

Population Processes

California State Polytechnic University, Pomona

and

Loyola Marymount University

Department of Mathematics Technical Report

Robert L. Bewernick*, Jeremy D. Dewar†, Eunice Gray‡, Nancy Y. Rodriguez§

Applied Mathematical Sciences Summer Institute
Department of Mathematics & Statistics,
California State Polytechnic University Pomona
3801 W. Temple Ave.
Pomona, CA 91768

Faculty Mentor: R. J. Swift¶

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*University of California, Los Angeles

†Loyola Marymount University

‡Sam Houston State University

§Loyola Marymount University

¶California State Polytechnic University, Pomona

Abstract

Deterministic population models describe population sizes and their dynamics. However, random chance plays a large part in the growth of real-life populations. In this technical report, birth-death formulations for single and competing populations are developed. It is shown that these stochastic processes have expected values that agree with the corresponding deterministic models. A representation for the partial differential equation that a probability generating function of a birth-death process with polynomial transition rates is derived. This representation is in terms of Stirling numbers and is used to develop some of the properties of these processes. The analysis in this report uses both analytical methods and simulations.

1 Single Population Models

1.1 The Pure Birth Process - A Motivating Example

Consider the differential equation

$$\frac{dN}{dt} = \lambda N(t),$$

where $N(t)$ is the size of a population at time t and λ is the growth rate constant. For a growing population, we will assume $\lambda > 0$, for a declining population we assume $\lambda < 0$, see Figure 1. This deterministic model works with the aggregate population and assumes not simply that each individual may reproduce but that it actually *does* reproduce. For instance, if the average number of births per individual over some time period is 0.8, then this model gives 0.8 offspring to each individual. We understand this as an average over the entire population, but this averaging process eliminates the natural variance in the population. Our work will focus upon a method that will allow us to model these natural variations.

$\lambda > 0$

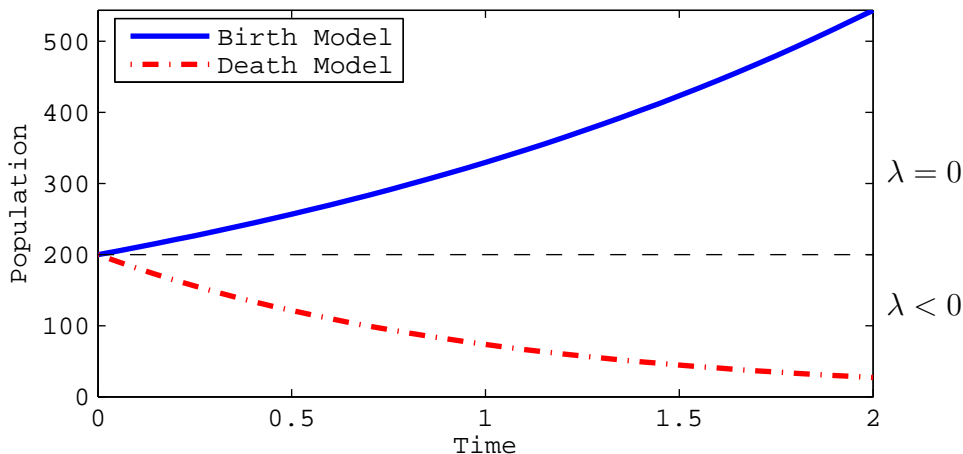


Figure 1: Graphs of the population model $\frac{dN}{dt} = \lambda N(t)$ for different growth rates λ .

We wish to consider the situation where an individual in our population has a chance of giving birth in a period of time. We assume that the probability of reproduction for one individual in a very short time interval of length Δt is proportional to Δt , that is

$$P[\text{one individual gives birth in } \Delta t] = \lambda \Delta t + o(\Delta t),$$

where $o(\Delta t)$ is “little o” notation. Note that

$$\lim_{\Delta t \rightarrow 0} \frac{o(\Delta t)}{\Delta t} = 0.$$

Using complements, we find

$$P[\text{individual does not give birth in } \Delta t] = 1 - \lambda\Delta t + o(\Delta t).$$

These probabilities are for each individual in the population; we need to know the probability of one birth's occurring for the population as a whole.

To do this, we will suppose that there were $n = 2$ individuals in the population. If we assume that births to each individual occur independently, then the probability of no births' occurring during the time interval Δt is

$$P[\text{no births occur in } \Delta t] = (1 - \lambda\Delta t + o(\Delta t))^2. \quad (1)$$

Thus, expanding the right-hand side of (1), we obtain

$$(1 - \lambda\Delta t + o(\Delta t))^2 = 1 - 2\lambda\Delta t + \lambda^2(\Delta t)^2 + o(\Delta t).$$

Since Δt is assumed small, $(\Delta t)^2$ is even smaller, in fact, essentially negligible. Thus we assume that

$$P[\text{no births occur in } \Delta t] = 1 - 2\lambda\Delta t + o(\Delta t). \quad (2)$$

Hence, the probability of one birth occurring in Δt in a population of size $n = 2$ is

$$P[\text{one birth occurs in } \Delta t] = 2\lambda\Delta t + o(\Delta t). \quad (3)$$

A similar argument using the binomial theorem shows that in a population of size n ,

$$P[\text{one birth occurs in } \Delta t] = n\lambda\Delta t + o(\Delta t). \quad (4)$$

We assume that the interval of time Δt is sufficiently small, so that at most one birth can occur with probability given by equation (4).

Let $X(t)$ be the number of individuals in the population at time t . Suppose that the population has n_0 individuals initially.

Then $X(0) = n_0$, and we seek to determine

$$P_n(t) = P[X(t) = n].$$

Here $X(t)$ has possible values $n_0, n_0 + 1, n_0 + 2, \dots$ since we have assumed that no deaths occur in this population.

We can represent our population as a state diagram. Each state represents the size of the population. The arcs between the states represent the chance that we move up one state during time Δt , with the probability of remaining in that state given by the complement.



As we can see, the probability to increase the population from 1 to 2 is $\lambda\Delta t$. From 2 to 3 is $2\lambda\Delta t$ and to increase from n to $n + 1$ is given by the chance of $n\lambda\Delta t$.

Transition	Probability
$1 \rightarrow 2$	$\lambda\Delta t$
$2 \rightarrow 3$	$2\lambda\Delta t$
\vdots	\vdots
$n \rightarrow n + 1$	$n\lambda\Delta t$

We can summarize this by saying that a transition up has the probability of the birth rate times the population. There is no chance to drop in state (lose population) in our pure birth model.

Transition	Rate
$i \rightarrow i + 1$	λi
$i \rightarrow i - 1$	0

We have chosen Δt to be so small that only one event can occur during time Δt . So

$$P[\text{one birth}|N(t) = 1] \approx \lambda\Delta t, \quad (5)$$

and

$$P[\text{no births in}(0, \Delta t)|N(t) = 1] = 1 - \lambda\Delta t.$$

Using this, we have that during a time interval Δt

$$P_i(t + \Delta t) = \lambda(i - 1)P_{i-1}(t)\Delta t + (1 - \lambda i\Delta t)P_i(t) \quad \text{for } i > N_0 \quad (6)$$

with the initial state N_0 having

$$P_{N_0}(t + \Delta t) = (1 - N_0\Delta t)P_{N_0}(t) \quad (7)$$

by rearranging (6) we obtain

$$P_i(t + \Delta t) - P_i(t) = \lambda(i - 1)P_{i-1}(t)\Delta t - \lambda i P_i(t)\Delta t, \quad (8)$$

then dividing through by Δt we have

$$\frac{P_i(t + \Delta t) - P_i(t)}{\Delta t} = \lambda(i - 1)P_{i-1}(t) - \lambda i P_i(t). \quad (9)$$

Letting Δt approach zero by taking a limit we have

$$P'_i(t) = \lim_{\Delta t \rightarrow 0} \frac{P_i(t + \Delta t) - P_i(t)}{\Delta t} = \lim_{\Delta t \rightarrow 0} [\lambda(i - 1)P_{i-1}(t) - \lambda i P_i(t)], \quad (10)$$

provided the limit exists. We have obtained the *forward Kolmogorov equations*, (c.f. Karlin and Taylor, 136)

$$P'_i(t) = \lambda(i-1)P_{i-1}(t) - \lambda iP_i(t) \quad \text{for } i > N_0 \quad (11)$$

and

$$P'_{N_0}(t) = -\lambda N_0 P_{N_0}(t). \quad (12)$$

1.2 Recursive solution

The system of equations(11)and(12) can be solved recursively. Using the equation for $P'_{N_0}(t)$ as

$$P'_{N_0}(t) + \lambda N_0 P_{N_0}(t) = 0.$$

We see that this is a first order differential equation which can be solved with the integrating factor

$$e^{\int \lambda N_0 dt} = e^{\lambda N_0 t}. \quad (13)$$

Using this gives

$$e^{\lambda N_0 t} P'_{N_0}(t) + \lambda N_0 e^{\lambda N_0 t} P_{N_0}(t) = 0,$$

so that integrating and solving for $P_{N_0}(t)$ gives

$$P_{N_0}(t) = c_1 e^{-\lambda N_0 t}.$$

Given that initially we're at population N_0 at $t = 0$ then $c_1 = 1$, so

$$P_{N_0}(t) = e^{-\lambda N_0 t}. \quad (14)$$

Fortunately for us this answer makes sense: the probability that we stay at the initial population decreases exponentially with time. Now let's look at the probability for the next state and substitute in what we found in (14).

Thus

$$P'_{N_0+1}(t) = N_0 \lambda P_{N_0}(t) - (N_0+1) \lambda P_{N_0+1}(t),$$

becomes

$$P'_{N_0+1}(t) + (N_0 + 1) \lambda P_{N_0+1}(t) = N_0 \lambda e^{-\lambda N_0 t}.$$

Again, we see that this is just a first order linear equation so that the integrating factor is (Go integrating factor!)

$$e^{\int \lambda(N_0+1)dt} = e^{\lambda(N_0+1)t} \quad (15)$$

Thus

$$e^{\lambda(N_0+1)t} P'_{N_0+1}(t) + \lambda(N_0+1)e^{\lambda(N_0+1)t} P_{N_0+1}(t) = e^{\lambda(N_0+1)t} N_0 \lambda e^{-\lambda N_0 t}$$

so that we have

$$P_{N_0+1}(t) = N_0 e^{-\lambda N_0 t} + c_2 e^{-\lambda(N_0+1)t}.$$

At $t = 0$ there is no chance that we're at population N_0+1 (as $P_{N_0}(0) = 1$) so $c_2 = -N_0$. This gives

$$P_{N_0+1}(t) = N_0 e^{-\lambda N_0 t} (1 + e^{-\lambda t}). \quad (16)$$

Once $P_{N_0+1}(t)$ is known, it is used to find $P_{N_0+2}(t)$.

$$P'_{N_0+2}(t) + (N_0+2)\lambda P_{N_0+2}(t) = (N_0+1)\lambda N_0 e^{-\lambda N_0 t} (1 - e^{-\lambda t}). \quad (17)$$

Equation (17) is again a first-order linear differential equation. If we multiply each side of the equation by $e^{\lambda(N_0+2)t}$, integrate, and use the initial condition that $P_{N_0+2}(0) = 0$, we obtain the solution

$$P_{N_0+2}(t) = \frac{(N_0+1)N_0}{2} e^{-N_0 \lambda t} (1 - e^{-\lambda t})^2.$$

We continue this procedure. The general formula, which may be checked by induction, is

$$P_N(t) = \binom{N-1}{N_0-1} e^{-N_0 \lambda t} (1 - e^{-\lambda t})^{n-N_0} \text{ for } n \geq N_0. \quad (18)$$

The equation (45) is the probabilistic model for a pure birth process. It gives the probability distribution of the size of the population at time t . While the deterministic model gives a single number as the prediction for the population size at time t , the probabilistic model gives the relative likelihood of each different possible population size at time t .

The deterministic model was much simpler to obtain than the probabilistic model. Is there a connection between these two models? The answer to this question is found by considering the expected value (or average) of the probabilistic model.

