Different Strokes For Different Folks: The Evolution Of The Distribution Of Traits Within Heterogeneous Populations

Kara Cunningham (California State University, Bakersfield)
Paul Hurtado (University of Southern Colorado)
Heather Watson (Claremont McKenna College)
Georgy Karev (Georgia Technical Institute)

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Abstract

Most population models assume that individuals within a given population are identical, that is, they ignore the fundamental role of variation. By understanding the dynamics within heterogeneous populations, we can more accurately predict population growth and composition. Using computational and analytical techniques, we consider Malthus, logistic and Allee growth models with several different initial parameter distributions. Our results highlight the importance of local dynamics on genetic diversity and, consequently, the role of natural selection on the evolution of traits.

1   Introduction

Many models assume homogeneous populations, that is, all individuals have identical traits. However, in reality this is not an accurate depiction. What is needed is a model that takes into account differences between individuals, that is, a model where selected traits have rates of increase that are different from the average individual [3]. The kinds of differences in attributes that will have the most impact are, for example, death rates and birth rates. In order to further develop what is known about heterogeneous population dynamics, we start with the framework for the model developed by Berezovsky *et al* [1].

Consider a population size $N(t)$ with a growth rate that depends on the total population size and a parameter a. Hence,

$$\frac{dN}{dt} = N(t) \cdot F(N(t), a).\tag{1}$$

The only case we consider in this paper is the case where $F(N(t), a) = f(N(t)) + a \cdot g(N(t))$ which includes the Malthus, logistic, and Allee growth models.

In a heterogeneous population, where each individual has its own growth parameter a, it is possible to group individuals with equivalent parameter values. Let $l(t, a)$ represent the number of individuals at time t with parameter a. By definition, the distribution function of a can be written as

$$P_t(a) = \frac{l(t, a)}{N(t)}\tag{2}$$

Then, with further calculations outlined later in the paper, the following equation is reached:

$$P_t(a) = e^{(a \cdot p(t))} \cdot q(t) \cdot \frac{P_0(a)}{M_0(p(t))}\tag{3}$$

where $p(t)$ and $q(t)$ are given by $\frac{dp}{dt} = g(N(t))$ and $\frac{dq}{dt} = q \cdot f(N(t))$ with initial conditions $p(0) = 0$ and $q(0) = 1$. $P_0(a)$ is the initial distribution of parameter a and $M_0(p(t))$ is the moment generating function of that initial distribution of a, evaluated at $p(t)$.

We want to see how different growth models and initial parameter distributions affect what the parameter distribution will be at a later time. (3) gives us the distribution function of parameter a at time t as a function of

the growth model and the initial distribution. Therefore, we study the impact of the populations dynamics on the evolution of the initial distribution of parameter a. By studying a distribution's evolution, we gain a better understanding of these local dynamics and their impact upon heterogeneous population models.

1.1 Background of Natural Selection

Natural selection occurs when the environment changes and the more reproductively successful forms are likely to increase in frequency [5]. Some factors that affect natural selection are fitness which includes birth rate or adaptability. We define fitness as a measure of an individual's ability to survive and reproduce [4]. Here, we focus on the impact of a gradient of fitness in a population. We interpret higher fitness of a specific trait to mean a higher net growth rate.

Fisher's Fundamental Theorem of Natural Selection states that, for a heterogeneous population, the rate of increase of the average fitness in the population is equal or roughly equal to the population's variance in fitness [3]. The equation,

$$\frac{dr(t)}{dt} = \sigma^2(t) \tag{4}$$

is used for haploid populations with Malthus growth, where r is the average growth rate of the individuals in the population [6]. Therefore, a population with a larger variance, will increase in average fitness at a greater rate than a population with a smaller variance. In other words, the rate at which natural selection acts upon a parameter distribution within a population is controlled by the variance of that parameter distribution [6].

2 Parameter Distribution Equation

The following discussion and equations are paraphrased from [1]. We begin with a general population dynamics model given by

$$\frac{dN(t)}{dt} = N(t) \cdot F(N(t), a),$$

where $N(t)$ is the total populations size and $F(N(t), a)$ is the growth factor of the population with parameter value a. Again, let $l(t, a)$ represent the

3

number of individuals at time t with parameter a. It follows that

$$N(t) = \int_A l(t, a)\,da, \tag{5}$$

where $A = \{\text{set of all possible } a \text{ values}\}$. For each different a-group $l(t, a)$, the rate of change of $l(t, a)$ is given by

$$\frac{d[l(t, a)]}{dt} = l(t, a) \cdot F(N(t), a). \tag{6}$$

Note that the growth factor is dependent on the size of the total population and not on the size of the a-group. For a more complete discussion on this rationale see [1].

In addition,

$$l(0, a) = l_0(a), \tag{7}$$

$$N_0 = N(0) = \int_A l_0(a)\,da. \tag{8}$$

Our goal is to compute $P_t(a)$, that is, the parameter distribution function at any time t. Where,

$$P_t(a) = \frac{l(t, a)}{N(t)}.$$

Hence, consider the growth factors $F(N(t), a)$ of the form

$$F(N(t), a) = f(N(t)) + a \cdot g(N(t)). \tag{9}$$

The functions $p(t)$ and $q(t)$ defined by,

$$\frac{dp}{dt} = g(N(t)), \tag{10}$$

$$\frac{dq}{dt} = q \cdot f(N(t)), \tag{11}$$

where $p(0) = 0$ and $q(0) = 1$ are quite useful. We solve for $l(t, a)$ by subsituting (9) into (6) to obtain the following:

$$\frac{d[l(t, a)]}{dt} = l(t, a) \cdot [f(N(t)) + a \cdot g(N(t))]$$

4

Using separations of variables and integrating with respect to t gives

$$\int \frac{d[l(t,a)]}{l(t,a)dt}dt = \int f(N(t))dt + \int a \cdot g(N(t))dt. \qquad (12)$$

Further substitution of (10) and (11) into Equation (12) gives

$$l(t,a) = q(t) \cdot e^{a \cdot p(t)} \cdot e^c. \qquad (13)$$

If we let $l_0(a) = e^c$, (13) becomes

$$l(t,a) = l_0(a) \cdot q(t) \cdot e^{a \cdot p(t)}. \qquad (14)$$

The moment generating function of $l(t,a)$ and $l_0(a)$ are given by

$$U_t(\lambda) = \int_A e^{\lambda \cdot a} \cdot l(t,a)da, \qquad (15)$$

$$U_0(\lambda) = \int_A e^{\lambda \cdot a} \cdot l_0(a)da. \qquad (16)$$

Hence,

$$M_t(\lambda) = \frac{U_t(\lambda)}{N(t)} \qquad (17)$$

where,

$$M_t(\lambda) = \int_A e^{\lambda \cdot a} \cdot P_t(a)da, \qquad (18)$$

which is the moment generating function of $P_t(a)$. From (17) and (18) we can find N(t). The subsitution of Equation (14) into (5) gives

$$N(t) = \int_A l_0(a) \cdot q(t) \cdot e^{a \cdot p(t)}da.$$

Using (18), (16), and (17), this implies that

$$N(t) = q(t) \cdot N_0 \cdot M_0(p(t)). \qquad (19)$$

Equations (10), (11) and (19) allows us to solve for $N(t)$ from the computation of $p(t)$ and $q(t)$. Substituting Equations (14) and (19) into (2) and using $P_0(a) = \frac{l_0(a)}{N_0}$ gives

$$P_t(a) = \frac{e^{a \cdot p(t)} \cdot P_0(a)}{M_0(p(t))}.$$

This is the primary equation used for determining the evolution of the parameter distributions studied throughout the remainder of this paper.

3 Methodology

To model the evolution of the distribution of parameter a, we use equation (3) and numerically study several different initial distributions. We designed a Matlab program that graphically displays changing distributions of a with respect to time. The program also outputs graphs of $p(t)$ with respect to time, and total population size with respect to time. This program consists of m-files that return values for the moment generating function and the density, or mass function for each distribution. In the case of logistic and Allee growth models, $p(t)$ can not be explicitly solved. Therefore, we chose to use computational techniques to solve $p(t)$ and look at its effect upon the distributions as they change with time. This capability allows us to analyze the effects of different growth models. It should be noted that $p(t)$ can be interpreted as an internal time for the models considered here.

The number of different distributions and cases of N_0 in some of the models, also influenced the decision to study these distributions computationally. By including the different distributions and their moment generating functions, we can generate a large number of different graphical representations of the changing distributions in a very short ammount of time.

In order to study the changes in a distribution over time we use equation (3), which was derived in a previous section, given by

$$P_t(a) = e^{(a \cdot p(t))} \cdot q(t) \cdot \frac{P_0(a)}{M_0(p(t))}.$$

This function uses an initial distribution and it's moment generating function to evaluate the distribution of a at a given time t. The changes in the distribution are influenced by $p(t)$, which is determined by the chosen growth model. To study these effects, we selected three different kinds of growth models: Malthus, logistic, and Allee. To see examples of these population models, please refer to part (**D**) of the Figures in the following sections.

We began our simulation with the simplest model, the Malthus model: $\frac{dN}{dt} = N(t) \cdot a$. Malthus growth is basically exponential and thus can be unbounded. For our equation, the Malthus form is $F(N(t), a) = a$. Since $F(N(t), a) = f(N(t)) + a \cdot g(N(t))$, we know $f(N(t)) = 0$ and $g(N(t)) = 1$, thus for $p(t)$ we have $\frac{dp}{dt} = 1$. That is, time is not rescaled and therefore

$$p(t) = t_0$$

6

In nature, Malthus growth exists in the first stages of an unrestricted population explosions such as algae blooms, but should not be valid for large time values due to environmental limitations.

Next we looked at the logistic growth model

$$\frac{dN(t)}{dt} = N(t) \cdot a \cdot \left(1 - \frac{N(t)}{K}\right).$$

This is usually considered a more useful model than Malthus, since it is often associated with simple population growth that is limited only by population density; for example, organisms growing under lab conditions. The carrying capacity of a logistic equation represents the stable equilibrium for the population size. For our purposes, we use the normalized logistic equation where $K = 1$. Hence

$$F(N(t), a) = a \cdot (1 - N(t)).$$

That is, $f(N(t)) = 0$ and $g(N(t)) = (1 - N(t))$. Here, $\frac{dp}{dt} = 1 - N(t)$. Since $N(t) = N_0 \cdot q(t) \cdot M_0(p(t))$, we have that

$$\frac{d[p(t)]}{dt} = 1 - N_0 \cdot q(t) \cdot M_0(p(t)).$$

Recall $K = 1$, $f(N(t)) = 0$, and $q(0) = 1$. Thus, it follows that $q(t) = 1$. Additionally $p(t)$ satisfies

$$\frac{d[p(t)]}{dt} = 1 - N(t),$$

where

$$N(t) = N_0 \cdot M_0(p(t)).$$

Hence, our initial population size is chosen for two cases; $N_0 < K = 1$ or $N_0 > 1$.

Then, we looked at the Allee growth model,

$$\frac{dN}{dt} = N(t) \cdot a \cdot \left(1 - \frac{N(t)}{K}\right) \cdot (N(t) - \alpha).$$

This model can also be considered more useful model since it takes into account the possibility of a population becoming too low in numbers to sustain

7

growth. Thus, the Allee model can be used for such situations as modeling the reintroduction of endangered species, where α is a threshold below which the population will die. We used the normalized Allee equation for our investigations where $K = 1$. This normalized Allee model is given by

$$F(N(t), a) = a \cdot (1 - N(t)) \cdot (N(t) - \alpha).$$

Thus, $f(N(t)) = 0$ and $g(N(t)) = (1 - N(t)) \cdot (N(t) - \alpha)$. Again $q(t) = 1$, and $p(t)$ satisfies

$$\frac{dp}{dt} = (1 - N(t)) \cdot (N(t) - \alpha), \tag{20}$$

$$N(t) = N_0 \cdot M_0(p(t)), \tag{21}$$

where our initial population size is either; $N_0 < \alpha, \alpha < N_0 < 1$, or $N_0 > 1$.

With these three models, we analyzed six continuous distributions: normal, truncated normal, exponential, uniform, truncated exponential, and a hybrid exponential x uniform distribution (see Appendix 7.1). We also include a brief analysis of a discrete distribution, the Poisson. The continuous distributions, exponential, uniform, and normal were chosen, because they well known and commonly used. It is often reasonable to assume that a limit exists on the variations available in a gene pool at any given time. The biological limit of variation of parameter a can be represented by using truncated distributions. To illustrate this view, we included the truncated normal distribution, truncated exponential distribution, and the previously mentioned hybrid distribution. A discrete distribution was included to show how the model could be extended to approximate discrete distributions for factors such as family size or fecundity [7]. Using additional equations from [1], we found the general mean and variance of each distribution at any $p(t)$ (see Appendix). These also aid us in understanding the dynamics of an evolving parameter distribution $P_t(a)$.

