_2)\|_T \leq \alpha \|P_1 - P_2\|_T$  for all  $P_1, P_2 \in D_T$ , for some  $\alpha < 1$ .

First we will show  $P_T$  maps  $D_T$  into itself. Let  $P \in D_T$ , then

$$B_T(P)(t) = \int_0^t \beta(t-a) \pi_1(P) B_T(P)(a) da + \int_0^\infty \beta(a+t) \pi_2(P) \phi(a) da$$

from the definition of  $B_0$  and the fact that  $\pi(P) < 1$ , we have

$$\begin{aligned} B_T(P)(t) &\leq \int_0^t \beta_0 B_T(P)(a) da + \int_0^\infty \beta_0 \phi(a) da \\ &\leq \beta_0 \int_0^t B_T(P)(a) da + \beta_0 P_0 \end{aligned}$$

and by Lemma 1 (Gronwall's Inequality)

$$B_T(P)(t) \leq \beta_0 P_0 e^{\beta_0 t}$$

Next we have

$$\begin{aligned} |P_T(P)(t) - P_0| &\leq \int_0^t |\pi_1(P) B_T(P)(a)| da + \\ &\quad \int_0^\infty |\pi_2(P) - 1| \phi(a) da \\ |\pi_2(P) - 1| &= \left| \exp\left(-\int_0^t \mu_2(P) d\tau\right) - 1 \right| \end{aligned}$$

Using the fact that  $|e^z - 1| \leq |z| e^{12\gamma}$ , we have:

$$\begin{aligned} \left| \pi_2(P) - 1 \right| &\leq \int_0^t \left| \mu_2(P) \right| d\tau \exp\left(\int_0^t \left| \mu_2(P) \right| d\tau\right) \\ &\leq \bar{\mu}t \exp(\bar{\mu}t) \end{aligned}$$

so, using the previous approximations, we have

$$\begin{aligned} \left| P_T(P)(t) - P_0 \right| &\leq \int_0^t \beta_0 P_0 e^{\beta_0 a} da + \sup_{\substack{a>0 \\ t \in [0, T]}} \left| \pi_2(P) - 1 \right| \int_0^\infty \phi(a) da \\ &\leq P_0 (e^{\beta_0 T} - 1) + P_0 \bar{\mu} T e^{\bar{\mu} T}, \end{aligned}$$

which for sufficiently small  $T$  can be made less than  $r$ . So

$P_T(P) \in D_T$ .

Now we will show that  $P_T$  is contractive. Let  $P_1, P_2 \in D_T$ , then

$$\|P_T(P_1) - P_T(P_2)\|_T = I + II + III, \quad \text{where}$$

$$I = \left| \int_0^t (\pi_1(P_2) - \pi_2(P_2)) B_T(P_2) da \right|$$

$$II = \left| \int_0^t \pi_1(P_2) (B_T(P_1) - B_T(P_2)) da \right|$$

$$III = \left| \int_0^\infty (\pi_2(P_1) - \pi_2(P_2)) \phi(a) da \right|$$

First let us look at III.

$$\begin{aligned} III &\leq \int_0^\infty \left| \pi_2(P_1) - \pi_2(P_2) \right| \phi(a) da \\ &\leq P_0 \sup_{\substack{a>0 \\ t \in [0, T]}} \left| \pi_2(P_1) - \pi_2(P_2) \right| \end{aligned}$$

$$\begin{aligned}
|\pi_2(P_1) - \pi_2(P_2)| &= \left| \exp\left(-\int_0^t \mu_2(P_1)d\tau\right) - \exp\left(-\int_0^t \mu_2(P_2)d\tau\right) \right| \\
&\leq \left| \exp\left(-\int_0^t \mu_2(P_1)d\tau\right) \right| \left| 1 - \exp\left(-\int_0^t \mu_2(P_1) - \mu_2(P_2)d\tau\right) \right| \\
&\leq \int_0^t |\mu_2(P_1) - \mu_2(P_2)| d\tau \exp\left(\int_0^t |\mu_2(P_1) - \mu_2(P_2)| d\tau\right) \\
|\mu_2(P_1) - \mu_2(P_2)| &= \left| \frac{\mu_2(P_1) - \mu_2(P_2)}{Q_T(P_1) - Q_T(P_2)} \right| \cdot |Q_T(P_1) - Q_T(P_2)| \\
&\leq \left| \frac{d}{dQ} \mu_2(P_1) \right| \cdot |Q_T(P_1) - Q_T(P_2)| \\
&\leq \bar{\mu}_Q \|Q_T(P_1) - Q_T(P_2)\|_T
\end{aligned}$$