To compute the expected value of a discrete random variable, let

$$m(t) = \sum_{n=N_0}^{\infty} n P_n(t). \quad (19)$$

Differentiating this expression gives the equation

$$m'(t) = \sum_{n=N_0}^{\infty} nP'_n(t). \quad (20)$$

If we substitute the equation for $P'_n(t)$ in (20), we obtain

$$\begin{aligned} m'(t) &= \sum_{n=N_0}^{\infty} nP'_n(t) \\ &= \sum_{n=N_0}^{\infty} n((n-1)\lambda P_{n-1}(t) - n\lambda P_n(t)) \\ &= \lambda \sum_{n=N_0}^{\infty} (n(n-1)P_{n-1}(t)) - n^2 P_n(t). \end{aligned} \quad (21)$$

Expanding the sum in the expression (21) and recalling that $P_n(t) = 0$ for $n < N_0$ gives

$$\begin{aligned} m'(t) &= \lambda (-N_0^2 P_{N_0}(t) + (N_0 + 1)N_0 P_{N_0}(t) - (N_0 + 1)^2 P_{N_0+1}(t) \\ &\quad + (N_0 + 2)(N_0 + 1)P_{N_0+1}(t) - (N_0 + 2)^2 P_{N_0+2}(t) + \dots) \\ &= \lambda (N_0 P_{N_0}(t) + (N_0 + 1)P_{N_0+1}(t) + (N_0 + 2)P_{N_0+2}(t) + \dots) \\ &= \lambda \sum_{n=N_0}^{\infty} nP_n(t) \\ &= \lambda m(t). \end{aligned} \quad (22)$$

Equation (22) is the exponential differential equation, the initial condition following from the initial population size's being N_0 . That is, since $P_{N_0}(0) = 1$, we have $m(0) = N_0$. The solution to the equation (22) with this initial condition is then

$$m(t) = N_0 e^{\lambda t}. \quad (23)$$

Equation (23) is also the deterministic model for the population. Thus, the deterministic model coincides with the mean of the probabilistic model. This is the motivation for the types of processes we will consider in this report.

The variance of the pure birth process is

$$v(t) = N_0 e^{\lambda t} (e^{\lambda t} - 1), \quad (24)$$

and is obtained similarly using the above approach. The variance provides a measure of spread for this model and is unavailable if the deterministic model is used alone.

1.3 The Generating Function Method

We will now present a useful method for analysis of systems of differential equation such as (11) and (12) We define the probability generating function (p.g.f.) of a process $X(t)$ as

$$\phi(r, t) = \sum_{i=0}^{\infty} P_i(t)r^i = P_0(t) + P_1(t)r + P_2(t)r^2 + \dots$$

Probability generating functions are power series (in r) whose coefficients are probabilities. We can use p.g.f.s to obtain the transient solution to systems such as (11). As an example of this idea, we use the pure birth process of the previous section. If we take the partial of ϕ with respect to t then

$$\frac{\partial \phi}{\partial t} = \sum_{i=0}^{\infty} P'_i(t)r^i,$$

Substituting in (11) we obtain

$$\frac{\partial \phi}{\partial t} = \sum_{i=0}^{\infty} \lambda(i-1)P_{i-1}(t)r^i - \sum_{i=0}^{\infty} \lambda i P_i(t)r^i. \quad (25)$$

Re-indexing the series we get

$$\frac{\partial \phi}{\partial t} = (r-1)\lambda \sum_{i=0}^{\infty} i P_i(t)r^i \quad (26)$$

Since

$$\frac{\partial \phi}{\partial r} = \sum_{i=0}^{\infty} i P_i(t)r^{i-1} \quad (27)$$

we can re-write (26) as

$$\frac{\partial \phi}{\partial t} = \lambda r(r-1) \frac{\partial \phi}{\partial r} \quad (28)$$

Before we solve this partial differential equation, we will present a method for obtaining some useful information about the process. Recalling that the p.g.f. is defined as

$$\phi(r, t) = \sum_{i=0}^{\infty} P_i(t)r^i \quad (29)$$

we see that

$$\frac{\partial \phi}{\partial r} = \sum_{i=0}^{\infty} i P_i(t)r^{i-1}, \quad (30)$$

so that

$$E[X(t)] = \left. \frac{\partial \phi}{\partial r} \right|_{r=1}. \quad (31)$$

where $X(t)$ is a stochastic random variable. Thus applying this idea to (28) we have

$$\begin{aligned} \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} &= \frac{\partial}{\partial r} \left[\lambda r(r-1) \frac{\partial \phi}{\partial r} \right] \\ &= \lambda(r-1) \frac{\partial \phi}{\partial r} + \lambda r \frac{\partial \phi}{\partial r} + \lambda r(r-1) \frac{\partial^2 \phi}{\partial r^2}, \end{aligned} \quad (32)$$

we then evaluate it at $r=1$ in order to obtain the expected value

$$\frac{d}{dt} E[X(t)] = \left. \frac{\partial}{\partial t} \frac{\partial \phi}{\partial r} \right|_{r=1} = \lambda E[X(t)]. \quad (33)$$

So as we had before, the expected value of the p.g.f. corresponds to the deterministic model

$$\frac{dx}{dt} = \lambda x(t).$$

This method of obtaining the expected value of the process using the p.g.f. will be used throughout the rest of this report. In the case of the pure birth process, we can actually solve the p.d.e.. Recalling the separation of variables method assume

$$\phi(r, t) = F(r)G(t) \quad \text{for all } r, t, \quad (34)$$

then

$$\frac{\partial \phi}{\partial t} = F(r)G'(t) \quad \text{and} \quad \frac{\partial \phi}{\partial r} = F'(r)G(t). \quad (35)$$

Substituting (35) into (28) gives

$$F(r)G'(t) = r(r-1)\lambda F'(r)G(t)$$

so that

$$\implies \frac{G'(t)}{G(t)} = r(r-1)\lambda \frac{F'(r)}{F(r)} \quad \text{for all } r, t. \quad (36)$$

Thus,

$$\frac{G'(t)}{G(t)} = C \quad r(r-1)\lambda \frac{F'(r)}{F(r)} = C \quad (37)$$

C is an arbitrary constant unchanged by negating it (this becomes useful later). The equation

$$\frac{G'(t)}{G(t)} = -C$$

has the solution

$$G(t) = k_1 e^{-Ct} \quad (38)$$

and the equation

$$r(r-1)\lambda \frac{F'(r)}{F(r)} = -C$$

has the solution

$$F(r) = k_2 \left(\frac{r-1}{r} \right)^{\frac{C}{\lambda}}. \quad (39)$$

Combining these two equations gives

$$F(r)G(t) = \phi(r, t) = k \left(\left(\frac{r-1}{r} \right)^{\frac{C}{\lambda}} e^{-Ct} \right). \quad (40)$$

A more general solution is obtained when k is a function to be determined.

$$\phi(r, 0) = r = k \left(\left(\frac{r-1}{r} \right)^{\frac{C}{\lambda}} \right) \quad (41)$$

Let $z = \left(\frac{r-1}{r} \right)^{\frac{C}{\lambda}}$ and solve for r , so that

$$r = k(z) = -\frac{1}{z^{\frac{\lambda}{C}} - 1} \quad (42)$$

We had defined r as $k(z)$, substituting in (40) and simplify to get

$$\phi(r, t) = -\frac{1}{\left(\left(\frac{r-1}{r} \right)^{\frac{C}{\lambda}} e^{-Ct} \right)^{\frac{\lambda}{C}} - 1} \quad (43)$$

$$= \frac{r e^{\lambda t}}{1 + r(e^{\lambda t} - 1)} \quad (44)$$

We now have a general closed form solution to the probability generating function. We now can obtain the probabilities by expanding ϕ as a power series and rearranging it gives us the form

$$P_N(t) = \binom{N-1}{N_0-1} e^{-N_0 \lambda t} (1 - e^{-\lambda t})^{n-N_0} \text{ for } n \geq N_0. \quad (45)$$

Simulation of a pure birth process

In analyzing these models, we use simulations as well as analytical techniques. Using the fact that the interevent time is exponentially distributed, we are able to generate times and events that as we will see solidify our analytical findings. A simulation of a pure birth process can be found in Figure 2.

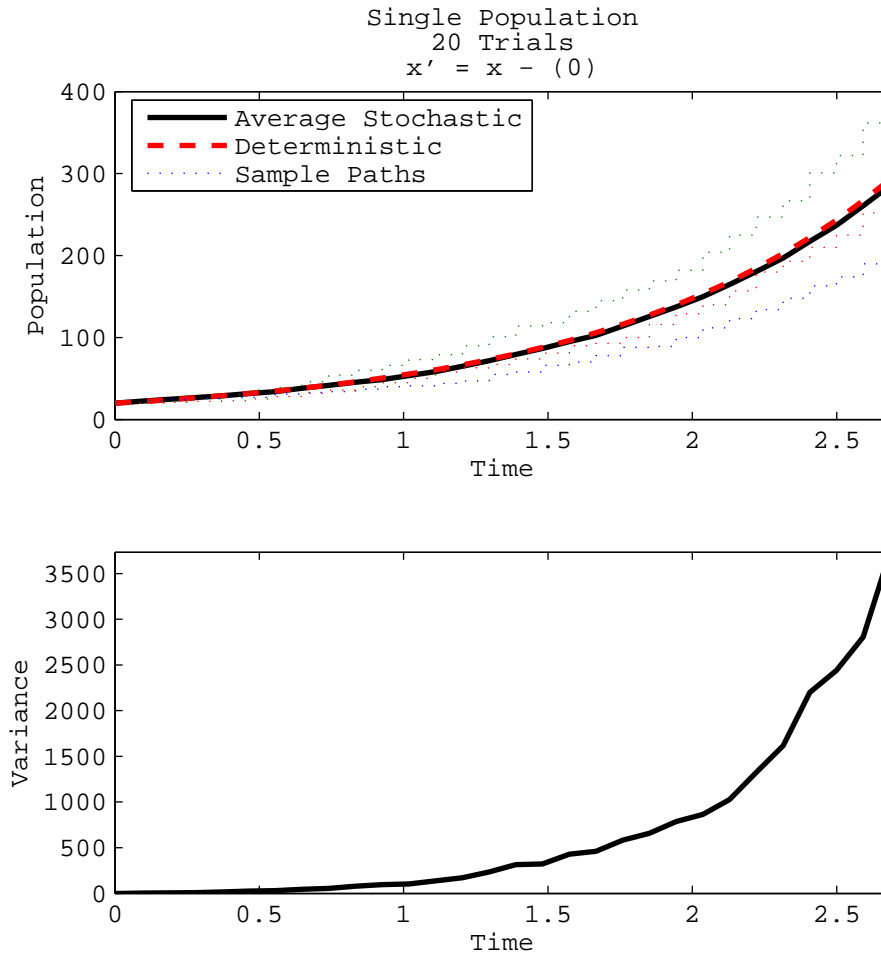


Figure 2: $\lambda = 1$

1.3.1 Birth-Death Process

Deterministic Model

In the birth-death model, we add a death term to the equation. This represents the rate at which people die. As far as the deterministic model is concerned, this has no qualitative effect on the function, as it will continue to look the same as our birth model. However, adding the concept of death to our stochastic process allows the possibility of extinction of the population.

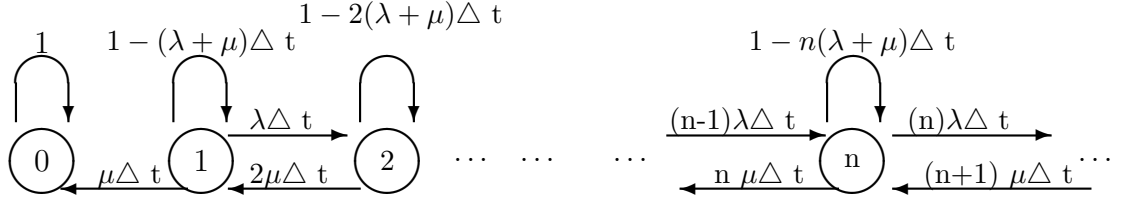
$$\frac{dN(t)}{dt} = (\lambda - \mu)N(t) \tag{46}$$

where $N(t)$ = population, λ = birth rate, μ = death rate

Stochastic Birth-Death (BD) Process

This time the table of transition probabilities has a rate going both ways: To transition up a state, the probability is the birth rate times the population. To transition down to a state that represents one less in the population the probability is the death rate times the population.

This state diagram represents increases or decreases in the population



Transition	Rate
$i \rightarrow (i + 1)$	λi
$i \rightarrow (i - 1)$	μi

The *forward Kolmogorov equations* are

$$P'_i(t) = \lambda(i - 1)P_{i-1}(t)r^i + \mu(i + 1)P_{i+1}(t)r^i - (\lambda i + \mu i)P_i(t)r^i \quad \text{for } i \geq 1 \quad (47)$$

Solving in the manner we are accustomed we find our p.d.e. to be

$$\frac{\partial \phi}{\partial t} = r(r - 1)\lambda \frac{\partial \phi}{\partial r} + r \left(\frac{1}{r} - 1 \right) \mu \frac{\partial \phi}{\partial r} \quad (48)$$

From the p.d.e. we take the partial with respect to r evaluate it at $r = 1$ in order to get the expected value of the $N(t)$ population.

$$\begin{aligned} \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} &= (r - 1)\lambda \frac{\partial \phi}{\partial r} + r\lambda \frac{\partial \phi}{\partial r} + r(r - 1)\lambda \frac{\partial^2 \phi}{\partial r^2} \\ &+ \left(\frac{1}{r} - 1 \right) \mu \frac{\partial \phi}{\partial r} - \frac{1}{r}\mu \frac{\partial \phi}{\partial r} + r(r - 1)\mu \frac{\partial^2 \phi}{\partial r^2} \end{aligned} \quad (49)$$

$$\begin{aligned} \left. \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} \right|_{r=1} &= \lambda \frac{\partial \phi}{\partial r} - \mu \frac{\partial \phi}{\partial r} \\ &= (\lambda - \mu)E[N(t)] \end{aligned} \quad (50)$$

which is similar to the deterministic birth-death model.