4 Analysis

Before we discuss specific parameter distributions, we introduce some of the general trends found. This will help focus our analysis on the specifics of each distribution.

When considering positive values of a, it may be helpful to assume that this parameter corresponds to the growth rate. With increasing population

8

size, we see a higher frequency of individuals with larger a values over time. The interpretation of negative parameter values is quite different. Their effect will be discussed later on.

To look at the effect $p(t)$ has on the parameter distribution, we focus on the Malthus model where $p(t) = t$. Under this model, the mean value of the parameter a increases with t. In general, whenever $N(t)$ is decreasing $p(t)$ decreases below 0, and the growth rate, $F(N(t), a)$, is negative. It is a net reproductive rate where the death rate is "winning". That is, with time there is an increase in the relative abundance of smaller a values within the population as the number of individuals with high parameter values decrease at a faster rate. The mean parameter value will also decrease in this case, and as above, for bounded distributions, the variance will decrease towards 0.

With logistic growth, the changes initially resemble those observed with Malthus growth. However, as $N(t) \to 1$, $p(t)$ and the density function $P_t(a)$ approach finite limits. Thus, as the population tends towards its carrying capacity, the trait distribution approaches an equilibrium.

The Allee model has dynamics similar to those of the logistic model (Compare Figure 4and Figure5). However, the eventual distribution depends strongly upon the initial population size. In the Allee growth models with threshold α and $\alpha < N_0 < 1$, the distributions behave in a similar manner to the logistic model for $N_0 < 1$. When $N_0 < \alpha$ or $N_0 > 1$, the population declines. For $N_0 < \alpha$, $N(t) \to 0$, and when $N_0 > 1$, $N(t) \to 1$. While these two situations have drastically different outcomes with respect to the population size, it is clear that the dynamics of the distribution of traits are essentially identical.

For positive a values, we consider the evolution of the parameter distribution to parallel the changes in total population size. A growing population will cause the distribution to evolve towards higher values. That is, the mean will increase. A decreasing population will have the reverse effect, that is a decreasing mean. Let us now compute the specific parameter distributions.

4.1   The Normal Distribution

The normal distribution with mean μ and variance σ^2, is the classic bell curve. Using Equation (3) for the normal distribution we obtain:

$$P_t(a) = \frac{1}{\sqrt{2\pi} \cdot \sigma} e^{-\frac{1}{2} \cdot \frac{(a - \mu + \sigma^2 \cdot p(t))^2}{\sigma^2}}$$
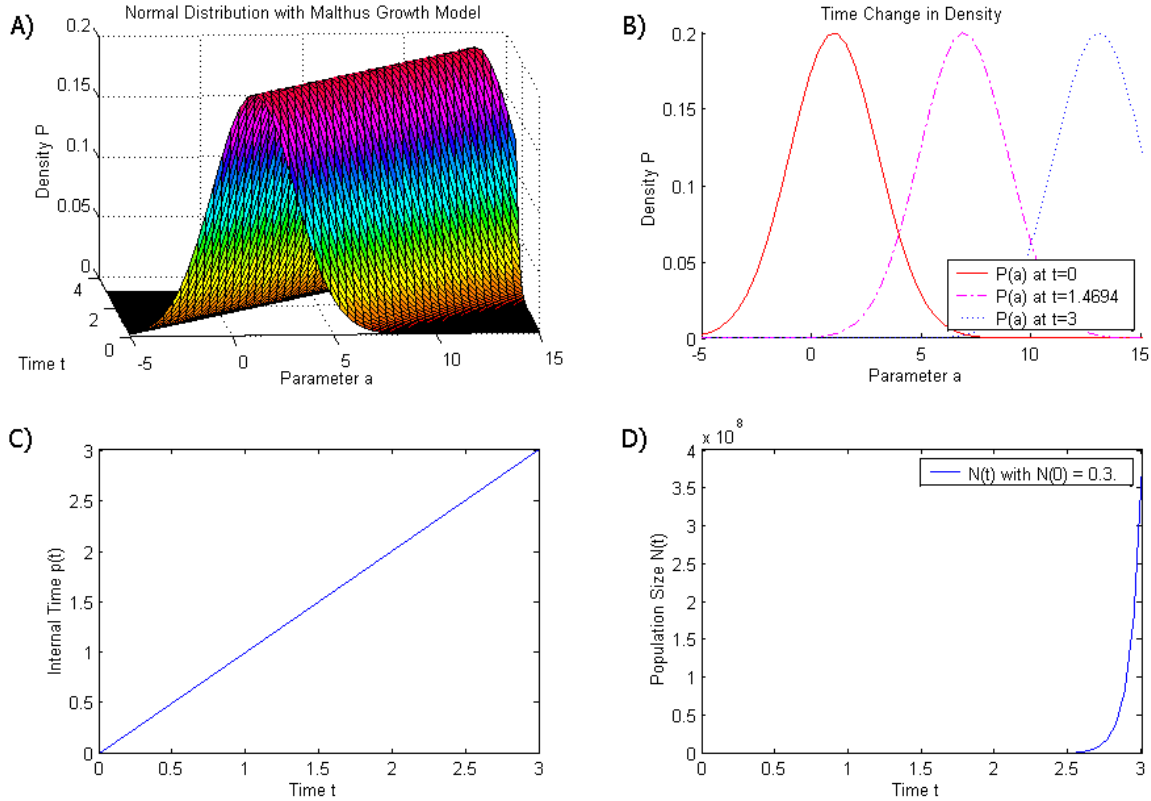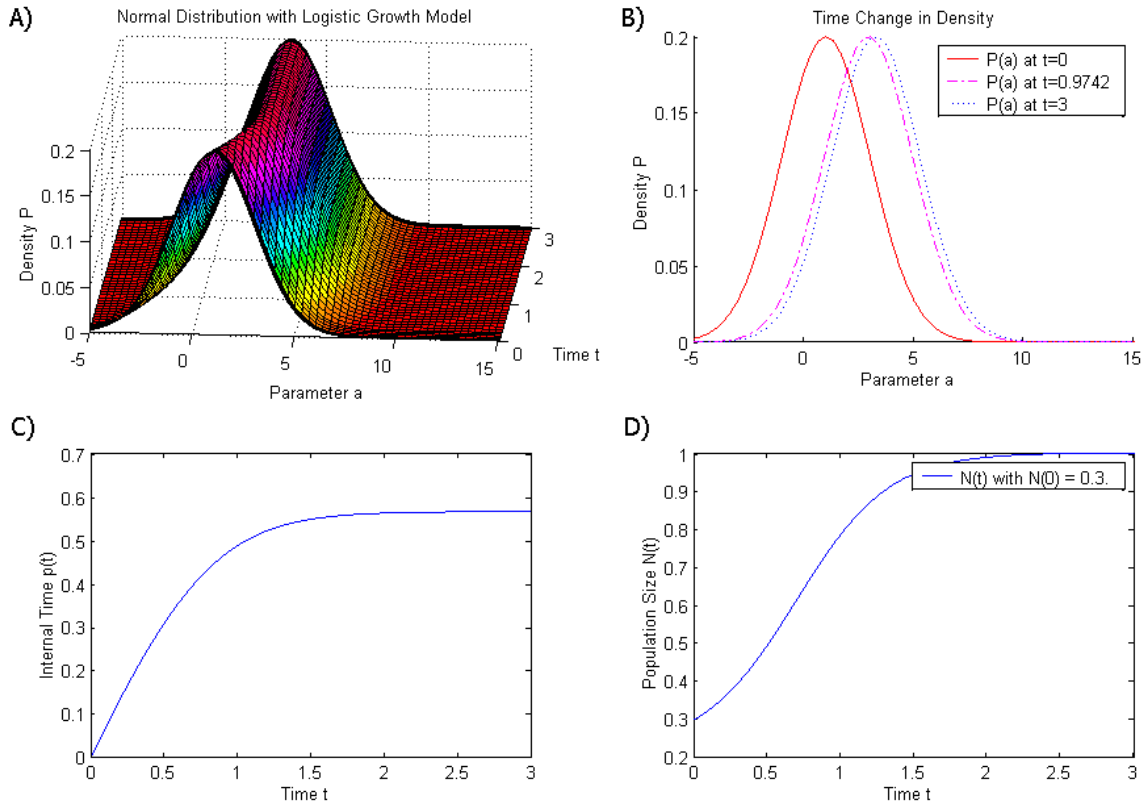
9

Figure 1: Normal Distribution with Malthus Growth: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval.

With the Malthus model, the mean shifts in the positive direction with velocity σ^2 and is unbounded since $p(t) = t$. From the graphs and calculations, an initial normal distribution remains a normal distribution with a changing mean $\mu_t = \mu_0 + \sigma^2 \cdot p(t)$ and a constant variance $\sigma_t^2 = \sigma^2$. In other words, the mean of $P_t(a)$ changes, but the varience and distribution type do not (see Figure 1). Note that the initial variance of our parameter distribution has a direct influence upon the rate of change of the normal distribution. Under the simple Malthus model, our biological interpretation of this distribution evolution is quite limited. Although this simplistic model does provide much insight into the dynamics of the changing normal distribution, it makes little

sense to have the mean diverge to infinity.

Refining our model from Malthus to logistic growth, an initial normal distribution again remains normal. For an initial population N_0 less than the carrying capacity, $p(t)$ approaches a limiting value. Therefore, the mean and varience of the distribution will asymptotically approach a limit value as $N(t) \to 1$ (see Figure 2). Starting with $N_0 > 1$, the population will decline and approach 1. Very similar dynamics occur under the Allee model, for $\alpha < N_0 < 1$.

Figure 2: Normal Distribution with Logistic Growth where $N_0 < 1$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval.

4.2   The Truncated Normal Distribution

The Truncated Normal Distribution with parameters μ and σ^2, truncated between c and d is of the form:

$$P_0(a) = \frac{-\sqrt{2} \cdot e^{-\frac{1}{2} \cdot (\frac{(a-\mu)^2}{(\sigma^2)})}}{(\sigma \cdot \sqrt{\pi} \cdot ((erf(\frac{1}{2} \cdot \sqrt{2} \cdot \frac{(-d+\mu)}{\sigma}) - erf(\frac{1}{2} \cdot \sqrt{2} \cdot \frac{(-c+\mu)}{\sigma})))}$$
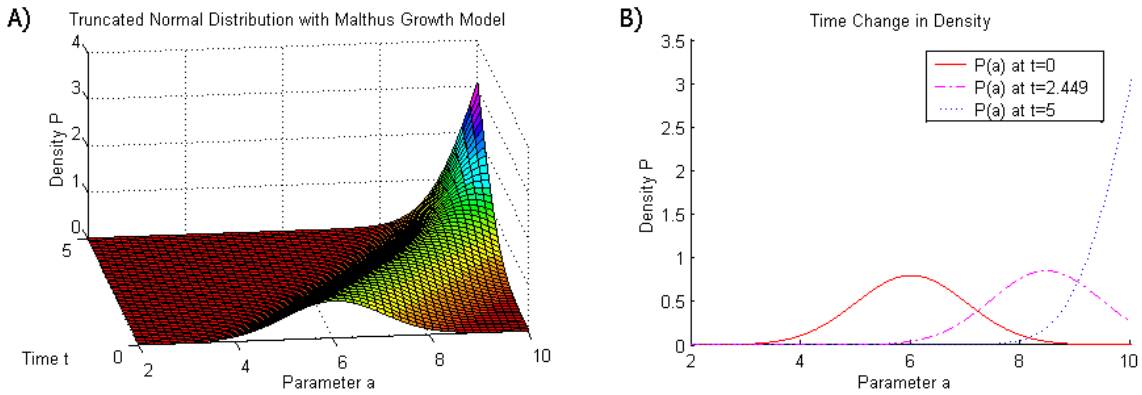
$P_t(a)$ is too large to put in the paper.

Figure 3:   Truncated Normal Distribution with Malthus Growth: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.