so

$$\begin{aligned}
\text{III} &\leq P_0 \bar{\mu}_Q T e^{2\bar{\mu}T} \|Q_T(P_1) - Q_T(P_2)\|_T \\
\|Q_T(P_1) - Q_T(P_2)\|_T &\leq \|e^{-ct}\|_T \|e^{\int_0^t P_1 d\tau} - e^{\int_0^t P_2 d\tau}\|_T \\
&\leq d \|P_1 - P_2\|_T e^{\|\int_0^t P dt\|_T} \\
&\leq dT \exp(P_0 T e^{\beta_0 T}) \|P_1 - P_2\|_T
\end{aligned}$$

Letting  $K(t) = d\bar{\mu}_Q T^2 \exp(3\bar{\mu}T + P_0 T e^{\beta_0 T})$  we have for sufficiently small  $T$ ,  $K(T) < \frac{1}{3P_0}$ , so:

$$\text{II} \leq P_0 K(T) \|P_1 - P_2\|_T < \frac{1}{3} \|P_1 - P_2\|_T.$$

Now for I:

$$I_1 \leq \|\pi_1(P_1) - \pi_2(P_2)\|_T \int_0^t \beta_0 P_0 e^{\beta_0 T}$$

from previous work we have

$$\|\pi_1(P_1) - \pi_1(P_2)\|_T \leq K(T) \|P_1 - P_2\|_T,$$

so

$$I \leq TK(T) \beta_0 P_0 e^{\beta_0 T} \|P_1 - P_2\|_T$$

which for sufficiently small  $T$  we have

$$I < \frac{1}{3} \|P_1 - P_2\|_T$$

Now for II:

$$II \leq T \|B_T(P_1) - B_T(P_2)\|_T$$

Let  $g(t) = B_T(P_1) - B_T(P_2)$ , then

$$\begin{aligned} g(t) &= \int_0^t \beta(t-a) \pi_1(P_2) g(a) da + \int_0^t \beta(t-a) [\pi_1(P_1) - \pi_2(P_2)] B_T(P_2) da \\ &\quad + \int_0^\infty \beta(a+t) [\pi_2(P_1) - \pi_2(P_2)] \phi(a) da \end{aligned}$$

Letting  $f(t)$  denote the last two integrals:

$$g(t) \leq \beta_0 \int_0^t g(a) da + |f(t)|$$

and by Lemma 1 (Gronwall's inequality)

$$|g(t)| \leq |f(t)| + \beta_0 \int_0^t |f(a)| e^{\beta_0(t-a)} da$$

We have from definition of  $f(t)$ :

$$\begin{aligned} |f(t)| &\leq \beta_0 (\beta_0 P_0 e^{\beta_0 T}) TK(T) \|P_1 - P_2\|_T \\ &\quad + \beta_0 P_0 K(T) \|P_1 - P_2\|_T \end{aligned}$$

$$\begin{aligned} |f(t)| &\leq K_0 \|P_1 - P_2\|_T \quad \text{where} \\ K_0 &< 1/3 \quad \text{for sufficiently small } T. \end{aligned}$$

Thus

$$|g(t)| \leq K_0 \|P_1 - P_2\|_T + K_0 \|P_1 - P_2\|_T e^{\beta_0 T}$$

which implies that for small  $T$ ,

$$II < \frac{1}{3} \|P_1 - P_2\|_T.$$

So we have

$$\begin{aligned} \|P_T(P_1) - P_T(P_2)\|_T &\leq I + II + III \\ &\leq \alpha \|P_1 - P_2\|_T \end{aligned}$$

where  $\alpha < 1$  for sufficiently small  $T$ .

Therefore we have shown that  $P_T(P)$  is contractive, and thus by Lemma 2 has a unique fixed point.