Simulation of a birth-death process

A simulation of a birth-death process can be found in Figure 3.

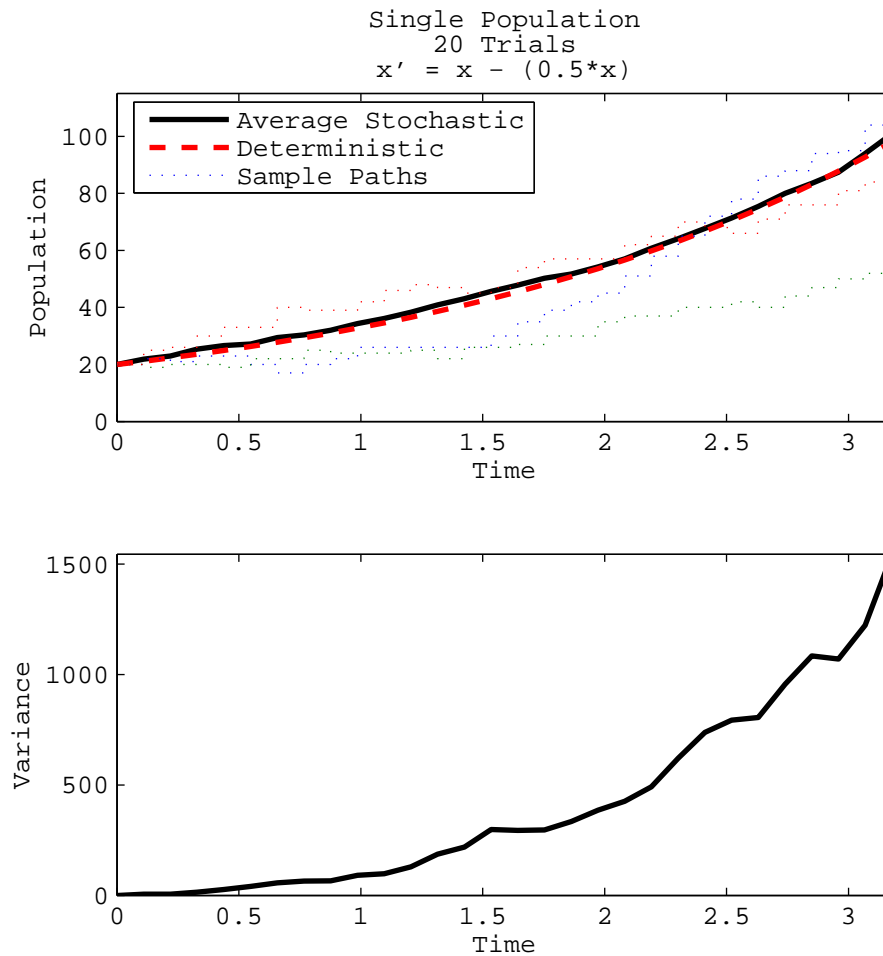


Figure 3: $\lambda = 1$ and $\mu = .5$

1.4 Birth-Death-Immigration

Stay with us now. Let's add immigration, a non-population dependent rate. Immigration allows the population to never stay extinct, as there will always be an influx of members into the population.

Deterministic BDI

$$\frac{dN(t)}{dt} = (\lambda - \mu)N(t) + \beta \quad (51)$$

where $\lambda =$ birth rate, $\mu =$ death rate,

$N(t) =$ population, $\beta =$ immigration rate

Stochastic Birth-Death-Immigration (BDI) Process

The table of transition probabilities has a rate going both ways: To transition up a state, the probability is the birth rate times the population plus an immigration rate. To transition down to a state that represents one less in the population the probability is the death rate times the population.

Transition	Rate
$i \rightarrow (i + 1)$	$\lambda i + \beta$
$i \rightarrow (i - 1)$	μi

The forward Kolmogorov equations are

$$P'_i(t) = (\lambda(i - 1) + \beta)P_{i-1}(t)r^i + \mu(i + 1)P_{i+1}(t)r^i - (\lambda i + \beta + \mu i)P_i(t)r^i \quad \text{for } i \geq 0 \quad (52)$$

Solving in the manner we are accustomed we find our p.d.e. to be

$$\frac{\partial \phi}{\partial t} = r(r - 1)\lambda \frac{\partial \phi}{\partial r} + \beta(r - 1)\phi(r, t) + r \left(\frac{1}{r} - 1 \right) \mu \frac{\partial \phi}{\partial r} \quad (53)$$

Differentiating with respect to r we have

$$\begin{aligned} \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} &= (r - 1)\lambda \frac{\partial \phi}{\partial r} + r\lambda \frac{\partial \phi}{\partial r} + r(r - 1)\lambda \frac{\partial^2 \phi}{\partial r^2} \\ &+ \beta \phi(r, t) + \beta(r - 1) \frac{\partial \phi}{\partial r} \\ &+ \left(\frac{1}{r} - 1 \right) \mu \frac{\partial \phi}{\partial r} - \frac{1}{r} \mu \frac{\partial \phi}{\partial r} + r(r - 1) \mu \frac{\partial^2 \phi}{\partial r^2}. \end{aligned} \quad (54)$$

We evaluate the partial at $r = 1$ in order to get the expected value of the population.

Since we know

$$\phi(1, t) \phi(r, t)|_{r=1} = \sum_{i=0}^{\infty} P_i(t) = 1 \quad (55)$$

so applying (55) to (54)

$$\begin{aligned} \left. \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} \right|_{r=1} &= \lambda \frac{\partial \phi}{\partial r} - \mu \frac{\partial \phi}{\partial r} + \beta \phi(r, t) \\ &= (\lambda - \mu) E[N(t)] + \beta \end{aligned} \tag{56}$$

we can see the result corresponds to the deterministic birth-death-immigration model.

1.4.1 Simulation of a birth-death-immigration

A simulation of the BDI process can be found in Figure 4.

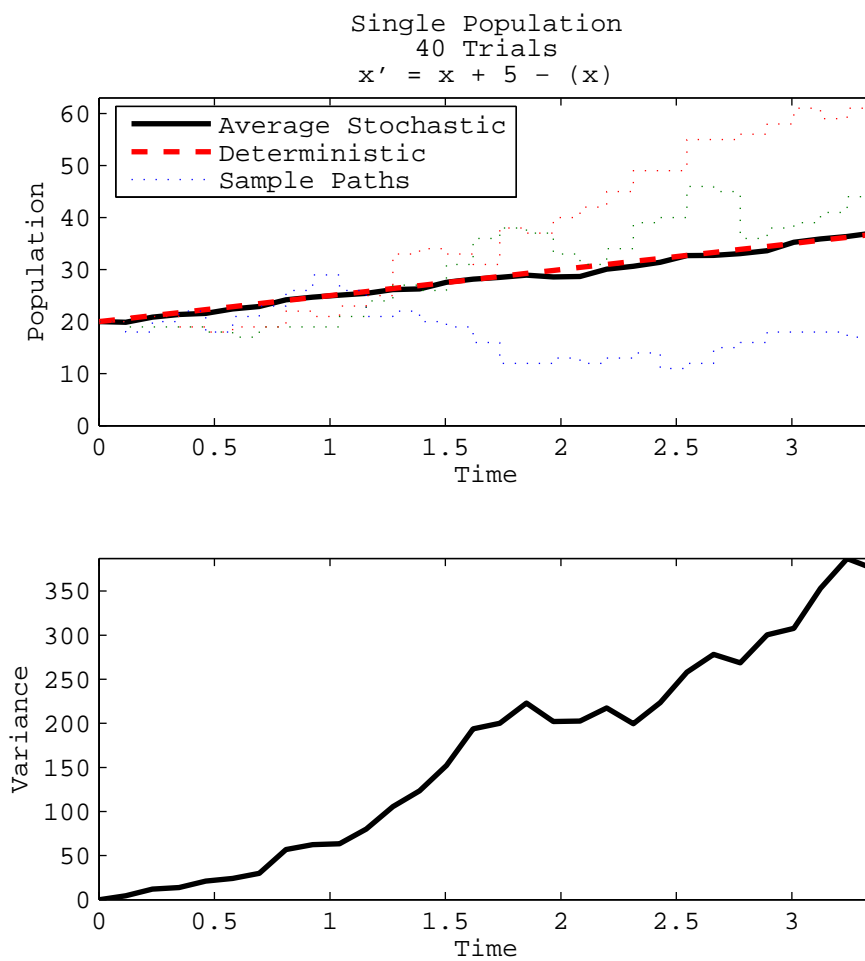


Figure 4: $\lambda = 1$, $\mu = 1$, and $\beta = 5$.

1.5 Birth-Death-Immigration-Emigration (BDIE) Process

To keep pace, we can now add an emigration term to the mix. This is not population dependent and will remove members from our population at a constant rate. As we will see, this produces a complicated term that cannot easily be ignored. A pure immigration and emigration process can be referred to in many other texts as a queueing process.

$$\frac{dN(t)}{dt} = (\lambda - \mu)N(t) + \beta - \gamma \quad (57)$$

where λ = birth rate, μ = death rate,

$N(t)$ = population, β = immigration rate, γ = emigration

Stochastic Birth-Death-Immigration-Emigration Process

The table of transition probabilities has a rate going both ways: To transition up a state, the probability is the birth rate times the population plus an immigration rate. To transition down to a state that represents one less in the population the probability is the death rate times the population plus an emigration rate.

Transition	Rate
$i \rightarrow (i + 1)$	$\lambda i + \beta$ for $i \geq 0$
$i \rightarrow (i - 1)$	$\mu i + \gamma$ for $i \geq 1$

The forward Kolmogorov equations are

$$\begin{aligned} P_i'(t) &= (\lambda(i - 1) + \beta)P_{i-1}(t)r^i + (\mu(i + 1) + \gamma)P_{i+1}(t)r^i \\ &- (\lambda i + \beta + \mu i + \gamma)P_i(t)r^i \quad \text{for } i \geq 0 \end{aligned} \quad (58)$$

Solving in the manner we are accustomed we find our p.d.e. to be

$$\begin{aligned} \frac{\partial \phi}{\partial t} &= r(r - 1)\lambda \frac{\partial \phi}{\partial r} + (r - 1)\beta \phi(r, t) + r \left(\frac{1}{r} - 1 \right) \mu \frac{\partial \phi}{\partial r} \\ &+ \left(\frac{1}{r} - 1 \right) \gamma \phi(r, t) - \gamma P_0(t)r^{-1}. \end{aligned} \quad (59)$$

Differentiating with respect to r we have

$$\begin{aligned} \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} &= r(r - 1)\lambda \frac{\partial \phi}{\partial r} + r\lambda \frac{\partial \phi}{\partial r} + r(r - 1) \frac{\partial^2 \phi}{\partial r^2} \\ &+ \beta \phi(r, t) + (r - 1)\beta \phi(r, t) \\ &+ \left(\frac{1}{r} - 1 \right) \mu \frac{\partial \phi}{\partial r} - \frac{1}{r} \mu \frac{\partial \phi}{\partial r} + r \left(\frac{1}{r} - 1 \right) \mu \frac{\partial^2 \phi}{\partial r^2} \\ &- \frac{1}{r^2} \gamma \phi(r, t) + \left(\frac{1}{r} - 1 \right) \gamma \frac{\partial \phi}{\partial r} + \frac{1}{r^2} \gamma P_0(t). \end{aligned} \quad (60)$$

We evaluate the partial at $r = 1$ to get the expected value of the population

$$\begin{aligned} \left. \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} \right|_{r=1} &= \lambda \frac{\partial \phi}{\partial r} + \beta \phi(r, t) - \mu \frac{\partial \phi}{\partial r} - \gamma \phi(r, t) + \gamma P_0(t) \\ &= (\lambda - \mu) E[N(t)] + \beta - \gamma + \gamma P_0(t) \end{aligned} \quad (61)$$

which doesn't look like the deterministic birth-death-immigration-emigration model. This is due to the emigration term, γ , being present. Any attempt to relate the deterministic model with a stochastic process when there is a non-population dependent rate (emigration) affecting their population's transition will result in this troublesome issue. For a detailed discussion of this situation, see the article by Switkes et.al [8].

Simulation of a birth-death-immigration-emigration process

A simulation of a BDIE process can be found in Figure 5.