For Malthus growth, the truncated normal initially behaves much like the regular normal distribution. However, as the mean comes closer to the truncation point of the initial distribution, the $\sigma^2 \to 0$. Note that this last effect is an marked difference from the standard Normal distribution described above, which had a constant variance. As t increases, the mean approaches the upper boundary, and the variance decreases (see Figure 3). If time were allowed to go to infinity, mathematically the parameter density function would tend towards having infinite height and infinitely small width (small variance), that is, it approaches something similar to the δ-function. Biologically speaking, this could mean that the curve keeps shifting to higher and higher parameters until it reaches the biological limit at the boundary.

For logistic, when $N_0 < 1$, and for Allee, when $\alpha < N_0 < 1$, the distribution starts out like the Malthus, but then slows down and tends towards a final parameter distribution, similar to the Normal Distribution.
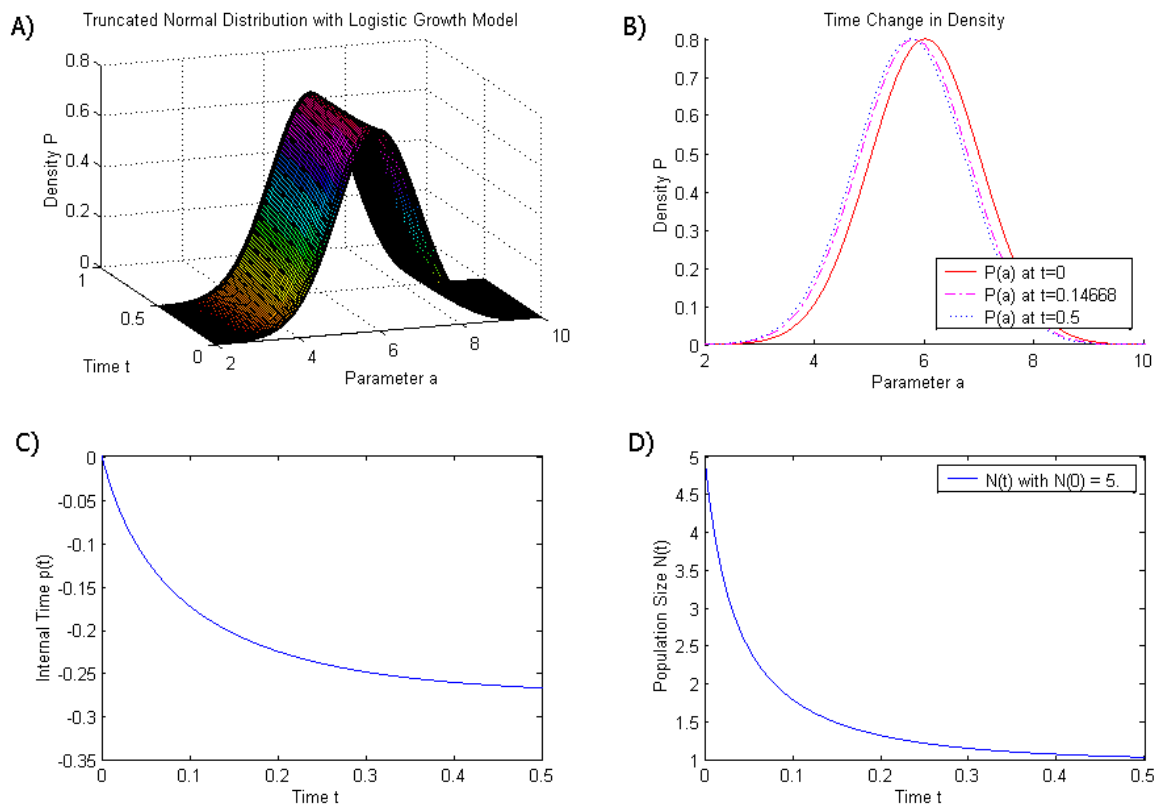
12

Figure 4: Truncated Normal Distribution with Logistic Growth and $N_0 > 1$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval.
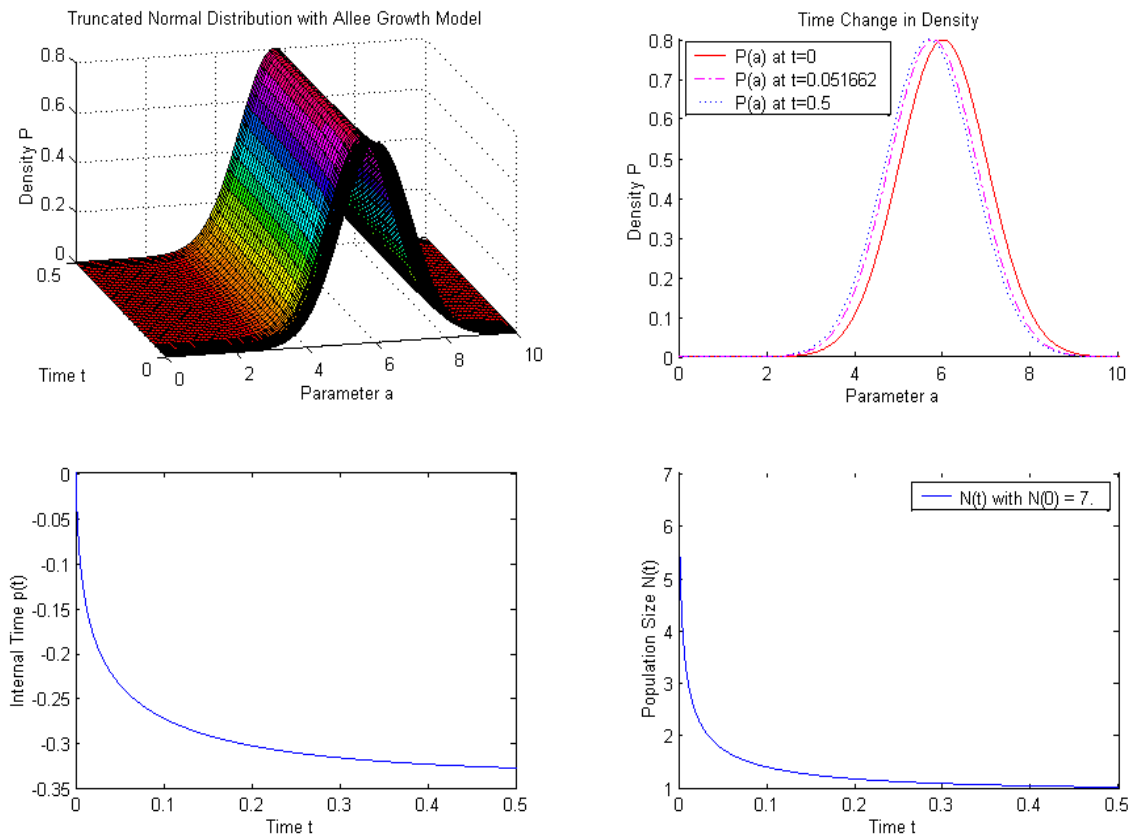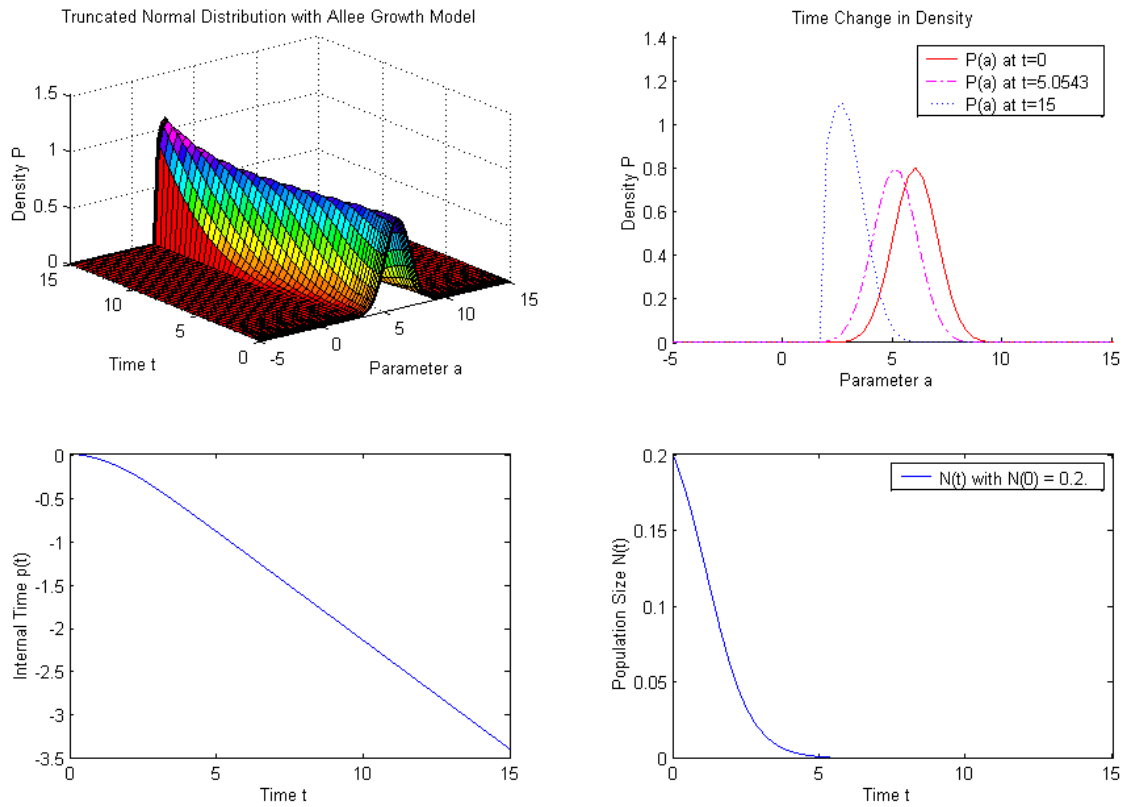
Figure 5: Truncated Normal Distribution with Allee Growth and $N_0 > 1$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval.

14

Figure 6: Truncated Normal Distribution with Allee Growth and $N_0 < \alpha$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval.

For logistic and Allee, when $N_0 > 1$, we see the reverse affects, as $N(t)$ tends back towards the carrying capacity (compare Figures 4 and 5).

For Allee, when $N_0 < \alpha$, $N(t)$ approaches 0, however, the dynamics are almost identical to the case where N_0 is greater than 1 (compare Figure 6 to Figures 4 and 5). We see that for any decreasing population, $F(N(t), a)$ can be perceived as a death rate or net growth rate. We have the same dynamics regardless of the value $N(t)$ is approaching.

4.3   The Exponential Distribution

The exponential distribution has the distribution function:

$$P_0(a) = \lambda \cdot e^{-\lambda \cdot a}$$

By applying Equation (3), we obtain the general equation

$$P_t(a) = e^{a \cdot (p(t) - \lambda)} \cdot (\lambda - p(t))$$

which is still exponential, but with parameter $\lambda - p(t)$. It should be pointed out that because of our moment generating function, this distribution is only valid for $p(t) < \lambda$.

As $p(t) \to \lambda$, this distribution will approach a uniform distribution, however it does not ever become uniform, due to the infinite range of parameter values. In fact, the exponential distribution tends towards 0 as $p(t) \to \lambda$ and is only defined for values of time $p(t) < \lambda$. More interesting results occur with the truncated exponential distribution, which is discussed later in this paper.

With Malthus growth, when $p(t) = t$, the exponential distribution remains exponential with parameter $\lambda - t$. Thus, as $t \to \lambda$, the mean and variance of the distribution go to infinity (see Figure 7).