### Proof of Theorem 2

Let

$$\begin{aligned} P_0 &= \int_0^\infty \phi(a) da \\ \beta_0 &= \sup_{a>0} \beta(a) < +\infty \\ \mu_0 &= \inf_{\substack{a>0 \\ t \in [0, L]}} \mu(a, t; Q) \\ \delta &= \beta_0 - \mu_0 \end{aligned}$$

then by definition

$$\begin{aligned}\pi(0, t-a, t; Q) &= \exp\left(-\int_a^t \mu(\tau-a, \tau; Q) d\tau\right) \\ &\leq \exp\left(-\int_a^t \mu_0 d\tau\right) = e^{-\mu_0(t-a)} \\ \pi(a, a+t, t; Q) &= \exp\left(-\int_0^t \mu(\tau+a, \tau; Q) d\tau\right) \\ &\leq \exp\left(-\int_0^t \mu_0 d\tau\right) = e^{-\mu_0 t}\end{aligned}$$

So

$$\begin{aligned}B(t) &\leq \int_0^t \beta_0 e^{-\mu_0(t-a)} B(a) da + \int_0^\infty \beta_0 e^{-\mu_0 t} \phi(a) da \\ &\leq \beta_0 e^{-\mu_0 t} \int_0^t e^{\mu_0 a} B(a) da + \beta_0 P_0 e^{-\mu_0 t}\end{aligned}$$

and by Lemma 1 (Gronwall's inequality)

$$B(t) \leq \beta_0 P_0 e^{-\mu_0 t} e^{\beta_0 t} = \beta_0 P_0 e^{\delta t}$$

Then

$$\begin{aligned}P(t) &\leq \int_0^t e^{-\mu_0(t-a)} \beta_0 P_0 e^{\delta a} da + \int_0^\infty e^{-\mu_0 t} \phi(a) da \\ &\leq \beta_0 P_0 e^{-\mu_0 t} \int_0^t e^{\mu_0 a} e^{(\beta_0 - \mu_0)a} da + P_0 e^{-\mu_0 t} \\ &\leq P_0 e^{-\mu_0 t} e^{\beta_0 t} = P_0 e^{\delta t}\end{aligned}$$

So  $B(t)$ ,  $P(t)$  can grow at most like a Malthusian population with growth factor  $\delta$ .

### Proof of Theorem 3

From the proof of Lemma 3 and hypothesis we have  $\bar{\mu}$ ,  $\bar{\mu}_Q$  and  $\beta_0$  as defined in Lemma 3, dependent on  $P_0$ , and as functions of  $P_0$  are



continuous. Since the time  $T$  (of Lemma 3) up to which a unique solution exists, is dependent on these parameters  $(\bar{\mu}, \bar{\mu}_0$  and  $\beta_0)$  continuously, we have  $T$  as a continuous function of  $P_0$ .

Define

$$T(P_1, P_2) = \min_{P_1 \leq P_0 \leq P_2} T(P_0).$$

We have existence of a unique solution for all  $t$  such that

$0 \leq t \leq T(P_1, P_2)$  as long as the initial population  $P_0$  is between  $P_1$  and  $P_2$ .

To show existence for all time, let  $\bar{T} > 0$ . If we can show existence up to time  $\bar{T}$ , then, since  $\bar{T}$  is arbitrary, we have global existence.

By theorem 2, as long as  $P(t)$  is a solution of our problem  $P(t) \leq P_0 e^{\delta \bar{T}}$ . Since  $e^{\delta \bar{T}} \geq 1$ , we have  $0 \leq P_0 \leq P_0 e^{\delta \bar{T}}$ , so the solution exists on  $0 \leq t \leq T(0, P_0 e^{\delta \bar{T}})$ . Now letting  $P_0 = P(T(0, P_0 e^{\delta \bar{T}}))$ , i.e. let the starting point be the ending point of the previous solution.

By the same argument as above we can extend our solution by  $T(0, P_0 e^{\delta \bar{T}})$ . Since  $P(t)$  is always bounded above by  $P_0 e^{\delta \bar{T}}$ , this procedure will extend the solution to  $\bar{T}$  in a finite number of steps. Therefore, we have global existence.

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