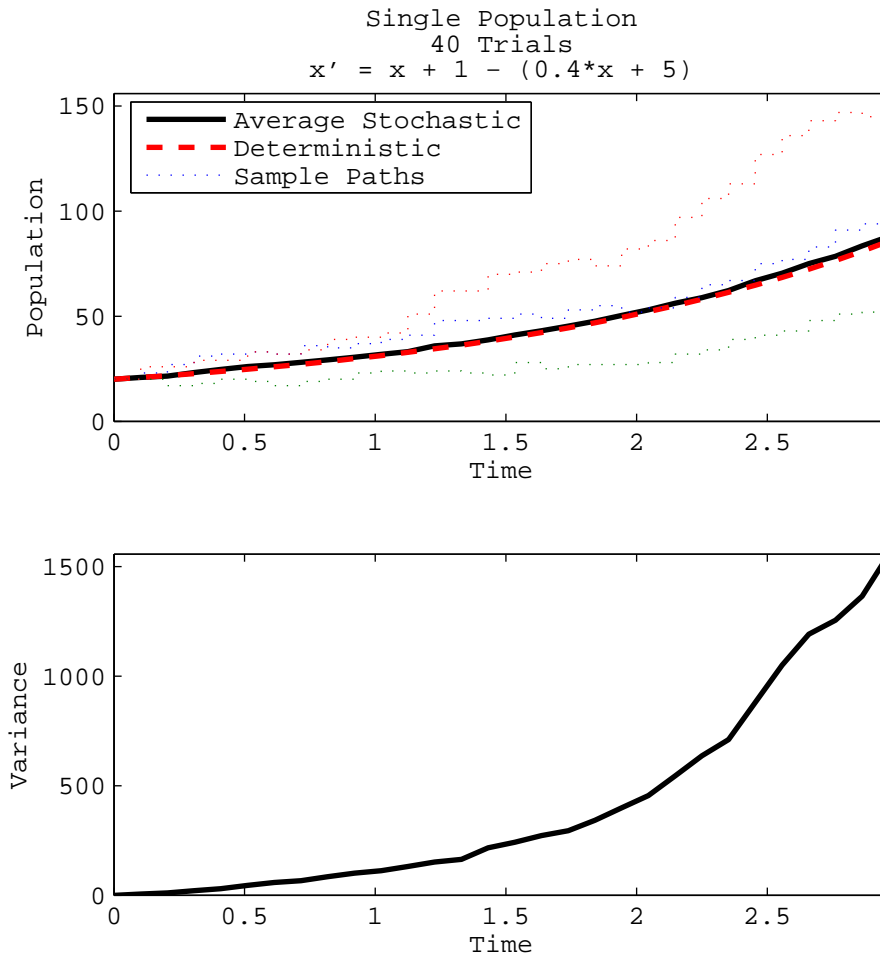


Figure 5: $\lambda = 1$, $\mu = .4$, $\beta = 1$, $\gamma = 5$.

1.6 Birth-Death Process with Polynomial Transition Rates

We now generalize the preceding sections by considering a population that is described by the differential equation

$$\frac{dx}{dt} = f(x, n) - g(x, m) \quad (62)$$

where $x(t)$ is the size of the population at time t and

$$f(i, n) = a_0 + a_1i + a_2i^2 + \dots + a_ni^n \quad (63)$$

$$g(i, m) = b_0 + b_1i + b_2i^2 + \dots + b_mi^m \quad (64)$$

Here f and g are the respective birth and death rates.

The work of the previous sections has motivated this population model and suggests that we can consider a birth-death formulation, however we noted the difficulty associated with having an emigration rate in considering the BDIE process so in the subsequent work, we will assume $b_0 = 0$.

Let $X(t)$ be a nonnegative, integer valued process with transition described in the following table

Transition	Rate
$i \rightarrow i + 1$	$f(i, n), i \geq 0$
$i \rightarrow i - 1$	$g(i, n), i \geq 1$

Then if

$$P_k(t) = P[X(t) = k | X(0) = 0], \quad (65)$$

we can derive the forward Kolmogorov equations in the usual manner. Specifically, we have for $k \geq 0$.

$$P'_k(t) = f(k-1, n)P_{k-1}(t) + g(k+1, m)P_{k+1}(t) - (f(k, n) + g(k, m))P_k(t). \quad (66)$$

Letting

$$\phi(r, t) = \sum_{k=0}^{\infty} P_k(t)r^k \quad (67)$$

be the probability generating function, we have

$$\begin{aligned} \frac{\partial \phi}{\partial t} &= \sum_{k=0}^{\infty} P'_k(t)r^k \\ &= \sum_{k=0}^{\infty} f(k-1, n)P_{k-1}(t)r^k + \sum_{k=0}^{\infty} g(k+1, m)P_{k+1}(t)r^k \\ &\quad - \sum_{k=0}^{\infty} (f(k, n) + g(k, m))P_k(t)r^k, \end{aligned} \quad (68)$$

upon substitution of equation (66). To simplify this expression for $\frac{\partial \phi}{\partial t}$ we need to evaluate series of the form

$$\sum_{k=0}^{\infty} k^n P_k(t) r^k \quad (69)$$

in terms of the p.g.f. $\phi(r, t)$. To get an idea of how to represent this series, we will consider a few cases (you will recognize these from the logistic and allee processes).

Specifically, when $n = 0$, then (69) becomes

$$\sum_{k=0}^{\infty} P_k(t) r^k = \phi(r, t), \quad (70)$$

as this is the definition of $\phi(r, t)$.

When $n = 1$, equation (69) can be expressed as a partial derivative of $\phi(r, t)$ with respect to r as follows

$$\sum_{k=0}^{\infty} k P_k(t) r^k = r \sum_{k=0}^{\infty} P_k(t) k r^{k-1} = r \frac{\partial \phi}{\partial r}. \quad (71)$$

If $n = 2$, equation (69) becomes

$$\begin{aligned} \sum_{k=0}^{\infty} k^2 P_k(t) r^k &= \sum_{k=0}^{\infty} [k(k-1) + k] P_k(t) r^k \\ &= \sum_{k=0}^{\infty} k(k-1) P_k(t) r^k + \sum_{k=0}^{\infty} k P_k(t) r^k. \end{aligned} \quad (72)$$

The first sum in this expression can be recognized as the second partial derivative with respect to r

$$\sum_{k=0}^{\infty} k(k-1) P_k(t) r^k = r^2 \sum_{k=0}^{\infty} k(k-1) P_k(t) r^{k-2} = r^2 \frac{\partial^2 \phi}{\partial r^2}. \quad (73)$$

The last sum in (72) is given by equation (71), so

$$\sum_{k=0}^{\infty} k^2 P_k(t) r^k = r^2 \frac{\partial^2 \phi}{\partial r^2} + r \frac{\partial \phi}{\partial r}. \quad (74)$$

For the case $n = 3$, the sum

$$\sum_{k=0}^{\infty} k^3 P_k(t) r^k \quad (75)$$

can be expressed as partial derivatives of $\phi(r, t)$ with respect to r by noting that

$$k^3 = k(k-1)(k-2) + 3k^2 - 2k, \quad (76)$$

so that

$$\begin{aligned}
\sum_{k=0}^{\infty} k^3 P_k(t) r^k &= \sum_{k=0}^{\infty} [k(k-1)(k-2) + 3k^2 - 2k] P_k(t) r^k \\
&= r^3 \sum_{k=0}^{\infty} k(k-1)(k-2) P_k(t) r^{k-3} \\
&\quad + 3 \sum_{k=0}^{\infty} k^2 P_k(t) r^k - 2 \sum_{k=0}^{\infty} k P_k(t) r^k \\
&= r^3 \frac{\partial^3 \phi}{\partial r^3} + 3r^2 \frac{\partial^2 \phi}{\partial r^2} - 2r \frac{\partial \phi}{\partial r},
\end{aligned} \tag{77}$$

by using equations (71) and (74).

To obtain a general formula for this pattern we will introduce some notation. The *falling factorial polynomial* is defined for a real x as

$$[x]_n = x(x-1)(x-2)\dots(x-n+1) \text{ for } n=1,2,\dots \tag{78}$$

with

$$[x]_0 = 1 \tag{79}$$

Using this notation one can show (c.f. Swift [6])

$$x^n = \sum_{j=0}^n S_2(n, j) [x]_j \tag{80}$$

where $S_2(n, j)$ is the *Stirling number of the second kind*. The Stirling number of the second kind $S_2(n, j)$ is defined as the number of ways of partitioning a set of n elements into j (nonempty) subsets. A detailed discussion of the properties of Stirling numbers can be found in Swift [6].

Using equation (80), we can write the sum in equation (69) as

$$\begin{aligned}
\sum_{k=0}^{\infty} k^n P_k(t) r^k &= \sum_{k=0}^{\infty} \sum_{j=0}^n S_2(n, j) [k]_j P_k(t) r^k \\
&= \sum_{j=0}^n r^j \sum_{k=0}^{\infty} S_2(n, j) [k]_j P_k(t) r^{k-j} \\
&= \sum_{j=0}^n r^j S_2(n, j) \sum_{k=0}^{\infty} [k]_j P_k(t) r^{k-j} \\
&= \sum_{j=0}^n r^j S_2(n, j) \frac{\partial^j \phi}{\partial r^j}.
\end{aligned} \tag{81}$$

Using this expression, we can write the first sum of equation (68) as

$$\begin{aligned}
\sum_{k=0}^{\infty} f(k-1, n) P_{k-1}(t) r^k &= \sum_{k=0}^{\infty} \sum_{l=0}^n a_l (k-1)^l P_{k-1}(t) r^k \\
&= \sum_{l=0}^n a_l \sum_{k=0}^{\infty} (k-1)^l P_{k-1}(t) r^k \\
&= \sum_{l=0}^n a_l \sum_{k=0}^{\infty} k^l P_k(t) r^{k+1} \\
&= r \sum_{l=0}^n a_l \sum_{j=0}^l r^j S_2(l, j) \frac{\partial^j \phi}{\partial r^j}. \tag{82}
\end{aligned}$$

Similarly for the second term of (68) have

$$\begin{aligned}
\sum_{k=0}^{\infty} g(k+1, m) P_{k+1}(t) r^k &= \sum_{k=0}^{\infty} \sum_{l=1}^m b_l (k+1)^l P_{k+1}(t) r^k \\
&= \sum_{l=1}^m b_l \sum_{k=0}^{\infty} (k+1)^l P_{k+1}(t) r^k \\
&= \sum_{l=1}^m b_l \sum_{k=0}^{\infty} k^l P_k(t) r^{k-1} \\
&= \frac{1}{r} \sum_{l=1}^m b_l \sum_{j=0}^m r^j S_2(m, j) \frac{\partial^j \phi}{\partial r^j}. \tag{83}
\end{aligned}$$

A very similar calculation gives

$$\sum_{k=0}^{\infty} f(k, n) P_k(t) r^k = \sum_{l=0}^n a_l \sum_{j=0}^n r^j S_2(n, j) \frac{\partial^j \phi}{\partial r^j} \tag{84}$$

and

$$\sum_{k=0}^{\infty} g(k, m) P_k(t) r^k = \sum_{l=1}^m b_l \sum_{j=0}^m r^j S_2(m, j) \frac{\partial^j \phi}{\partial r^j}. \tag{85}$$

Combining these expressions in the representation for $\frac{\partial \phi}{\partial t}$ in equation (68) gives

$$\begin{aligned}
\frac{\partial \phi}{\partial t} &= \left(\frac{1}{r} - 1 \right) \sum_{l=1}^m b_l \sum_{j=1}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} r^j \\
&\quad + (r-1) \sum_{l=0}^n a_l \sum_{j=1}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} r^j. \tag{86}
\end{aligned}$$

This last expression is the p.d.e. for the p.g.f. of a birth death process with polynomial transition rates. This expression is extremely difficult to solve, only special cases can be

pursued. We can, however obtain some useful and interesting information. We can find the expected population size, as usual we take the partial with respect to r , to obtain

$$\begin{aligned}
\frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} &= -\frac{1}{r^2} \sum_{l=1}^m b_l \sum_{j=1}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} r^j \\
&+ \left(\frac{1}{r} - 1\right) \frac{\partial}{\partial r} \left[\sum_{l=1}^m b_l \sum_{j=1}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} r^j \right] \\
&+ \sum_{l=0}^n a_l \sum_{j=1}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} r^j \\
&+ (r-1) \frac{\partial}{\partial r} \left[\sum_{l=0}^n a_l \sum_{j=1}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} r^j \right]. \tag{87}
\end{aligned}$$

Interchanging the order of the derivatives and evaluating this expression at $r = 1$ we have

$$\frac{d}{dt} E[X(t)] = - \sum_{l=1}^m b_l \sum_{j=1}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} \Big|_{r=1} + \sum_{l=0}^n a_l \sum_{j=1}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} \Big|_{r=1}. \tag{88}$$

But recalling that ϕ is a p.g.f., the j th partial derivative at $r = 1$ is

$$\frac{\partial^j \phi}{\partial r^j} \Big|_{r=1} = E[X(X-1)(X-2)\dots(X-j+1)] \tag{89}$$

that is, in falling factorial polynomial notation

$$\frac{\partial^j \phi}{\partial r^j} \Big|_{r=1} = E[[X]_j]. \tag{90}$$

Substitution of (90) into (88) yields

$$\frac{d}{dt} E[X(t)] = - \sum_{l=1}^m b_l \sum_{j=1}^l S_2(l, j) E[[X]_j] + \sum_{l=0}^n a_l \sum_{j=1}^l S_2(l, j) E[[X]_j]. \tag{91}$$