With logistic growth, for an initial population below 1, the exponential distribution behaves as discussed above for the Malthus model. However, due to $p(t)$ approaching a limiting value, the parameter $\lambda - p(t)$ approaches a limiting value as well. Observe that $p(t)$ is still restricted to values less than λ, however it can be shown that $p(\infty) = \lambda \cdot (1 - N_0)$. Therefore, for the logistic model, there are no time restrictions since $p(\infty) = \lambda \cdot (1 - N_0) < \lambda$. By solving $\frac{dp}{dt} = 0$ to find the limiting value, the distribution is a fixed exponential distribution with the parameter approaching $\lambda - p(\infty) = (\lambda \cdot N_0)$ as the population size approaches 1. For an N_0 greater than 1, the $p(t)$ values
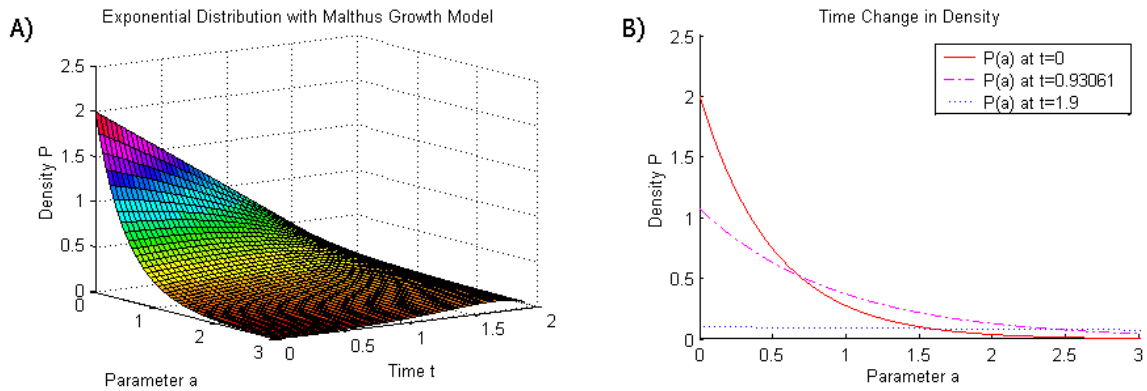
Figure 7: Exponential Distribution with Malthus Growth: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.
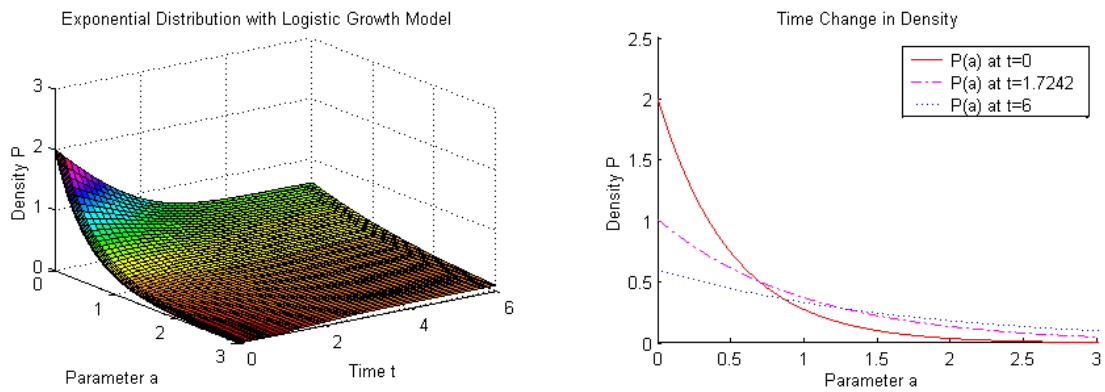

Figure 8: Exponential Distribution with Logistic Growth, $N_0 < 1$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.
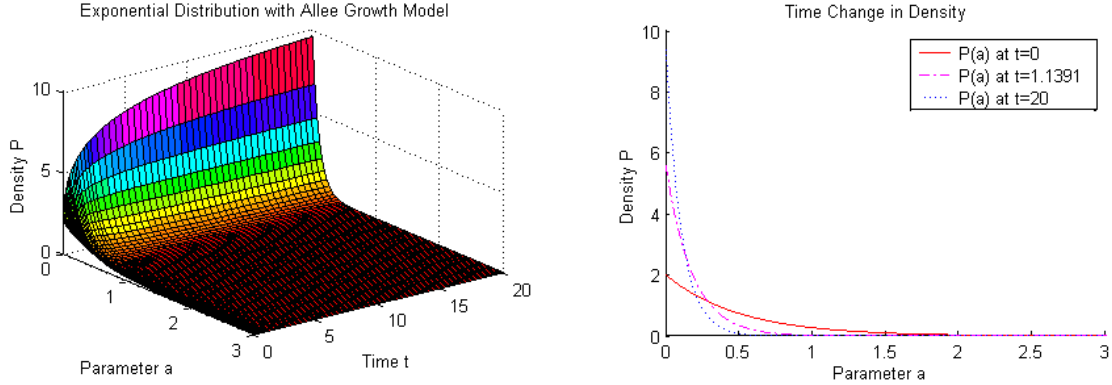
Figure 9: Exponential Distribution with Allee Growth, $N_0 > 1$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.

move with the decrease in population and approach a negative limiting value. Thus, the parameter $\lambda - p(t)$ is increasing towards the limiting value $\lambda \cdot N_0$ as the population size approaches 1 (see Figure 8).

For the Allee model when N_0 is between the threshold value and 1, the evolution of the distribution resembles the evolution seen with logistic growth above. It can be shown that for $N_0 > 1$, the distribution is an exponential distribution with the parameter approaching $N_0 \cdot \lambda$ (see Figure 9). Below the threshold condition, the population dies out as $(N(t) \to 0)$ and the distribution is an exponential distribution with the parameter approaching $\frac{N_0}{\alpha} \cdot \lambda$. Again, we see similar dynamics with these two cases.

4.4 The Uniform Distribution

Consider the uniform distribution with boundary values c and d such that $c < d$:

$$P_0(a) = \frac{1}{(d - c)}$$

This means each parameter value is equally represented within the population initially. Therefore, using Equation (3), we have:

$$P_t(a) = \frac{(p(t) \cdot e^{a \cdot p(t)})}{(e^{d \cdot p(t)} - e^{c \cdot p(t)})}.$$

18

As will be shown later, we see that $P_t(a)$ is of the form of a truncated exponential distribution with $t > 0$. See Equation (22) in the Appendix for details.
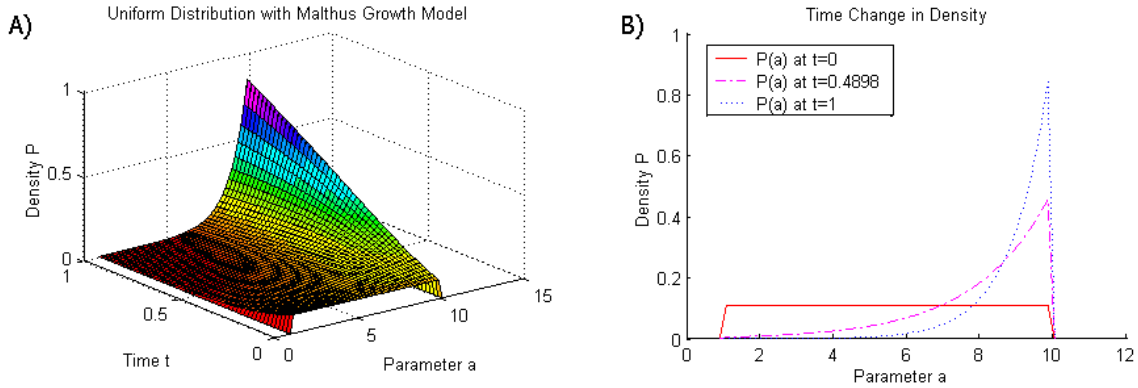

Figure 10: Uniform Distribution with Malthus Growth: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.

For the Malthus growth model, the distribution starts uniform and over time the parameter distribution increases for higher values of our parameter a. Thus, the distribution begins to resemble a positive exponential curve (see Figure 10). The mean tends towards the positive boundary and variance tends to 0 as $p(t) \to \infty$; an expected but still unrealistic result for most applications.

Next we consider the logistic and Allee models. For the logistic model when $N_0 < 1$ for the Allee model when $\alpha < N_0 < 1$, the population still evolves into a distribution resembling a positive exponential curve. The velocity of the change approaches 0 as $p(t)$ approaches its limiting value (see Figure 11). For $N_0 > 1$ for both the logistic and Allee models, and for $N_0 < \alpha$ in the Allee model, the behavior observed is identical to the behavior described at the beginning of the Analysis section for decreasing populations. As can be seen in the next section, the Truncated Exponential Distribution at time t remains truncated exponential but with parameter $\lambda - p(t)$ and when $\lambda - p(t) = 0$ the distribution is uniform. Therefore, for a uniform distrubiton where $p(t)$ is negative, $P_t(a)$ is exponential with parameter $\lambda = -p(t)$ (see Figure 12).
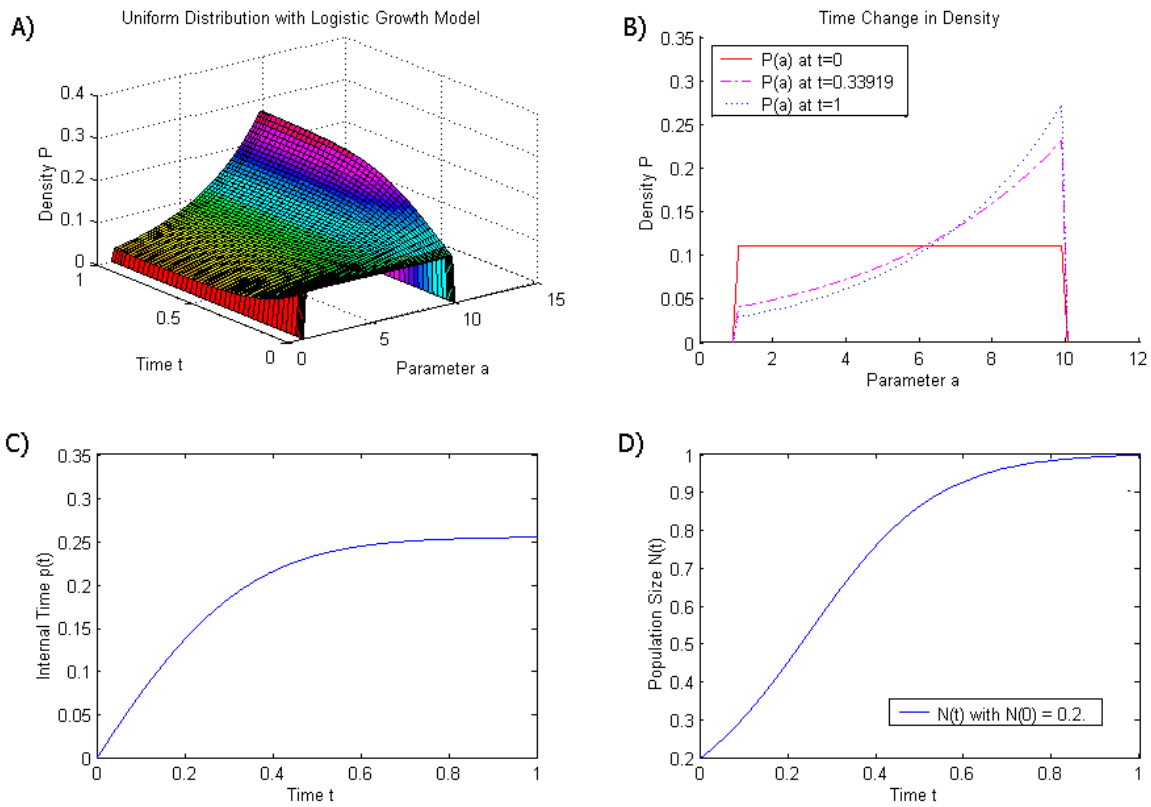
19