Falling factorials $[x]_j$ can be expressed as

$$[x]_j = \sum_{h=0}^{\infty} S_1(j, h) x^h \tag{92}$$

where $S_1(j, h)$ is the *Stirling number of the first kind* and is defined as the coefficient of x^h in $[x]_j$ (c.f. Swift [6]). Thus

$$E[[X]_j] = \sum_{h=0}^{\infty} S_1(j, h) E[X^h], \tag{93}$$

which substituting into (91) gives

$$\begin{aligned} \frac{d}{dt}E[X(t)] &= - \sum_{l=1}^m b_l \sum_{j=1}^l S_2(l, j) \sum_{h=0}^{\infty} S_1(j, h) E[X^h] \\ &\quad + \sum_{l=0}^n a_l \sum_{j=1}^l S_2(l, j) \sum_{h=0}^{\infty} S_1(j, h) E[X^h]. \end{aligned} \quad (94)$$

Fortunately, we can reduce this expression as there is a very useful orthogonal relation between Stirling numbers of the first and second kind. In particular

$$\sum_j S_2(l, j) S_1(j, h) = \begin{cases} 0 & \text{for } l \neq h \\ 1 & \text{for } l = h \end{cases}. \quad (95)$$

So

$$\begin{aligned} \frac{d}{dt}E[X(t)] &= - \sum_{l=1}^m b_l \sum_{h=0}^{\infty} \sum_{j=1}^l S_2(l, j) S_1(j, h) E[X^h] \\ &\quad + \sum_{l=0}^n a_l \sum_{h=0}^{\infty} \sum_{j=1}^l S_2(l, j) S_1(j, h) E[X^h] \\ &= \sum_{l=0}^n a_l E[X^l] - \sum_{l=1}^m b_l E[X^l], \end{aligned} \quad (96)$$

which corresponds to the deterministic model given in equation (62). Thus, birth-death process with polynomial transition rates correspond to the deterministic population size in a natural way.

We can summarize the preceding as the following Theorem:

Theorem 1.1. *If $X(t)$ is a non-negative integer valued stochastic process with transition rates given by*

Transition	Rate
$i \rightarrow i + 1$	$f(i, n), i \geq 0$
$i \rightarrow i - 1$	$g(i, n), i \geq 1$

where

$$f(i, n) = a_0 + a_1 i + a_2 i^2 + \dots + a_n i^n, a_i \geq 0 \quad \text{for } i = 0, 1, \dots, n \quad (97)$$

and

$$g(i, m) = b_1 i + b_2 i^2 + \dots + b_m i^m, b_i \geq 0 \quad \text{for } i = 1, \dots, m \quad (98)$$

and if

$$\phi(r, t) = \sum_{k=0}^{\infty} P_k(t) r^k. \quad (99)$$

Then

$$\begin{aligned} \frac{\partial \phi}{\partial t} &= \left(\frac{1}{r} - 1 \right) \sum_{l=1}^m \sum_{j=0}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} \\ &\quad + (r - 1) \sum_{l=0}^n a_l \sum_{j=1}^l S_2(l, j) \frac{\partial^j \phi}{\partial r^j} r^j \end{aligned} \quad (100)$$

where $S_2(l, j)$ is the Stirling number of the second kind. The expected value $E[X(t)]$ of the process $X(t)$ satisfies the differential equation

$$\frac{d}{dt} E[X(t)] = \sum_{l=0}^n a_l E[X^l(t)] - \sum_{l=1}^m b_l E[X^l(t)]. \quad (101)$$

Here we have examples of this process.

Example 1: Logistic Birth-Death

As in the simple birth-death process, births occur proportional to the population size with a birth rate $\lambda > 0$. To introduce the logistic effect in the population, we will assume that population crowding and competition for resources increases the death rate. Mimicking the deterministic logistic model, we increase the usual death rate $\mu > 0$, with an additional term $\varepsilon > 0$ which is proportional to the square of the population size.

Deterministic

$$\frac{dx(t)}{dt} = (\lambda - \mu)x - \varepsilon x^2 \quad (102)$$

where x = population, λ = birth rate, μ = death rate,
 $\varepsilon = \frac{\lambda - \mu}{k}$, k = carrying capacity

Thus, this logistic birth-death process can be described as having the following transitions and rates:

Transition	Rate
$i \rightarrow i + 1$	λi
$i \rightarrow i - 1$	$\mu i + \varepsilon i^2$

The forward Kolmogorov equations are

$$\begin{aligned} P'_n(t) &= \lambda(i-1)P_{i-1}(t)r^i + \mu(i+1)P_{i+1}(t)r^i + \varepsilon(i+1)^2P_{i+1}(t)r^i \\ &- (\lambda i + \mu i + \varepsilon i^2)P_i(t)r^i. \end{aligned} \quad (103)$$

Solving in the manner we are accustomed we find our p.d.e. to be

$$\begin{aligned} \frac{\partial \phi}{\partial t} &= r(r-1)\lambda \frac{\partial \phi}{\partial r} + r \left(\frac{1}{r} - 1 \right) \mu \frac{\partial \phi}{\partial r} \\ &+ r^2 \left(\frac{1}{r} - 1 \right) \varepsilon \frac{\partial^2 \phi}{\partial r^2} + r \left(\frac{1}{r} - 1 \right) \varepsilon \frac{\partial \phi}{\partial r} \end{aligned} \quad (104)$$

Differentiating with respect to r we have

$$\begin{aligned} \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} &= (r-1)\lambda \frac{\partial \phi}{\partial r} + r\lambda \frac{\partial \phi}{\partial r} + r(r-1)\lambda \frac{\partial^2 \phi}{\partial r^2} \\ &+ \left(\frac{1}{r} - 1 \right) \mu \frac{\partial \phi}{\partial r} - \frac{1}{r} \mu \frac{\partial \phi}{\partial r} + r \left(\frac{1}{r} - 1 \right) \frac{\partial^2 \phi}{\partial r^2} \\ &+ 2r \left(\frac{1}{r} - 1 \right) \varepsilon \frac{\partial^2 \phi}{\partial r^2} - \varepsilon \frac{\partial^2 \phi}{\partial r^2} + r^2 \left(\frac{1}{r} - 1 \right) \varepsilon \frac{\partial^3 \phi}{\partial r^3} \\ &+ \left(\frac{1}{r} - 1 \right) \varepsilon \frac{\partial \phi}{\partial r} - \frac{1}{r} \varepsilon \frac{\partial \phi}{\partial r} + r \left(\frac{1}{r} - 1 \right) \varepsilon \frac{\partial^2 \phi}{\partial r^2} \end{aligned} \quad (105)$$

We evaluate the partial at $r = 1$ to get the expected value of the population.

$$\begin{aligned} \left. \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} \right|_{r=1} &= \lambda \frac{\partial \phi}{\partial r} - \mu \frac{\partial \phi}{\partial r} - \varepsilon \frac{\partial^2 \phi}{\partial r^2} - \varepsilon \frac{\partial \phi}{\partial r} \\ &= (\lambda - \mu)E[X(t)] - \varepsilon E[X(t)(X(t) - 1)] - \varepsilon E[X(t)] \\ &= (\lambda - \mu)E[X(t)] - \varepsilon E[X(t)^2] + \varepsilon E[X(t)] - \varepsilon E[X(t)] \\ &= (\lambda - \mu)E[X(t)] - \varepsilon E[X(t)^2] \end{aligned} \quad (106)$$

which is similar to the deterministic logistic model.

Simulation of a logistic birth-death process

A simulation of the logistic process can be found in Figure 6.

Example 2: Allee Birth-Death

The purpose of the allee model is to include the fact that a certain population size is needed to sustain growth.

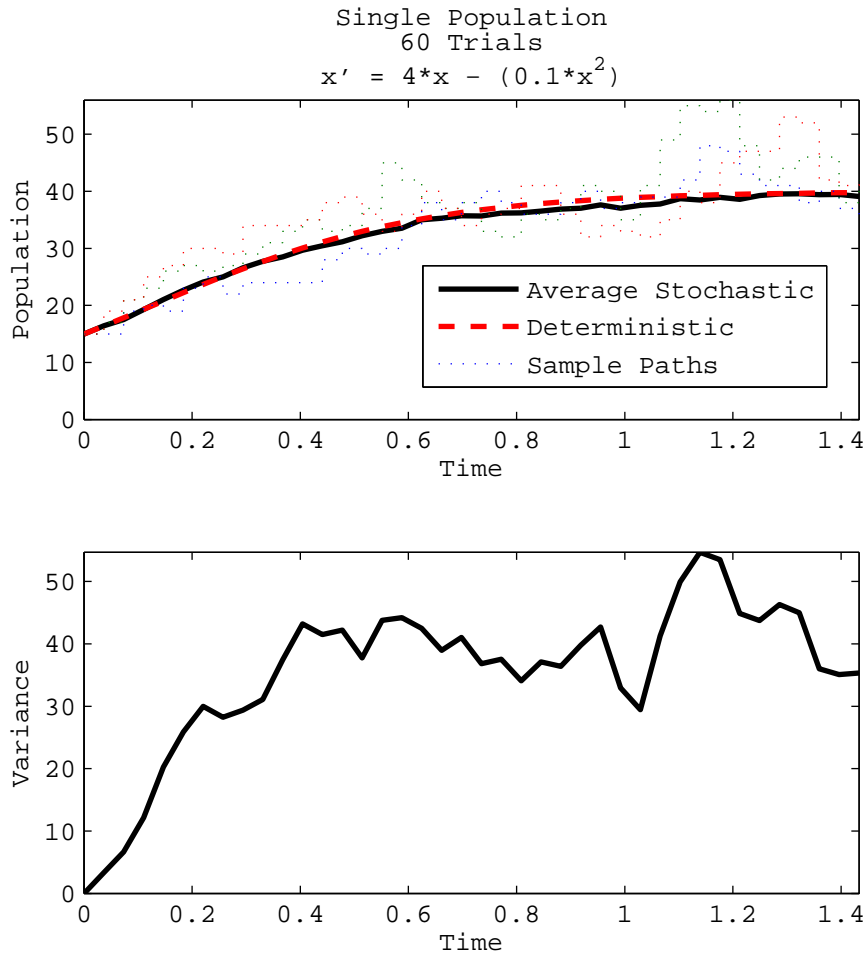


Figure 6: $(\lambda - \mu) = 4$ and $\varepsilon = .1$.

Deterministic

$$\frac{dx(t)}{dt} = \omega x(a - x)(x - b) \quad (107)$$

where x = population, ω = growth rate,
 a = population required to sustain growth, b = carrying capacity

This logistic birth-death process can be described as having the following transitions and rates:

Transition	Rate
$i \rightarrow i + 1$	$\omega(a + b)i^2$
$i \rightarrow i - 1$	$\omega a b i + \omega i^3$

Increase can occur through birth, a proportional increase dependent on population size $\lambda i > 0$,. A decrease in population size will come through death $\mu i + \omega i^3$.

For notation purposes we will use

$$\begin{aligned}
\alpha &= \omega(a+b) \\
\beta &= \omega ab \\
\gamma &= \omega
\end{aligned} \tag{108}$$

The forward Kolmogorov equations are

$$\begin{aligned}
P_i'(t) &= \alpha(i-1)^2 P_{i-1}(t) r^i + \beta(i+1) P_{i+1}(t) + \gamma(i+1)^3 P_{i+1}(t) \\
&- (\alpha i^2 + \beta i + \gamma i^3) P_i(t).
\end{aligned} \tag{109}$$

Solving in the manner we are accustomed we find our p.d.e. to be

$$\begin{aligned}
\frac{\partial \phi}{\partial t} &= \alpha(r-1) \left(r^2 \frac{\partial^2 \phi}{\partial r^2} + r \frac{\partial \phi}{\partial r} \right) + \beta r \left(\frac{1}{r} - 1 \right) \frac{\partial \phi}{\partial r} \\
&+ \gamma \left(\frac{1}{r} - 1 \right) \left(r^3 \frac{\partial^3 \phi}{\partial r^3} + 3r^2 \frac{\partial^2 \phi}{\partial r^2} + r \frac{\partial \phi}{\partial r} \right).
\end{aligned} \tag{110}$$

Differentiating with respect to r we have

$$\begin{aligned}
\frac{\partial}{\partial r} \frac{\partial \phi}{\partial r} &= \alpha \left(r^2 \frac{\partial^2 \phi}{\partial r^2} + r \frac{\partial \phi}{\partial r} \right) + \alpha(r-1) \frac{d}{dr} \left[r^2 \frac{\partial^2 \phi}{\partial r^2} + r \frac{\partial \phi}{\partial r} \right] \\
&+ \beta \left(\frac{1}{r} - 1 \right) \frac{\partial \phi}{\partial r} - \beta \frac{1}{r} \frac{\partial \phi}{\partial r} + \beta r \left(\frac{1}{r} - 1 \right) \frac{\partial^2 \phi}{\partial r^2} \\
&- \gamma \frac{1}{r^2} \left(r^2 \frac{\partial^3 \phi}{\partial r^3} + 3r^2 \frac{\partial^2 \phi}{\partial r^2} + r \frac{\partial \phi}{\partial r} \right) \\
&+ \gamma \left(\frac{1}{r} - 1 \right) \frac{d}{dr} \left[r^2 \frac{\partial^3 \phi}{\partial r^3} + 3r^2 \frac{\partial^2 \phi}{\partial r^2} + r \frac{\partial \phi}{\partial r} \right].
\end{aligned} \tag{111}$$

We evaluate the partial at $r = 1$ to get the expected value of the population.

$$\begin{aligned}
\left. \frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} \right|_{r=1} &= \alpha \frac{\partial^2 \phi}{\partial r^2} + \alpha \frac{\partial \phi}{\partial r} - \beta \frac{\partial \phi}{\partial r} - \gamma \frac{\partial^3}{\partial r^3} - 3\gamma \frac{\partial^2 \phi}{\partial r^2} - \gamma \frac{\partial \phi}{\partial r} \\
&= \alpha E[X(t)(X(t) - 1)] + \alpha E[X(t)] - \beta E[X(t)] \\
&\quad - \gamma E[X(t)(X(t) - 1)(X(t) - 2)] - 3\gamma E[X(t)(X(t) - 1)] \\
&\quad - \gamma E[X(t)] \\
&= \alpha E[X(t)^2] - \alpha E[X(t)] + \alpha E[X(t)] - \beta E[X(t)] \\
&\quad - \gamma E[X(t)^3] + 3\gamma E[X(t)^2] - 2\gamma E[X(t)] \\
&\quad - 3\gamma E[X(t)^2] + 3\gamma E[X(t)] - \gamma E[X(t)] \\
&= \alpha E[X(t)^2] - \beta E[X(t)] - \gamma E[X(t)^3].
\end{aligned} \tag{112}$$

Recalling that

$$\begin{aligned}
\alpha &= \omega(a+b) \\
\beta &= \omega ab \\
\gamma &= \omega
\end{aligned}$$

gives (112) to be

$$\frac{d}{dt}E[X(t)] = \omega(a + b)E[X(t)^2] - \omega abE[X(t)] - \omega E[X(t)^3] \quad (113)$$

which is similar to the deterministic Allee model.

Simulation of a Allee birth-death process

A simulation of the Allee model can be found in Figure 7.

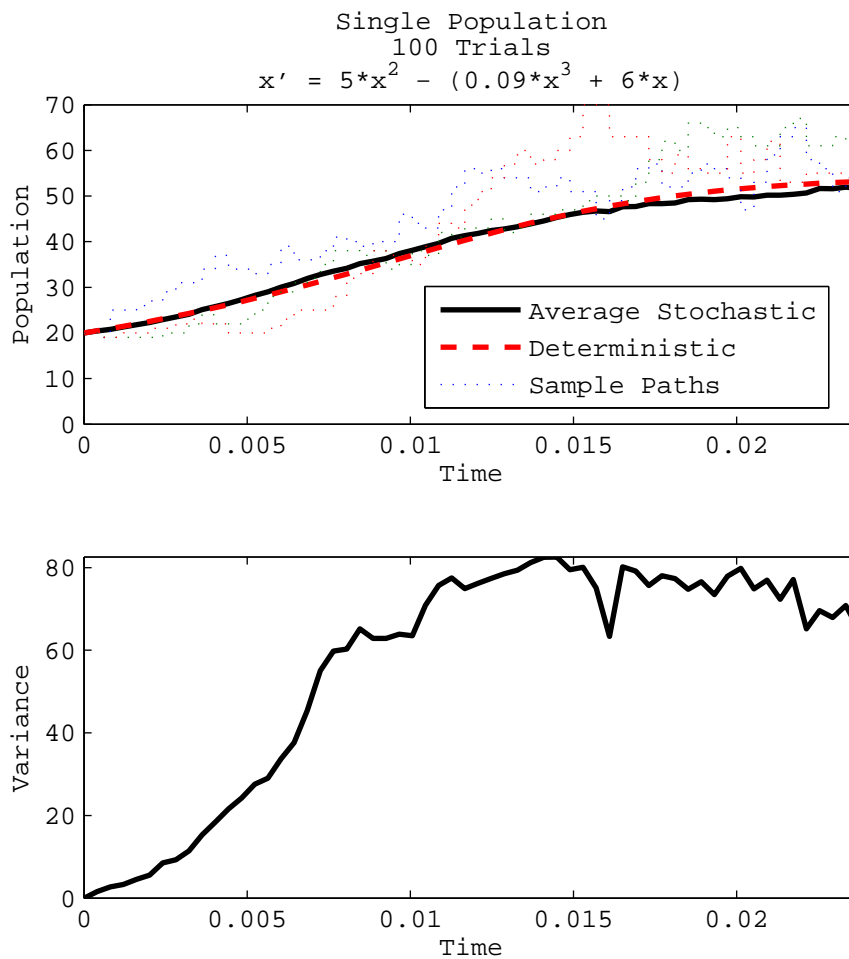


Figure 7: $\omega(a + b) = 5$, $\omega ab = 6$, and $\omega = .09$.

1.7 Extinction

The behavior of birth-death processes with polynomial transition rates is rather interesting and as shown in the previous section generalizes a large class of deterministic population

models. Our work with simulating these processes uncovered some surprising behavior. While simulating Allee models with low carrying capacities we noticed that the averages were ever so slightly smaller than the deterministic model as time went on. This led to the discovery that some of the simulations were becoming extinct. This outcome is by no means unreasonable with small populations, but it raises a curious question. Exactly what is the probability of extinction for our stochastic population processes?

To develop the appropriate tools to analyze these processes, we consider a general birth-death process $X(t)$ with transitions and rates given in the following table

Transition	Rate
$i \rightarrow i + 1$	$\lambda_i, i \geq 0$
$i \rightarrow i - 1$	$\mu_i, i \geq 1$

here $\lambda_i \geq 0$ is the state-dependent birth rate and $\mu_i \geq 0$ is the state-dependent death rate. In this notation we can state a well-known result, the proof of which can be found in either Allen [76] or Karlin and Taylor [76].

Theorem 1.2. *Consider a birth and death process with birth and death rates $\lambda_n > 0$ and $\mu_n > 0, n \geq 1$, where $\lambda_0 = 0$ so that 0 is an absorbing state. The probability of absorption into state 0 from an initial state m is*

$$\begin{cases} \frac{\sum_{i=m}^{\infty} \prod_{j=1}^i \frac{\mu_j}{\lambda_j}}{1 + \sum_{i=m}^{\infty} \prod_{j=1}^i \frac{\mu_j}{\lambda_j}} & \text{if } \sum_{i=1}^{\infty} \prod_{j=1}^i \frac{\mu_j}{\lambda_j} < \infty, \\ 1 & \text{if } \sum_{i=1}^{\infty} \prod_{j=1}^i \frac{\mu_j}{\lambda_j} = \infty. \end{cases} \quad (114)$$

We can apply this result to birth-death with polynomial transition rates. Let

$$\lambda(i, n) = f(i, n) = a_0 + a_1 i + a_2 i^2 + \dots + a_n i^n \quad (115)$$

$$\mu(i, m) = g(i, m) = b_0 + b_1 i + b_2 i^2 + \dots + b_m i^m \quad (116)$$

Let $a_0 = 0$, so that there is no immigration rate and hence state 0 is absorbing.

$$W_k = \prod_{i=1}^k \frac{\mu_i}{\lambda_i}. \quad (117)$$

So

$$\begin{aligned} \frac{W_{k+1}}{W_k} &= \frac{\prod_{i=1}^{k+1} \frac{\mu_i}{\lambda_i}}{\prod_{i=1}^k \frac{\mu_i}{\lambda_i}} \\ &= \frac{\mu_{k+1}}{\lambda_{k+1}} = \frac{b_0 + b_1(k+1) + b_2(k+1)^2 + \dots + b_m(k+1)^m}{a_1(k+1) + a_2(k+1)^2 + \dots + a_n(k+1)^n}. \end{aligned} \quad (118)$$

Thus

$$\begin{aligned}\lim_{k \rightarrow \infty} \frac{W_{k+1}}{W_k} &= \lim_{k \rightarrow \infty} \frac{b_0 + b_1(k+1) + b_2(k+1)^2 + \dots + b_m(k+1)^m}{a_1(k+1) + a_2(k+1)^2 + \dots + a_n(k+1)^n} \\ &= \lim_{k \rightarrow \infty} \frac{b_m k^m}{a_n k^n}.\end{aligned}\tag{119}$$

This limit will be greater than 1 if $m = n$ and $b_m > a_m$ or if $m > n$, so if either of these conditions are satisfied then

$$\lim_{k \rightarrow \infty} \frac{W_{k+1}}{W_k} > 1\tag{120}$$

so that by the ratio test, the series

$$\sum_{k=1}^{\infty} W_k = \sum_{k=1}^{\infty} \prod_{i=1}^k \frac{\mu_i}{\lambda_i}\tag{121}$$

diverges. This by (114) of Theorem 1.2 gives that extinction is certain, More specifically

$$\lim_{t \rightarrow \infty} P_0(t) = 1.\tag{122}$$

We summarize this result in the following proposition.

Proposition 1.3. *If $X(t)$ is a nonnegative integer valued process with transition given by*

<i>Transition</i>	<i>Rate</i>
$i \rightarrow i + 1$	$f(i, n)$, for $i \geq 1$
$i \rightarrow i - 1$	$f(i, m)$, for $i \geq 1$

where

$$f(i, n) = a_1 i + a_2 i^2 + \dots + a_n i^n\tag{123}$$

and

$$g(i, m) = b_1 i + b_2 i^2 + \dots + b_m i^m\tag{124}$$

if $m = n$ and $b_m > a_n$ or if $m > n$.

Then

$$\lim_{t \rightarrow \infty} P_0(t) = 1\tag{125}$$

so that extinction is certain.

We present two examples that are relevant to our previous work.

Example 1: Logistic Birth Death Process

Recall the deterministic Logistic Model

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{k}\right) \text{ where } r > 0 \text{ and } k > 0 \quad (126)$$

We can write the change in x as the change due to growth so

$$\lambda_i - \mu_i = ri \left(1 - \frac{i}{k}\right). \quad (127)$$

Since the right hand side of this expression is a second degree polynomial, it is reasonable to suppose λ_i and μ_i are quadratic polynomials of the form

$$\lambda_i = b_1i + b_2i^2 \quad (128)$$

$$\mu_i = d_1i + d_2i^2. \quad (129)$$

where b_1, b_2, d_1, d_2 are constants.

The difference $\lambda_i - \mu_i$ is

$$\lambda_i - \mu_i = (b_1 - d_1)i + (b_2 - d_2)i^2. \quad (130)$$

Substituting in (127) into (130) we get

$$\begin{aligned} \lambda_i - \mu_i &= (b_1 - d_1)i + (b_2 - d_2)i^2 \\ &= ri \left(1 - \frac{i}{k}\right) \\ &= ri - \frac{ri^2}{k}. \end{aligned} \quad (131)$$

Now comparing coefficients gives

$$b_1 - d_1 = r \quad (132)$$

and

$$b_2 - d_2 = \frac{-r}{k}. \quad (133)$$

Solving for k we find

$$k = \frac{d_1 - b_1}{b_2 - d_2}. \quad (134)$$

Since $k > 0$ we can say

$$b_2 - d_2 < 0 \text{ as } b_1 - d_1 > 0$$

so

$$b_2 < d_2.$$

Thus, by our proposition, extinction is certain in the logistic birth-death process.

Example 2: Allee Birth Death Process

The deterministic Allee model is given by

$$\frac{dx}{dt} = rx(a-x)(x-b) \quad (135)$$

where $r > 0$, $a > 0$, $b < 0$. We can write the change as

$$\lambda_i - \mu_i = ri(a-i)(i-b). \quad (136)$$

As the Allee model has the right hand side as a cubic polynomial it is reasonable to suppose that λ_i and μ_i are cubic polynomials of the form

$$\lambda_i = b_1i + b_2i^2 + b_3i^3 \quad (137)$$

$$\mu_i = d_1i + d_2i^2 + d_3i^3, \quad (138)$$

begincenter with $b_1, b_2, b_3, d_1, d_2, d_3$ as constants. The difference $\lambda_i - \mu_i$ is the change in population, so

$$\lambda_i - \mu_i = (b_1 - d_1)i + (b_2 - d_2)i^2 + (b_3 - d_3)i^3 \quad (139)$$

Thus,

$$\begin{aligned} \lambda_i - \mu_i &= ri(a-i)(i-b) \\ &= rabi + (ra - rb)i^2 - ri^3 \\ &= (b_1 - d_1)i + (b_2 - d_2)i^2 + (b_3 - d_3)i^3 \end{aligned} \quad (140)$$

so that comparing coefficients gives

$$b_1 - d_1 = rab \quad (141)$$

and

$$b_2 - d_2 = r(a-b) \quad (142)$$

and

$$b_3 - d_3 = -r. \quad (143)$$

Since $r > 0$

$$b_3 - d_3 = r < 0 \quad (144)$$

so that

$$b_3 < d_3 \quad (145)$$

Thus, by our proposition, extinction is certain in the Allee birth-death process.