Figure 11: Uniform Distribution with Logistic Growth and $N_0 < 1$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval.
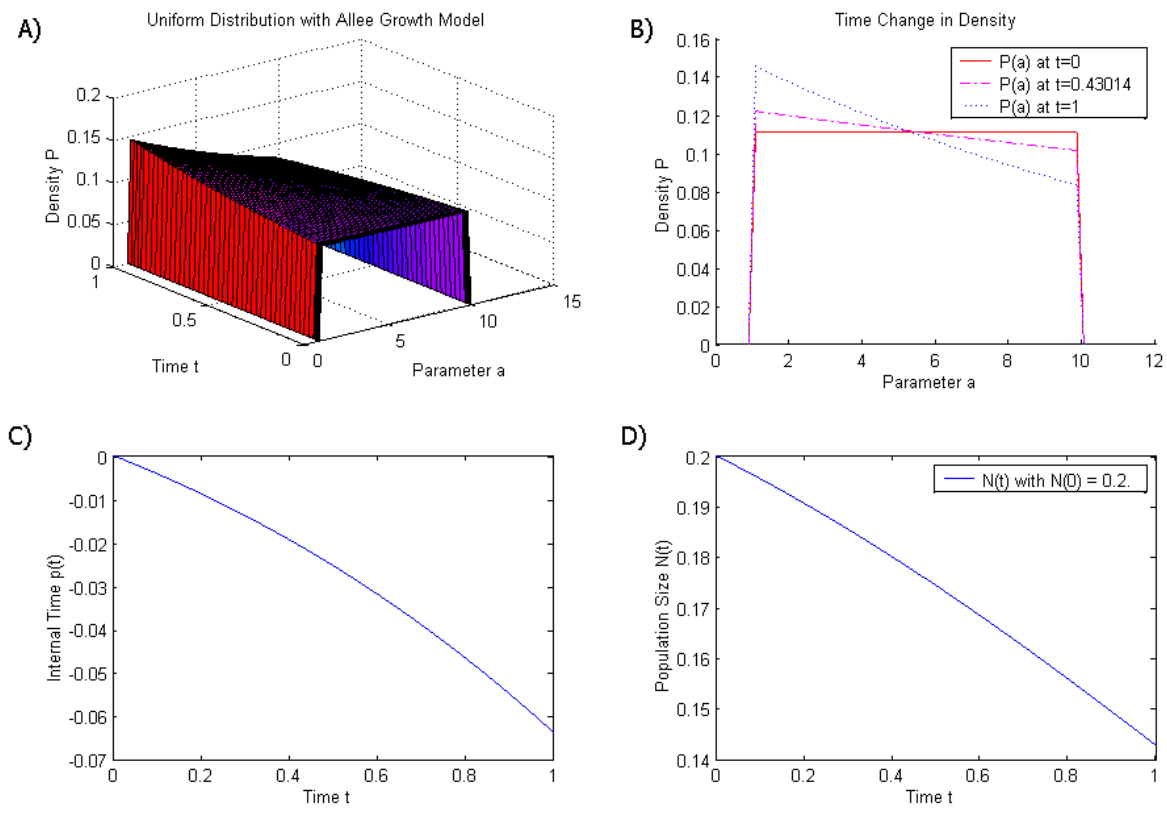
Figure 12: Uniform Distribution with Allee Growth and $N_0 < \alpha$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval.
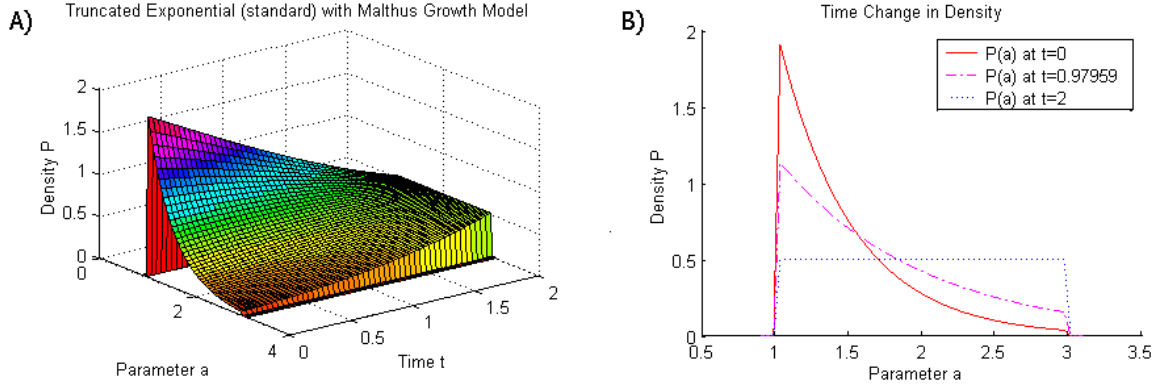
4.5　The Truncated Exponential Distribution

Figure 13: Truncated Exponential Distribution with Malthus Growth. The time ranges from $t = 0..2$: Note the uniform distribution at $t = \lambda$, where $\lambda = 2$. A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.

The truncated exponential distribution with parameter λ, truncated from c to d, is given by the equation:

$$P_0(a) = \lambda \cdot \frac{e^{-\lambda \cdot a}}{e^{-\lambda \cdot c} - e^{-\lambda \cdot d}}$$

Therefore using Equation (3), we see that $P_t(a)$ rearranges to the equation:

$$P_t(a) = \frac{((p(t) - \lambda) \cdot e^{a \cdot (p(t) - \lambda)})}{(e^{d \cdot (p(t) - \lambda)} - e^{c \cdot (p(t) - \lambda)})}. \tag{22}$$

Under Malthus growth, as with the exponential distribution, the truncated exponential distribution tends towards a uniform distribution as $p(t) \to \lambda$ (see Figure 13). However, due to the truncation, the moment generating function is now defined for any $p(t)$ value. This means that the truncated exponential distribution actually does become a uniform distribution at $p(t) = \lambda$ and continues towards an exponential curve (see Figure 15). Furthermore, it can be shown (see Appendix) these distributions are actually identical, in that the uniform distribution at time t is equal to the truncated exponential distribution at time $t + \lambda$. See The Uniform Distribution in the section above for the dynamics of the truncated exponential distribution, and compare Figure 14 with the Uniform distribution in Figure 11.
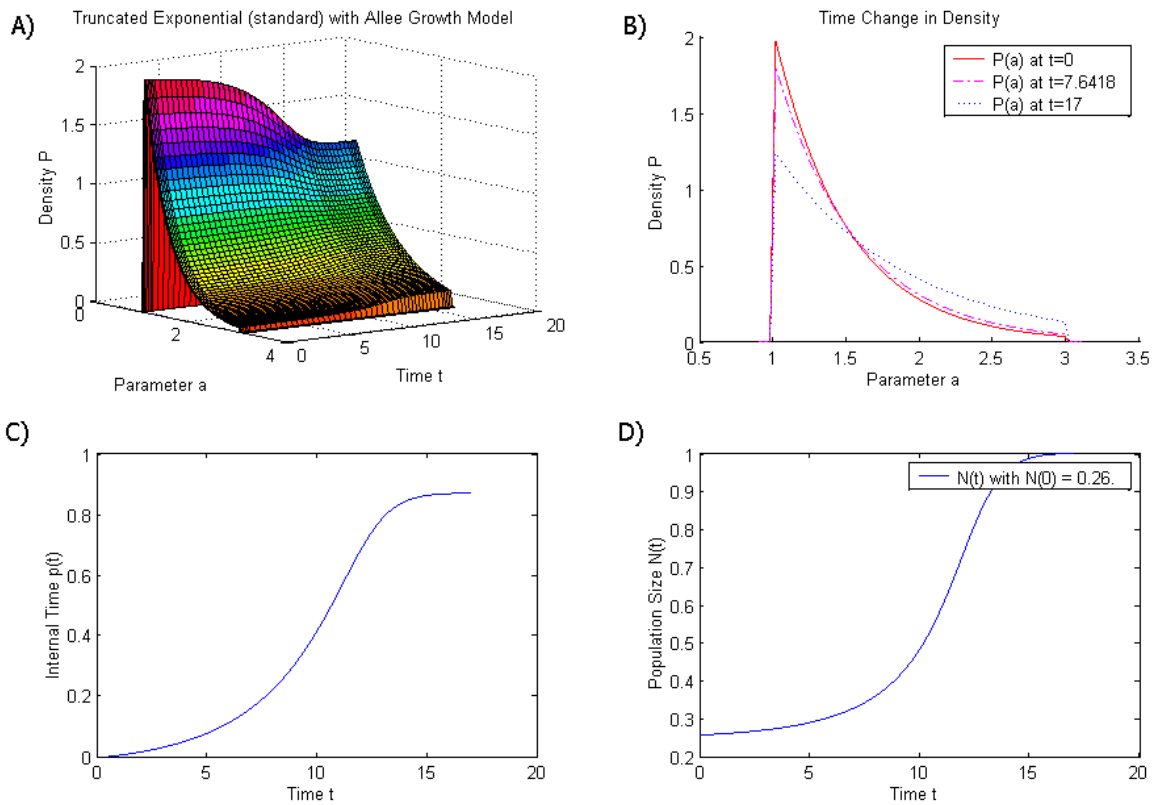
Figure 14: Truncated Exponential Distribution with Alee Growth, $\alpha < N_0 < 1$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval.
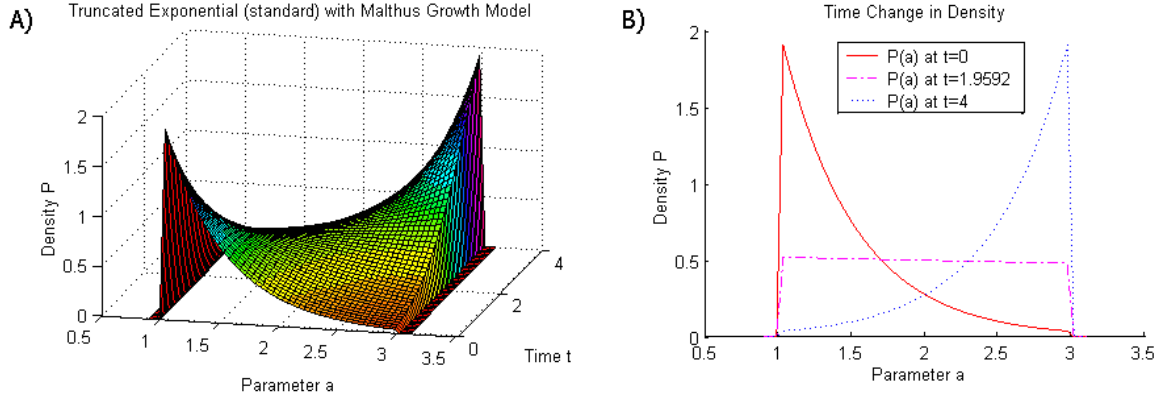
Figure 15: Truncated Exponential Distribution with Malthus Growth. The time ranges from $t = 0..4$: Observe that we can compute distributions for $t > \lambda$. A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.

4.6 The Hybrid Uniform x Truncated Exponential Distribution

As seen in the Appendix 7.1, we derived a different version of the truncated exponential distribution, which is given by:

$$P_0(a) = \lambda \cdot e^{-\lambda \cdot a} + \frac{1 + e^{-\lambda \cdot d} - e^{-\lambda \cdot c}}{d - c}$$

We see that this distribution has characteristics of both the exponential and uniform distribution, therefore the resulting dynamics reflect properties of both distributions. While the graphs of these two distributions appear quite similar, for $p(t) = \lambda$, we observe the slight difference. Whereas the standard distribution is uniform, our hybrid distribution has a slightly higher density for the larger parameter values (see Figure 16) and compare to Figure 13. We see from the previous comparison of the truncated exponential and uniform distributions that this is an expected result.
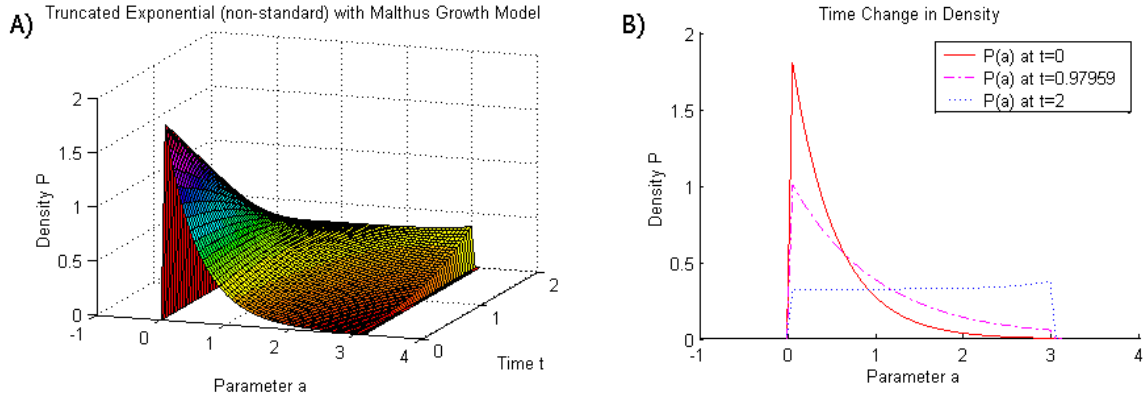
Figure 16: Hybrid Uniform x Truncated Exponential Distribution with Malthus Growth: Observe that at $t = \lambda$, where $\lambda = 2$, the distribution is not quite uniform as in trucated exponential. Compare with Figure 13. A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.

4.7 Discrete Distributions

Some biological traits are better modeled by a continuous gradient. However some traits may have discrete outcomes, such as the number of offspring per reproductive episode (fecundity). These distributions and their moment generating functions can be approximated by considering them continuous. While we did not study these distributions extensively, we look at a case here to show how this can be done. More discrete distributions can be explored using our Matlab program (see Appendix 7.3).