2 Competing Population Models

2.1 The Classic Predator-Prey Model

We will now consider a classical model describing the interaction between two species: a predator and its prey. This model was originally proposed by A. J. Lotka and V. Volterra in the 1920s.

The model assumptions, simplifications, and notation.

1. There are two species interacting: a prey species x and a predator species y . For the purposes of this model no other species interact with these two.
2. In the absence of the predator, the prey exhibits pure exponential growth. In particular $\frac{dx}{dt} = \alpha x$ where $\alpha > 0$. Implicit in this assumption is that there is sufficient food and space to allow the prey species to grow indefinitely.
3. In the absence of the prey, the predator species dies out exponentially. In particular, $\frac{dy}{dt} = -\gamma y$ where $\gamma > 0$. Thus although it is not explicitly mentioned, there is other food for the predators, but not enough to sustain the population.
4. When the two species are in the presence of each other, the predators kill the prey in such a way that the predator population increases at a rate proportional to the product of the number of predators and the number of prey (i.e., xy). Similarly the prey population is decreased by an amount proportional to the product of the population sizes.

$$\frac{dx}{dt} = \alpha x - \beta xy \quad (146)$$

$$\frac{dy}{dt} = -\gamma y + \delta xy \quad (147)$$

where $\alpha, \beta, \gamma, \delta$ are growth rates.

Factoring gives

$$\frac{dx}{dt} = x(\alpha - \beta y)$$

$$\frac{dy}{dt} = y(\delta x - \gamma).$$

Phase plane of a predator prey model

The nullclines for $\frac{dx}{dt} = 0$ are $x = 0$ and $y = \alpha/\beta$. The nullclines for $\frac{dy}{dt} = 0$ are $y = 0$ and $x = \gamma/\delta$. Graphing these in the phase plane reveals two fixed points $(\bar{x}, \bar{y}) = (0, 0)$ and $(\bar{x}, \bar{y}) = (\gamma/\delta, \alpha/\beta)$. (The points $(\gamma/\delta, 0)$ and $(0, \alpha/\beta)$ are not points of intersection of different nullclines.) A phase plane is shown in Figure 8. Naturally, we are not interested in the $(0, 0)$ solution. The $(\gamma/\delta, \alpha/\beta)$ solution has trajectories circling about it, though it is

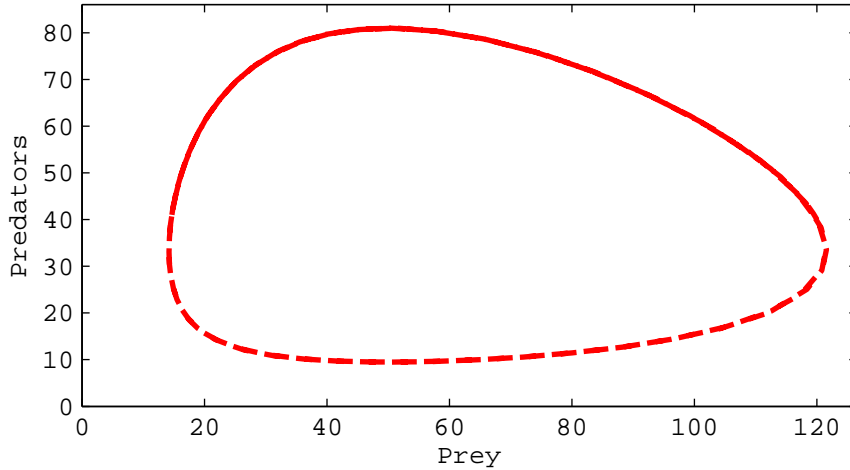


Figure 8: The initial populations are 120 for the prey population and 40 for the predator population. The growth rates are $\alpha = 1$, $\beta = .03$, $\gamma = 1$, and $\delta = .02$

not clear from this analysis if the solutions are spiraling in or out, or if they are circling in pure oscillatory motion. Jacobian analysis determines this.

To help in the analysis of this model we will “linearize” it.

$$F(x, y) = \alpha x - \beta xy \quad (148)$$

$$G(x, y) = -\gamma y + \delta xy \quad (149)$$

We will replace these functions with their Taylor series approximations. Here is the linearization of both populations at the point (\bar{x}, \bar{y}) .

$$F(x, y) \approx F(\bar{x}, \bar{y}) + \frac{\partial F}{\partial x}(\bar{x}, \bar{y})(x - \bar{x}) + \frac{\partial F}{\partial y}(\bar{x}, \bar{y})(y - \bar{y}) \quad (150)$$

$$G(x, y) \approx G(\bar{x}, \bar{y}) + \frac{\partial G}{\partial x}(\bar{x}, \bar{y})(x - \bar{x}) + \frac{\partial G}{\partial y}(\bar{x}, \bar{y})(y - \bar{y}). \quad (151)$$

Here u and v are the distance from x and y to the critical point, \bar{x} and \bar{y} , that is

$$u = x - \bar{x} \quad (152)$$

$$v = y - \bar{y}. \quad (153)$$

We use u and v to obtain new functions of the two populations for the linearized form

$$\frac{du}{dt} \approx \frac{\partial F}{\partial x}(\bar{x}, \bar{y})u + \frac{\partial F}{\partial y}(\bar{x}, \bar{y})v \quad (154)$$

$$\frac{dv}{dt} \approx \frac{\partial G}{\partial x}(\bar{x}, \bar{y})u + \frac{\partial G}{\partial y}(\bar{x}, \bar{y})v \quad (155)$$

The partials with respect to x and y for both functions are

$$\frac{\partial F}{\partial x} = \alpha - \beta y \quad (156)$$

$$\frac{\partial F}{\partial y} = -\beta x \quad (157)$$

$$\frac{\partial G}{\partial x} = \delta y \quad (158)$$

$$\frac{\partial G}{\partial y} = \gamma + \delta x. \quad (159)$$

Using the above equations, we can write

$$\begin{pmatrix} u'(t) \\ v'(t) \end{pmatrix} \approx \begin{pmatrix} \frac{\partial F}{\partial x}(\bar{x}, \bar{y}) & \frac{\partial F}{\partial y}(\bar{x}, \bar{y}) \\ \frac{\partial G}{\partial x}(\bar{x}, \bar{y}) & \frac{\partial G}{\partial y}(\bar{x}, \bar{y}) \end{pmatrix} \begin{pmatrix} u(t) \\ v(t) \end{pmatrix}, \quad (160)$$

where

$$J(x, y) = \begin{pmatrix} \frac{\partial F}{\partial x} & \frac{\partial F}{\partial y} \\ \frac{\partial G}{\partial x} & \frac{\partial G}{\partial y} \end{pmatrix} \quad (161)$$

is the Jacobian of F and G .

The critical point is $(\frac{\gamma}{\delta}, \frac{\alpha}{\beta})$ and when we evaluate the Jacobian we have

$$J\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right) = \begin{pmatrix} 0 & -\frac{\beta\gamma}{\delta} \\ \frac{\alpha\delta}{\beta} & 0 \end{pmatrix}. \quad (162)$$

After solving the Jacobian we end up with two differential equations,

$$\frac{du}{dt} = u' = -\frac{\beta\gamma}{\delta}v \quad (163)$$

$$\frac{dv}{dt} = v' = \frac{\alpha\delta}{\beta}u. \quad (164)$$

The chain rule from calculus implies that

$$\frac{du}{dv} = \frac{du}{dt} \frac{dt}{dv};$$

thus

$$\frac{du}{dv} = -\frac{\gamma\beta^2}{\alpha\delta^2} \frac{v}{u}.$$

The key to this analysis is that this is a separable differentiable equation. Thus

$$\alpha\delta^2 u \, du = -\gamma\beta^2 v \, dv.$$

Integrating both sides yields

$$\frac{\alpha\delta^2 u^2}{2} = -\frac{\gamma\beta^2 v^2}{2} + C.$$

Rearranging gives

$$\frac{\alpha\delta^2u^2}{2} + \frac{\gamma\beta^2v^2}{2} = C \quad \text{or} \quad \frac{u^2}{\beta^2\gamma} + \frac{v^2}{\alpha\delta^2} = C.$$

Substituting to get back our to our original variables yields

$$\frac{(x - \frac{\gamma}{\delta})^2}{\beta^2\gamma} + \frac{(y - \frac{\alpha}{\beta})^2}{\alpha\delta^2} = C.$$

This is, of course, the equation for an ellipse centered at the fixed point with axes parallel to the coordinate axes. The implication is that close to the fixed point, the trajectories look like ellipses; which confirms our prior determination that the fixed point was a center. Indeed, close to the fixed point the trajectories are ellipses, further away they still oscillate about the fixed point, but with a more complicated shape. A time plane of the predator prey is in Figure 9

Predator prey model

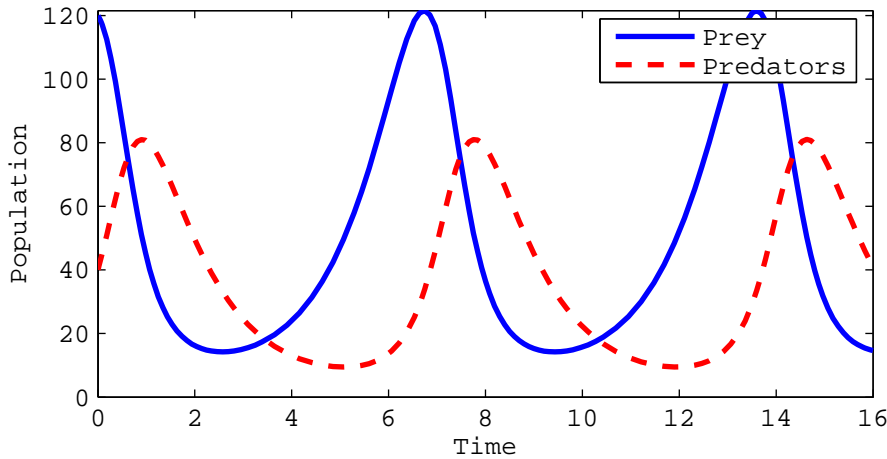


Figure 9: The initial populations are 120 for the prey population and 40 for the predator population. The growth rates are $\alpha = 1$, $\beta = .03$, $\gamma = 1$, and $\delta = .02$

2.2 Stochastic Classic Predator-Prey

Let $X(t)$ be the size of the prey population at time t and $Y(t)$ be the size of the predator population at time t . In the model to be formulated, it is now assumed that instead of a (deterministic) rate of predator and prey births and deaths, there is a probability of a predator and prey birth or death. Thus $X(t)$ and $Y(t)$ are time dependent random variables.

Let the probability of there being i preys and j predators at time t be denoted by

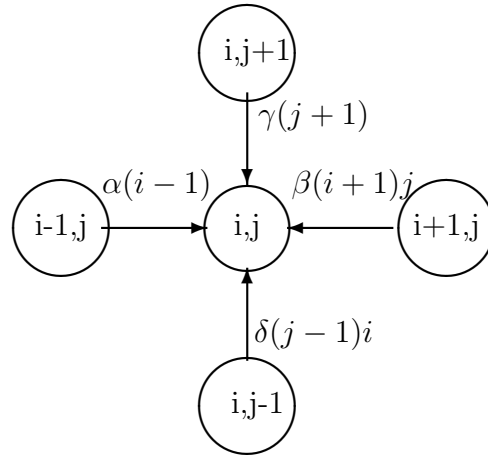
$$P_{i,j}(t) = P[X(t) = i, Y(t) = j], \text{ for } i = 0, 1, 2, \dots, j = 0, 1, 2, \dots$$

As in the simple birth-death process for a single species, births and deaths in this process occur proportional to the population size. We assume that the infinitesimal probability of an individual prey birth during the small time interval Δt is $\alpha i \Delta t + o(\Delta t)$, where $\alpha > 0$ is the prey birth rate. Similarly, we assume that the infinitesimal probability of an individual predator death during the small time interval Δt is $\gamma j \Delta t + o(\Delta t)$, where $\delta > 0$ is the predator death rate.