The Poisson distribution with parameter λ is given by the density function

$$P_0(a) = \frac{e^{-\lambda} \cdot \lambda^a}{a!}.$$

Using Equation 3 and $n! = \Gamma(n+1)$ yields

$$P_t(a) = \frac{\lambda^a \cdot e^{a \cdot p(t) - \lambda \cdot e^{p(t)}}}{\Gamma(p(t))}.$$

For a Poisson distribution with Malthus growth, the mean increases as in the previous distributions. However this distribution has some interesting dynamics. This can be clearly understood when we look at the mean and variance, since both are $\lambda \cdot e^{(p(t))}$.
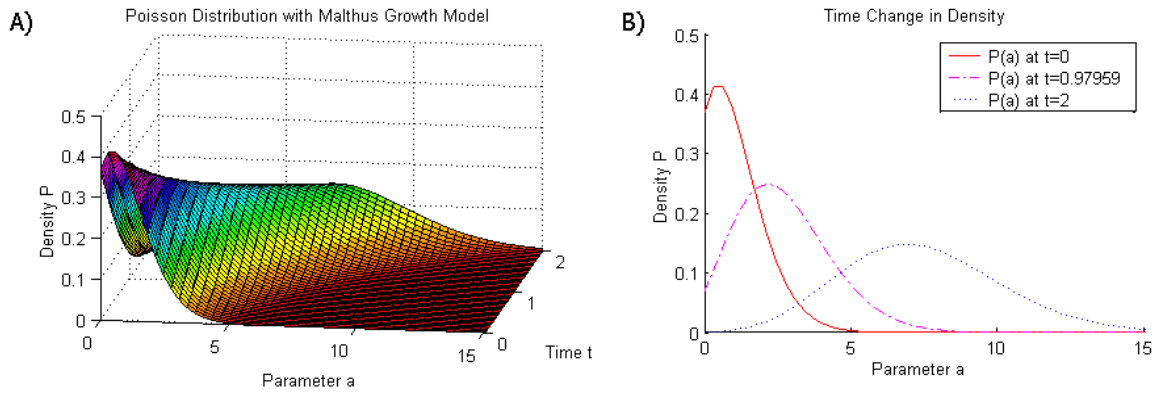
25

Figure 17: Poisson Distribution with Malthus Growth: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.
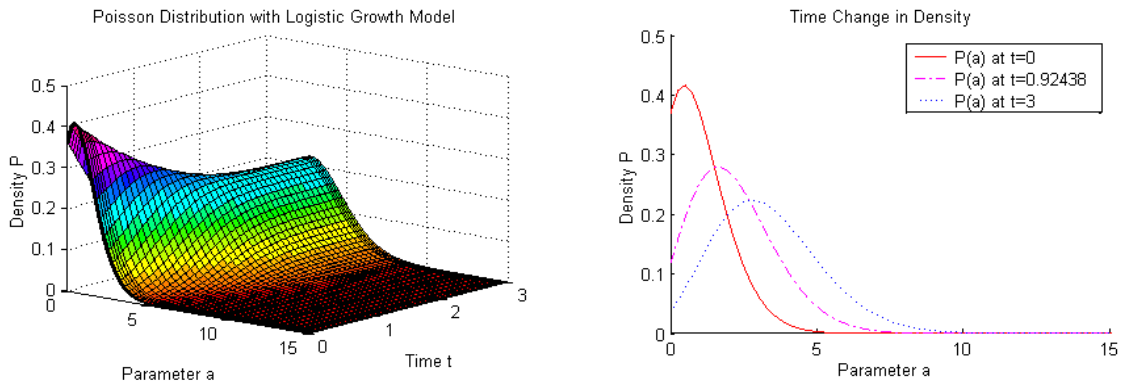

Figure 18: Poisson Distribution with Logistic Growth, $N_0 < 1$: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A.

Since the mean and variance increase with time, the density of parameters near the mean decreases as the mean increases, due to the growing variance. Therefore, the distribution becomes uniform as time increases. For the more reasonable logistic model, the Poisson distribution approaches some finite limiting value as $N(t) \to 1$, as can be seen in Figure 18.

4.8   Negative Parameter Values

Negative parameter values are also of interest for some problems. For example, the homegeneous Malthus model of extinction models the important process of tree population self-thinnning [1]. As mentioned in the analysis of the different distributions, these values are particularly interesting in the study of the logistic and Allee growth models.

We begin by taking a second look at the interpretation of our paramater a. In both the logistic and Allee models $a > 0$ is usually interpreted as a growth rate. For negative a values, we can consider the parameter a as a death rate, or a negative net growth rate of the population. More specifically, this parameter represents the magnitude of the effect that the current population size has on the rate of change of the population. In our individual based models, this parameter has the effect of controling how the current state of the total population impacts the rate of change of an a-group, or sub-population. It is this connection between the state of the overall population and the growth or decline of an individual a-group that brings to light the cause of the dynamics observed under the models studied.

We first consider a heterogeneous population as described in the Introduction. We see from [1] that for $E_t(a)$, the mean parameter value of the population, the rate of change of the population for both logistic and Allee models is given by the equation

$$\frac{d[N(t)]}{dt} = N(t) \cdot E_t(a) \cdot g(N(t)),$$

where the form of $g(N(t))$ is determined by either the Allee or logistic models. When assuming $E_t(a)$ is positive, it follows $g(N(t))$ is negative.

If we consider the various a-groups which are given by the equation

$$\frac{d[l(t,a)]}{dt} = l(t,a) \cdot a \cdot g(N(t))$$

as described in earlier sections, it can be observed that for those a-groups with negative a values, $\frac{d[l(t,a)]}{dt}$ is positive. Therefore the a-groups with negative parameter values will actually grow as $N(t)$ declines!

Figure 19: Normal Distribution with Allee Growth: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval. Note that the population drops down in numbers at first, then increases towards the threshold value $\alpha = 0.25$.

The result of this phenomena can be see in populations with a paramater distribution containing some negative values, such as in Figure 19. Initially, the majority of the population begins to decrease. However, after a period of time the growth of those a-groups with negative parameter values begins to overtake the decreasing effect of the a-groups with positive a values and

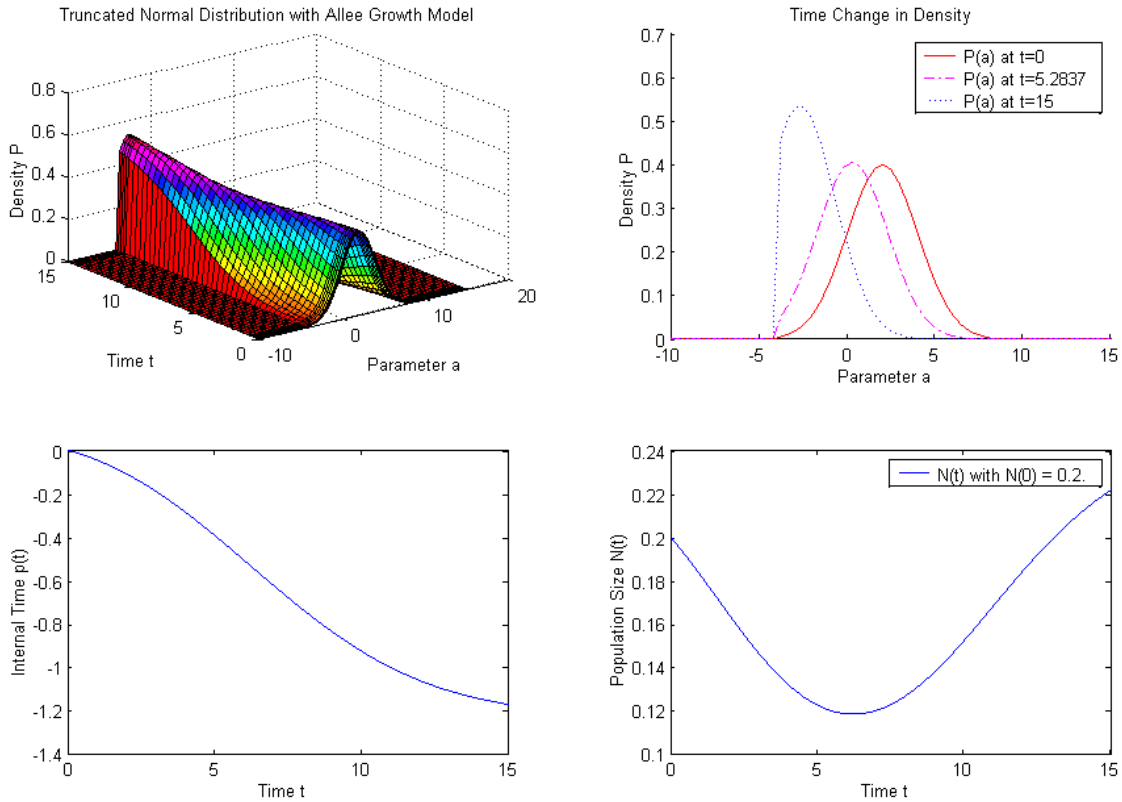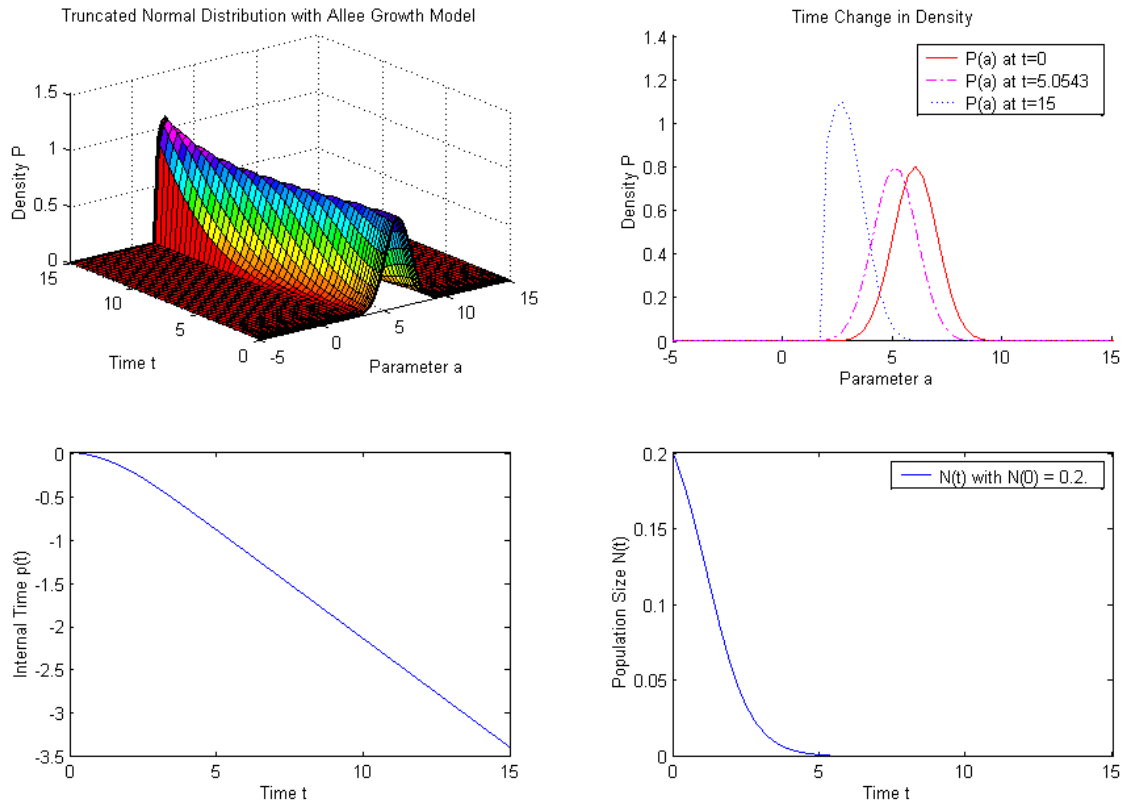Figure 20: Truncated Normal Distribution with Allee Growth: A) A graph of the distribution as it changes with respect to time. B) A two dimensional representation of graph A. C) A graph of $p(t)$ vs t. D) A graph of the total population size $N(t)$ over the given time interval. Note that the population does not drop down in numbers at first, but decreases towards $N(t) = 0$. Compare with Figure 19.

$E_t(a) \to 0$. This results in the population increasing to the threshold value α. For example, under an Allee model with $N_0 < \alpha$, the total population size is increasing due to the negative parameter values and is still less than α. Therefore $g(N(t)) = (1 - N(t)) \cdot (N(t) - \alpha)$ remains negative and approaches 0.

Regardless of the population dynamics in this case, the dynamics of the distributions are very similar to those we would see with a population containing only a-groups with positive parameter values (see Figures 19 and 20).

4.9 Applications to Biology

So far this paper has involved mostly abstract mathematical discussions and simulations. In this section we will now apply the model developed in [1] to a hypothetical biological situation.

First, let us look at how this work impacts Fisher's Fundamental Theorem of Natural Selection (4). The definition stated previously for a haploid population is:

$$\frac{d[r(t)]}{dt} = \sigma(t)^2$$

which biologically signifies that the increase of fitness in one generation is equal to the additive genetic variance of fitness [2]. This is usually taken to mean that a population with a larger variation is able to change faster, that is, it adapts quickly. From Karev's studies using Equation (3), we see how a distribution, and subsequently its variance, changes over time. By following how that variation is changing, it is possible to see how Fisher's theorem can be studied over time. Through this application, not only can one understand what trend an organisms fitness composition will lean towards, but also this can be used to mathematically understand why and how the variance is changing.

Note that in the framework of a heterogeneous model, equation (4) is valid if and only if the growth model of the population is Malthus. In the more general and realistic cases where $F(N(t), a) = f(N(t)) + a \cdot g(N(t))$, we have the more general form of Fisher's equation [1].

$$\frac{dE_t(a)}{dt} = g(N(t)) \cdot \sigma(t)^2.$$

30

This equation can be considered as a generalizaton of the Fundamental Theorem of Natural Selection for haploid populations [6].

Very rarely is Malthus growth experienced for long periods of time, so we will only focus on the logistic and Allee growth models. To better understand the results of this heterogeneous population model and how it relates to natural selection, we will briefly present a hypothetical biology example.

Suppose we have a population of fireflies with a variation of bioluminescence (brightness) from very dim to very bright. For our situation, let us assume that the brighter the firefly the more fit the organism is, that is, the faster the growth for that trait. Now let us say that there is a uniform distribution of this trait within the population and that each individual has its own rate of Malthus growth in correspondence to this variation. Using the equation by Karev, we find as time goes on, that the distribution of dim and bright variations will have a distribution resembling a positive exponential curve. This makes sense because we start by having equal numbers of all variants of fireflies, and as time goes on, the faster growth (brighter) individuals increase substantially in their numbers where the relative number of the slower growth individuals decreases. From our model we would expect to see higher numbers of bright (more fit) fireflies within the population over time, with this trait distributed according to a positive exponential curve.

5   Conclusions

In our investigation, we discovered there is a significant change over time in the distribution of a trait within a heterogeneous population. We also found that the initial distribution does indeed determine the dynamics of a changing distribution. The growth model used for the population also plays a vital role by controlling the final equilibrium distribution of the trait. As illustrated in the Allee and logistic growth models, the initial population size also has an effect upon the evolution of a trait within a population, as dictated by the growth model.

Under logistic growth, the parameter $p(t)$ slows down after some time and the distribution's rate of change slows down as well. With Allee growth, the distribution strongly depends on the initial parameters as to the survival or decline of the individuals in the population and the initial population size. This research helps us understand the role of heterogeneity in population modelling and the role of different distributions of traits and their influence

on natural selection.

6   Acknowledgements

7   Appendix

7.1   Hybrid Uniform x Truncated Exponential Distribution

Our version of the truncated exponential differs from traditional methods. This version consists of truncating the exponential at point K, and then adding the excised tail to the truncated exponential, thus shifting the graph up and making the area under the curve equal to 1. C(t) is the constant to be added.

$$\int_0^K P_0(a)da = \int_0^K (\lambda \cdot e^{-\lambda \cdot a})da + \int_0^K Cda = 1$$

For the above equation to be true,

$$\int_0^K Cda = e^{-\lambda \cdot K}$$

Only then will the area under the curve equal 1. Thus,

$$C = \frac{e^{-\lambda \cdot K}}{K}.$$

Our parameter distribution function for this distribution is therefore,

$$P_0(a) = \lambda e^{-\lambda \cdot a} + \frac{e^{-\lambda \cdot K}}{K}.$$

The Moment Generating Function for the truncated exponential is given by:

$$MGF = \int_0^K e^{t \cdot a} \cdot \lambda e^{-\lambda \cdot a} + \frac{e^{-\lambda \cdot K}}{K} da,$$

and with some calculations, we have:

$$M_0(t) = \frac{\lambda}{\lambda - t} \cdot (1 - e^{-K \cdot (\lambda - t)}) - \frac{e^{-\lambda \cdot K}}{K} \cdot (1 - e^{K \cdot t}).$$

7.2 Relation of the Truncated Exponential Distribution to the Uniform Distribution

We mention in the body of the paper that under this system the Truncated Exponential Distribution for $a \in [c, d]$ and the Uniform Distribution for $a \in [c, d]$ are essensially the same equation, only time offsets from one another. The following is included as a proof of this statement.

First we look at the initial parameter distribution of the truncated exponential,

$$P_0(a) = \frac{\lambda \cdot e^{-\lambda a}}{e^{-\lambda c} - e^{-\lambda d}}$$

Using the definition (20) we find that the general moment generating function for this pdf is

$$M_0(p(t)) = \frac{\lambda(e^{c(p(t)-\lambda)} - e^{d(p(t)-\lambda)})}{(p(t) - \lambda)(e^{-\lambda c} - e^{-\lambda d})},$$

and the case when $p(t) = \lambda$ we get the following equation

$$M_0(\lambda) = \frac{\lambda(d - c)}{e^{-\lambda c} - e^{-\lambda d}}.$$

Applying (3) to the above equalities we obtain

$$P_\lambda(a) = \frac{e^{\lambda a} \cdot \frac{\lambda \cdot e^{-\lambda a}}{e^{-\lambda c} - e^{-\lambda d}}}{\frac{\lambda(d-c)}{e^{-\lambda c} - e^{-\lambda d}}}$$

and after simplification we have

$$P_\lambda(a) = \frac{1}{(d-c)}, \tag{23}$$

which is the parameter distribution function for uniform. This shows that as truncated exponential distribution approaches λ it actually becomes uniform.

If you recall, the initial uniform distribution at time t_u becomes

$$P_{t_u}(a) = \frac{p(t_u) \cdot e^{p(t_u) \cdot a}}{e^{p(t_u) \cdot d} - e^{p(t_u) \cdot c}}. \tag{24}$$

Now for a truncated exponential distribution over the range (c, d) at time t_e, $P_{t_e}(a)$ is given by:

$$P_{t_e}(a) = \frac{e^{a(p(t_e) - \lambda)} \cdot ((p(t_e) - \lambda)}{e^{c \cdot (p(t_e) - \lambda)} - e^{d \cdot (p(t_e) - \lambda)}}.$$

Making the subsitution $p(t_e) = \lambda + p(t_u)$ into the density function for the exponential distribution, $P_{t_e}(a)$, we see that:

$$P_{t_e}(a) = \frac{p(t_u) \cdot e^{a \cdot p(t_u)}}{e^{d \cdot p(t_u)} - e^{c \cdot p(t_u)}} \tag{25}$$

Comparing (24) and (25) we see that when conditions are such that $p(t_e) = \lambda + p(t_u)$, the truncated exponential distribution with paramater λ and the uniform distribution are essentially equivelent distributions.

7.3   MatLab Program Files

The Following MatLab M-files were created to model the changing distributions studied in this paper. They were used on PC's running Matlab R12 with the Microsoft Windows 98 operating system. Copies of the program can be obtained from the authors or through the Mathematical and Theoretical Biology Institute at Cornell University.

The main function *probdist()* calls the other three functions *mass()*, *moment()* and *p()* and from them constructs graphs of the changing parameter distributions. All interested parties are encouraged to experiment with new distributions by including their density functions and moment generating functions in *mass.m* and *moment.m*, respectively.

Matlab M-File: probdist.m

```
function [a,x,P]=probdist(tmin,tmax,ai,aj,model,n0,dist)
%Usage:  [a,x,P]=probdist(tmin,tmax,ai,aj,MODEL,n0,dist);
%
% ***You also need files:  p.m, mass.m, and moment.m****
% Also note that our population is NORMALIZED
%This function plots our parpameter distribution as it evolves over time.
%It returns
% a = range of parameter values
% x = p(t) values (the internal time of our model)
% P(p(t),a) = Parameter values over the given range of t and a
%The arguments are
% (tmin,tmax) = range of time values.
% (ai,aj) = range of parameter values.
% MODEL= Either 'malthus' or 'logistic' models for parameter evolution.
% n0 = value of N0, our initial population size (0..1)
% dist = distribution number (below)
%
% *** Here's a list of different parameters ***
%1) Exponential:  probdist(0,2,0,3,'malthus',.5,1);
% probdist(0,1,0,3,'logistic',.2,1); probdist(0,3,0,3,'logistic',2,1);
% probdist(0,11,0,3,'allee',.2,1); probdist(0,12,0,3,'allee',.5,1);
% probdist(0,3,0,3,'allee',2,1);
%
%2) Truncated Exponential (std.):  probdist(0,2,0,3,'malthus',.5,2);
% probdist(0,2,0,3,'logistic',.3,2); probdist(0,2,0,3,'logistic',2,2);
% probdist(0,3,0,3,'allee',.3,2); probdist(0,3,0,3,'allee',.5,2);
% probdist(0,3,0,3,'allee',2,2);
%3) Truncated Exponential (our version):
% *** See Truncated Exponential (std.)  above for these parameters.  ***
%
%4) Normal probdist(0,3,-5,15,'malthus',.3,4);
% probdist(0,3,-5,15,'logistic',.2,4); probdist(0,2.5,-15,10,'logistic',1.1,4);
% probdist(0,15,-10,15,'allee',.2,4); probdist(0,17,-10,15,'allee',.45,4);
% probdist(0,25,-25,15,'allee',1.1,4);
%
% probdist(0,25,-15,10,'logistic',1.1,4); With negative aplha, check MU=1 vs
% 0
%
%5) Truncated Normal
% probdist(0,5,0,10,'malthus',.3,5);
%
%6) Uniform probdist(0,1,-11,10.01,'malthus',.2,6);
% probdist(0,1,-11,11,'logistic',.2,6); probdist(0,.45,-11,10.01,'logistic',1.3,6);
% probdist(0,1,-11,11,'allee',.2,6); probdist(0,1,-11,11,'logistic',.2,6);
```

```
% probdist(0,.35,-11,10.01,'allee',1.3,6);
%
%7) Binomial probdist(0,3,0,10,'malthus',.2,7);
%
%8) Poisson probdist(0,2,0,15,'malthus',.5,8);
% probdist(0,1.5,0,15,'allee',.5,8);
%
%9) Geometric
% probdist(0,2,0,2,'malthus',.5,9);
%
% More Graph Parameters.
%
%>> probdist(0,3,-5,15,'malthus',.3,4);
%>> probdist(0,3,-5,15,'logistic',.3,4);
%>> probdist(0,3,-5,15,'malthus',.3,4);
%>> probdist(0,5,2,10,'malthus',.3,5);
%>> probdist(0,.5,2,10,'logistic',5,5);
%>> probdist(0,9,2,10,'allee',.24,5);
%>> probdist(0,1.9,0,3,'malthus',.5,1);
%>> probdist(0,1,.9,10.01,'malthus',.2,6);
%>> probdist(0,1,.9,10.01,'logistic',.2,6);
%>> probdist(0,1,.9,10.01,'allee',.2,6);
%
%>> probdist(0,1.9,0,3,'malthus',.5,2);
%>> probdist(0,1.9,.9,4.1,'malthus',.5,2);
%>> probdist(0,1.9,.9,3.1,'malthus',.5,2);
%>> probdist(0,2,.9,3.1,'malthus',.5,2);
%>> probdist(0,1.999,.9,3.1,'malthus',.5,2);
%>> probdist(0,2,.9,3.1,'malthus',.5,2);
%
%>> probdist(0,4,.9,3.1,'malthus',.5,2);
%
%>> probdist(0,17,.9,3.1,'allee',.26,2);
%>> probdist(0,2,-.01,3.1,'malthus',.5,3);
%>> probdist(0,2,0,15,'malthus',.5,8);

% Before we begin, we need some global variables to make things easy.
global MODEL N0 K;
MODEL=model;
N0=n0;

%First lets choose the growth model & then solve for our p(t) values.
if (strcmp(model,'malthus')==1) %Avoid ode45 for malthus since p(t)=t
    t=linspace(tmin,tmax,50);
    x=transpose(t); %set up x as ode45() would
```

```matlab
else if (strcmp(model,'logistic')==1 | strcmp(model,'allee')==1)
    %Generate p(t) values with p(0)=0.  p.m needs to know 'dist'
    [t,x]=ode45(@p,[tmin tmax],0,[],dist);
else
    error(['Argument #5:  Please specify 'logistic' or 'malthus' models.  ;-]']);
    end;
end;
pts = size(x); %pts(1) is the number of a values to use between ai and aj

a = linspace(ai,aj,pts(1)); %a is the range of parameters from ai to aj

for i=1:pts(1) %For each x value,
    for j=1:pts(1) %For all the a values...
    %calculate the distribution Pt(a)
    P(i,j) = exp(x(i)*a(j))*mass(a(j),dist)/moment(x(i),dist);
    end;
end;

%-------------------------Now we display our graphs!-------------------------%
%3D graph (Pt(a) vs t vs a), 2D graph (Pt(a) vs t), p(t) vs t and N(t) vs t%
%----------------------------------------------------------------------------%

figure, hold on
subplot(2,2,1), surf(a,t,P) % The 3D Graph
ylabel('Time t'), xlabel('Parameter a'), zlabel('Density P')
grid on, shading faceted %or 'shading interp'
colormap(sqrt(hsv)) %We can modify the color matrix by exponentiation ;-]
axis xy
switch (model) %Pretty things up a little ;-]
case 'allee', model = 'Allee';
case 'malthus', model = 'Malthus';
case 'logistic', model = 'Logistic';
end;

%Add a title to our Figure and graph
switch (dist)
case 1, A=['Exponential Distribution with ',model,' Growth Model'];
case 2, A=['Truncated Exponential with ',model,' Growth Model'];
case 3, A=['Hybrid Uniform x Truncated Exponential with ',model,' Growth Model'];
case 4, A=['Normal Distribution with ',model,' Growth Model'];
case 5, A=['Truncated Normal Distribution with ',model,' Growth Model'];
case 6, A=['Uniform Distribution with ',model,' Growth Model'];
case 7, A=['Binomial Distribution with ',model,' Growth Model'];
case 8, A=['Poisson Distribution with ',model,' Growth Model'];
case 9, A=['Geometric Distribution with ',model,' Growth Model'];
```

```
otherwise, A=['[Un-named, see mass.m] with ',model,' Growth Model'];
end;
%Set the graph title, figure window title and maximize the figure.
title(A),
set(figure(gcf),'Numbertitle','off','Name',A,'Position',[1 29 1024 672])

%----------And now the 2D graph----------
subplot(2,2,2)
%Get 3 Distribution curves, t=0, one from the middle, and at t=tmax
t0=1;t1=round(pts(1)/2);t2=pts(1);
hold on, plot(a,P(t0,:),'r-'),plot(a,P(t1,:),'m-.'),plot(a,P(t2,:),'b:')
xlabel('Parameter a'), ylabel('Density P')
title('Time Change in Density')
S1=['P(a) at t=',num2str(t(t0))]; S2=['P(a) at t=',num2str(t(t1))];
S3=['P(a) at t=',num2str(t(t2))];
legend(S1,S2,S3)

%Graph p(t) (internal time) vs time
subplot(2,2,3), plot(t,x)
xlabel('Time t'), ylabel('Internal Time p(t)')

%Graph our Populations size N(t) vs.  time
subplot(2,2,4)
for i=1:pts(1)
   N(i)=(N0)*moment(x(i),dist);
end;
plot(t,N), xlabel('Time t'), ylabel('Population Size N(t)')
S1=['N(t) with N(0) = ',num2str(N0),'.'];
legend(S1) %No ; so the figure can be modified from the command line

% AND THEY ALL LIVED HAPPILY EVER AFTER,
%             T H E   E N D.
```

Matlab M-File: mass.m
```
function p=mass(a,dist)
%Usage:  mass(a,dist)
%
%Density/mass function used by probdist() to calculate Pt(a).
%See 'help probdist' for more details.
% a = parameter value
% p = Po(a) where Po() is the initial distribution given by 'dist'.
% dist = 1,2,...  see 'help probdist'

%PLEASE SEE MOMENT.M FOR VARIABLE DESCRIPTIONS.
```

```
%----- 1 = Exponential.
switch (dist)
case 1
L = 2.000000000001; % parameter lambda
p=L*exp(-L*a);

%----- 2 = Truncated Exponential.
case 2
L=2;
% Truncate from c to d
c=1; d=3;
if (a>=c & a<=d)
    p=(L*exp(-L*a))/(exp(-L*c)-exp(-L*d));
else
    p=0;
end;

%----- 3 = Truncated Exponential x Uniform hybrid (a 'custom' distribution.)
% ******* VALID only for t<L ********
case 3
L=2.000000000001;
k=3;
if (a>k | a<0)
    p=0;
else
    p=L*exp(-L*a) + exp(-L*k)/k;
end;

%----- 4 = Normal.
case 4
u=1; s=2;
p=(1/(s*sqrt(2*pi))*exp(-(a-u)^2/(2*s^2)));

%----- 5 = Truncated Normal.
case 5
u=6; s=1; c=2; d=10;
if(a<c) | (a>d)
    p=0;
else
p=sqrt(2)*exp(-1/2*(a-u)^2/(s^2))/(s*sqrt(pi)*(erf(1/sqrt(2)*
        (-c+u)/s-erf(1/sqrt(2)*(-d+u)/s))));
end;

%----- 6 = Uniform.
```

```matlab
case 6
alpha=1; %parameter a
b=10; %parameter b
if (a>b | a<alpha)
    p=0;
else
    p=1/(b-alpha);
end;


% -------------------------------------------------------------- %
% --------------- Some DISCRETE Distributions.  ---------------%
% -------------------------------------------------------------- %
% Note:  use n!  = gamma(n+1), to interpolate our distribution ;-)

%----- 7 = Binomial.
case 7
% *** FOR a<k only!!!
k=10; %parameter k = number of trials...
P=.3; %probability P
%p=((factorial(k))/(factorial(A)*factorial(k-A)))*P^A*(1-P)^(k-A);
p=((gamma(k+1))/(gamma(a+1)*gamma(k-a+1)))*P^a*(1-P)^(k-a);

%----- 8 = Poisson.
case 8
L=1; % parameter lambda
%p=exp(-L)*(L^A)/(factorial(A));
p=exp(-L)*(L^a)/(gamma(a+1));

%----- 9 = Geometric.
case 9
P=.9; % probability parameter P
p=P*(1-P)^(a-1);

end; % end our switch
```

Matlab M-File: moment.m

```matlab
function m=moment(x,dist)
%Usage:  moment(x,dist)
%
%Moment gerenating function for probdist(), see 'help probdist'
% x = some p(t) value
% m = moment(p(t) for the distribution given.
% dist = 1,2,...  see 'help probdist'
```

```
switch (dist)
%----- 1 = Exponential.
case 1
L = 2.000000000001; %parameter lambda = just over 2 ;-)
m=L/(L-x);
% Note that we're only valid for x->Lambda...

%----- 2 = Truncated Exponential.
case 2
L=2; c=1; d=3; %truncated between c and d
if (x==L), m=L*(d-c)/(exp(-L*c)-exp(-L*d));
    %The Mo(p(t)) value for p(t)=L
else, m=(L*(exp(c*(x-L))-exp(d*(x-L))))/((L-x)*(exp(-L*c)-exp(-L*d)));
    %General Mo(p(t)) for p(t)!=L
end;

%----- 3 = Truncated Exponential x Uniform hybrid (a 'custom' distribution.)
case 3
L=2; k=3; %Exponential part has paramaeter L, truncated from 0 to k
if x==L
    m=(1+$L^2$*$k^2$-exp(-L*k))/(L*k);
else
    if x==0, m=1;
    else, m=L/(L-x)*(1-exp(-k*(L-x)))-exp(-L*k)/(k*x)*(1-exp(k*x));
end;end; %end if statements.

%----- 4 = Normal.
case 4
u=1; s=2; %parameter mean = u, standard dev.  = s
m=exp((u*x)+(($s*x)^2$/2));

%----- 5 = Truncated Normal.
case 5
u=6; s=1; c=2; d=10; %mean u, std.  dev.  s, and truncated from -k to k
m=exp(1/2*x*(x*$s^2$+2*u))*(-erf(1/2*(-d+x*$s^2$+u)*sqrt(2)/s)+erf(1/2*(-c+x*$s^2$+u)*
      sqrt(2)/s))/(-erf(1/2*sqrt(2)*(-d+u)/s)+erf(1/2*sqrt(2)*(-c+u)/s));

%----- 6 = Uniform.
case 6
c=1; d=10; %Truncated from c to d.
if (x==0), m=1;
else, m=(exp(x*d)-exp(x*c))/(x*(d-c));
end;

%----------- Some DISCRETE Distributions...  -----------
```

```
%----- 7 = Binomial.
case 7
% *** FOR a<k only!!!
P=.3; % probability parameter
k=10; % number of trials.
m=(P*exp(x)+(1-P))^k;


%----- 8 = Poisson.
case 8
L=1;
m=exp(L*(exp(x)-1));


%----- 9 = Geometric.
case 9
P=.9;
m=(P*exp(x))/(1-(1-P)*exp(x));


end; %end the switch statement
```

Matlab M-File: p.m
```
%Used by probdist() -- please see 'help probdist'
function dx=p(t,x,dist) %x is p(t)
global MODEL N0
if (strcmp(MODEL,'logistic')==1)
    % differential equation for finding p(t) (determined by "moment")
    % K = 1, normailzed carrying capacity, N = initial population...
    % our ODE to return to ODE45...
    dx=1-N0*moment(x,dist);
else if (strcmp(MODEL,'allee')==1)
    % look at the allee model, with critical population value alpha,
    % carrying capacity K and initial population N.
    alpha=.25;
    m=moment(x,dist);
    %K=3.9; N0=4.5; alpha =5; aplha>N0, die out.  N0<aplha, like logistic.
    dx=(N0*m-alpha)*(1-N0*m);
end; end;
```

7.4 Distribution Means and Variances of $P_t(a)$

General Mean Equation:	$E_t(a) = \frac{d}{d\lambda}ln(M_0(\lambda))$
General Variance Equation:	$\sigma^2(t) = \frac{d^2}{d\lambda^2}\frac{M_0(\lambda)}{M_0(p(t))} - \frac{d}{d\lambda}\frac{M_0(\lambda)}{(M_0(p(t)))^2}$

Table 1: These are the general equations used to find the means and variances below. Please note that for these general equations that $\lambda = p(t)$.

Distribution	Computed Mean
Uniform	$\frac{p(t)de^{(p(t)d)} - p(t)ce^{(p(t)c)} - e^{(p(t)d)} + e^{(p(t)c)}}{p(t)(e^{(p(t)d)} - e^{(p(t)c)})}$
Exponential	$\frac{1}{\lambda - p(t)}$
Normal	$\mu + \sigma^2 p(t)$
Binomial*	$\frac{nre^{p(t)}}{re^{p(t)} + 1 - r}$
Poisson	$\lambda e^{p(t)}$
Geometric*	$\frac{1}{1 - e^{p(t)} + re^{p(t)}}$
Truncated Exponential	Too large for table
Hybrid Uniform X Trunc. Exp.	Too large for table
Truncated Normal	Too large for table

Table 2: These are the calculated means of the evolving distribution equations.

Distribution	Computed Variance
Uniform	$\frac{p(t)^2 d^2 e^{(p(t)(d+c))} + p(t)^2 c^2 e^{(p(t)(d+c))} - e^{(2td)} + 2e^{(p(t)(d+c))} - e^{(2p(t)c)} - 2p(t)^2 de^{(p(t)(d+c))}c}{p(t)^2(e^{(p(t)d)} - e^{(p(t)c)})^2}$
Exponential	$\frac{1}{(\lambda - p(t))^2}$
Normal	σ^2
Binomial*	$\frac{nre^{p(t)}(-1+r)}{(re^{p(t)} + 1 - r)^2}$
Poisson	$\lambda e^{p(t)}$
Geometric*	$\frac{(-1+r)e^{p(t)}}{(1 - e^{p(t)} + re^{p(t)})^2}$
Truncated Exponential	Too large for table
Uniform X Trunc. Exp.	Too large for table
Truncated Normal	Too large for table

* Here, r is the parameter for the distribution. Traditionally this parameter or probability is denoted as p.

Table 3: These are the calculated variances of the evolving distribution equations.

8 Reference List

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