To mimic the deterministic model interaction term, we assume that the infinitesimal probability of a prey death occurring during Δt is $\beta ij \Delta t + o(\Delta t)$, where $\beta > 0$ is the prey death rate. Similarly, a predator birth occurs during Δt with infinitesimal probability $\delta ij \Delta t + o(\Delta t)$, with $\gamma > 0$. These rates are summarized in the following table.

Transition	Rate
$(i, j) \rightarrow (i + 1, j)$	αi
$(i, j) \rightarrow (i - 1, j)$	βij
$(i, j) \rightarrow (i, j - 1)$	γj
$(i, j) \rightarrow (i, j + 1)$	δij

These transitions occur on the nonnegative integer lattice and can be visualized in the following way:



The standard argument using the forward Kolmogorov equations is used to obtain $P_{i,j}(t)$, by considering the probability $P_{i,j}(t + \Delta t)$. This probability is obtained as the sum of the probabilities of the following mutually exclusive events:

- a) There are i prey and j predators by time t and no birth or deaths of either species occur in $(t, t + \Delta t)$.

- b) There are $i - 1$ prey and j predators by time t and a prey birth occurs in $(t, t + \Delta t)$.
- c) There are i prey and $j - 1$ predators by time t and a predator birth occurs in $(t, t + \Delta t)$.
- d) There are $i + 1$ prey and j predators by time t and one prey death occurs in $(t, t + \Delta t)$.
- e) There are i prey and $j + 1$ predators and one predator death occurs in $(t, t + \Delta t)$. This gives

$$\begin{aligned}
P'_{i,j}(t) &= \alpha(i-1)P_{i-1,j}(t) + \beta(i+1)jP_{i+1,j}(t) \\
&+ \gamma(j+1)P_{i,j+1}(t) + \delta(j-1)iP_{i,j-1}(t) \\
&- (\alpha i + \beta i j + \gamma j + \delta i j)P_{i,j}(t).
\end{aligned} \tag{165}$$

This doubly infinite system of differential equations is not easily solved and in fact, it appears to be an open problem to obtain its closed form solution. The system can however, be studied by letting

$$\phi(r, s, t) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_{i,j}(t) r^i s^j \tag{166}$$

be the probability generating function for this system. We do not have $P_{ij}(t)$ but we do have $P'_{ij}(t)$ so we plug that into the p.g.f.

$$\frac{\partial \phi}{\partial t}(r, s, t) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P'_{i,j}(t) r^i s^j \tag{167}$$

Using in equation (165) in equation (167) we have

$$\begin{aligned}
\frac{\partial \phi}{\partial t}(r, s, t) &= - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} (\alpha i + \beta i j + \gamma j + \delta i j) P_{i,j}(t) r^i s^j \\
&+ \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \alpha(i-1) P_{i-1,j}(t) r^i s^j \\
&+ \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \beta(i+1) j P_{i+1,j}(t) r^i s^j \\
&+ \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \gamma(j+1) P_{i,j+1}(t) r^i s^j \\
&+ \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \delta(j-1) i P_{i,j-1}(t) r^i s^j
\end{aligned} \tag{168}$$

We expand the summation through the first term and combine rates, so that

$$\sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \alpha(i-1) P_{i-1,j}(t) r^i s^j - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \alpha i P_{i,j}(t) r^i s^j \tag{169}$$

by re-indexing with $i \leftarrow i + 1$

$$= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \alpha i P_{ij}(t) r^{i+1} s^j - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \alpha i P_{ij}(t) r^i s^j \quad (170)$$

Factoring out common terms, this sum becomes

$$\begin{aligned} &= r(r-1)\alpha \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_{ij}(t) r^{i-1} s^j \\ &= r(r-1)\alpha \frac{\partial \phi}{\partial r}. \end{aligned} \quad (171)$$

Now we do this same procedure for the next term

$$\begin{aligned} &\sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \beta(i+1)j P_{i+1,j}(t) r^i s^j - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \beta i j P_{i,j}(t) r^i s^j \\ &= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \beta i j P_{ij}(t) r^{i-1} s^j - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \beta i j P_{i,j}(t) r^i s^j \\ &= r s \left(\frac{1}{r} - 1 \right) \beta \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_{i,j}(t) r^{i-1} s^{j-1} \\ &= r s \left(\frac{1}{r} - 1 \right) \beta \frac{\partial^2 \phi}{\partial r \partial s}. \end{aligned} \quad (172)$$

Similarly

$$\begin{aligned} &\sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \gamma(j+1) P_{i,j+1}(t) r^i s^j - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \gamma j P_{ij}(t) r^i s^j \\ &= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \gamma j P_{ij}(t) r^i s^{j-1} - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \gamma j P_{ij}(t) r^i s^j \\ &= s \left(\frac{1}{s} - 1 \right) \gamma \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_{ij}(t) r^i s^{j-1} \\ &= s \left(\frac{1}{s} - 1 \right) \gamma \frac{\partial \phi}{\partial s}. \end{aligned} \quad (173)$$

Finally,

$$\begin{aligned} &\sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \delta(j-1) i P_{i,j-1}(t) r^i s^j - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \delta i j P_{i,j}(t) r^i s^j \\ &= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \delta i j P_{i,j}(t) r^i s^{j+1} - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \delta i j P_{i,j}(t) r^i s^j \\ &= r s (s-1) \delta \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_{i,j}(t) r^{i-1} s^{j-1} \\ &= r s (s-1) \delta \frac{\partial^2 \phi}{\partial r \partial s}. \end{aligned} \quad (174)$$

Combining the four terms above, we obtain the p.d.e.,

$$\begin{aligned}\frac{\partial \phi}{\partial t} &= r(r-1)\alpha \frac{\partial \phi}{\partial r} + rs \left(\frac{1}{r} - 1\right) \beta \frac{\partial^2 \phi}{\partial r \partial s} \\ &+ s \left(\frac{1}{s} - 1\right) \gamma \frac{\partial \phi}{\partial s} + rs(s-1) \delta \frac{\partial^2 \phi}{\partial r \partial s}.\end{aligned}\quad (175)$$

We analyze this p.d.e. as we did in the single population case by taking the partial with respect to r and evaluating it at $r = 1$ and $s = 1$ to get the expected value for the prey population. That is,

$$\begin{aligned}\left. \frac{\partial \phi}{\partial r} \right|_{r=s=1} &= \alpha \frac{\partial \phi}{\partial r} - \beta \frac{\partial^2 \phi}{\partial r \partial s} \\ &= \alpha E[X(t)] - \beta E[X(t)Y(t)]\end{aligned}\quad (176)$$

Similarly we can also take the partial with respect to s and evaluate it at $r = 1$ and $s = 1$ to get the expected value for the predator population,

$$\begin{aligned}\left. \frac{\partial \phi}{\partial s} \right|_{r=s=1} &= -\gamma \frac{\partial \phi}{\partial s} + \delta \frac{\partial^2 \phi}{\partial r \partial s} \\ &= -\gamma E[Y(t)] + \delta E[X(t)Y(t)].\end{aligned}\quad (177)$$

As we can see the equations of the expected values correspond to the differential equations for the deterministic predator-prey.

Simulation of a predator-prey process

A simulation of the time portrait, phase portrait and variance of the predator-prey process can be found in Figure 10.

2.3 Linearized Stochastic Predator-Prey Model

Since the partial differential equation we obtained from the probability generating function is not readily solved, we will consider a stochastic version of the linearized Predator-Prey model. It may be easier to work with a linear function. It will be of interest to know how the linearized model behaves and how much it differs from the stochastic non linearized model. The linearized predator prey model of the previous section is given here as

$$u'(t) = -\frac{\beta\gamma}{\delta}v \quad (178)$$

$$v'(t) = \frac{\alpha\delta}{\beta}u. \quad (179)$$

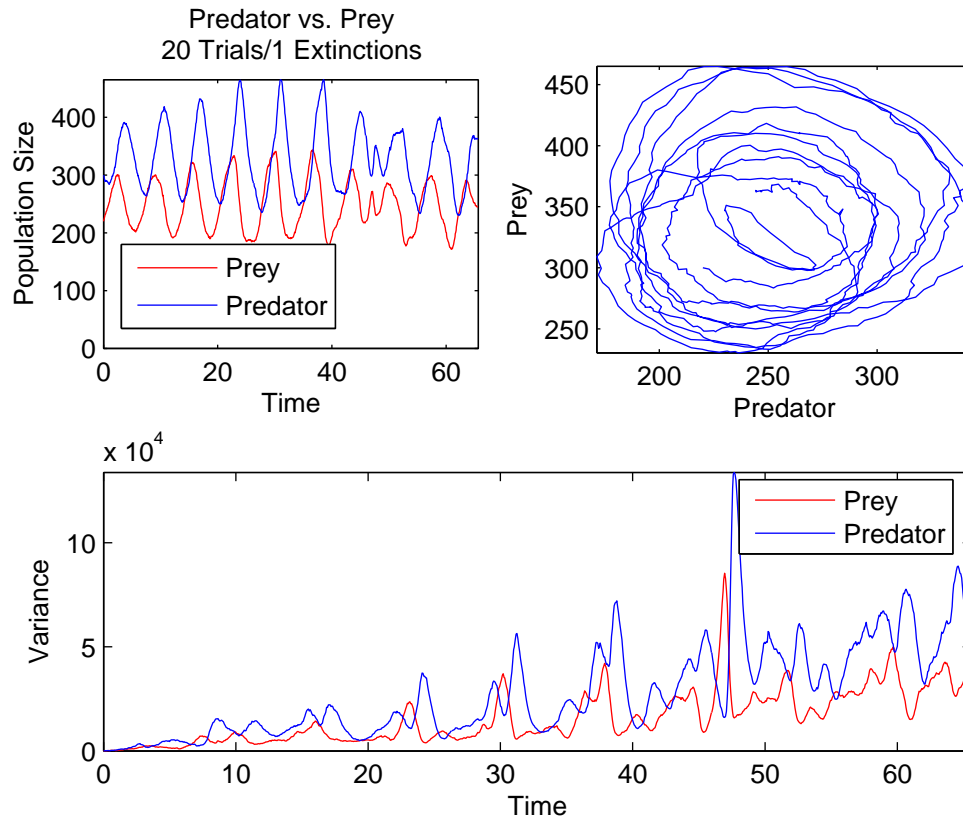
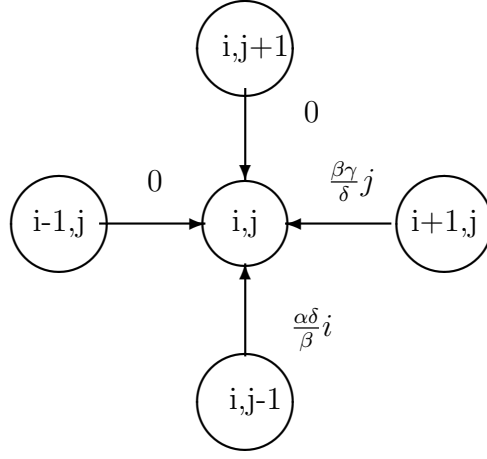


Figure 10: The initial populations 220 for the prey population and 300 for the predator population. The growth rates are $\alpha = 1$, $\beta = .003$, $\gamma = 1$, and $\delta = .004$.

Letting $(U(t), V(t))$ be a bivariate nonnegative integer valued process, then we can mimic the growth rates in this linearized model as in the following table

Transition	Rate
$(i, j) \rightarrow (i + 1, j)$	0
$(i, j) \rightarrow (i - 1, j)$	$\frac{\beta\gamma}{\delta}j$
$(i, j) \rightarrow (i, j + 1)$	$\frac{\alpha\delta}{\beta}i$
$(i, j) \rightarrow (i, j - 1)$	0

Now we can visualize these transitions on the nonnegative integer lattice



Again letting $P_{i,j}(t) = P[U(t) = i, V(t) = j]$ and using these transition rates, we write the probability of being in some i, j state. The rate of change of probability for the linearized predator-prey model is obtained as

$$P'_{ij}(t) = \frac{\beta\gamma}{\delta} j P_{i+1,j}(t) + \frac{\alpha\delta}{\beta} i P_{i,j-1}(t) - \left(\frac{\beta\gamma}{\delta} j + \frac{\alpha\delta}{\beta} i \right) P_{i,j}(t). \quad (180)$$

So if

$$\phi(r, s, t) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_{i,j}(t) r^i s^j \quad (181)$$

is the probability generating function, then we have

$$\frac{\partial \phi}{\partial t}(r, s, t) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P'_{ij}(t) r^i s^j. \quad (182)$$

By substituting in equation (180) into (182) we then have

$$\begin{aligned} \frac{\partial \phi}{\partial t}(r, s, t) = & - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \left(\frac{\beta\gamma}{\delta} j + \frac{\alpha\delta}{\beta} i \right) P_{i,j}(t) r^i s^j \\ & + \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \frac{\beta\gamma}{\delta} j P_{i+1,j}(t) r^i s^j \\ & + \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \frac{\alpha\delta}{\beta} i P_{i,j-1}(t) r^i s^j. \end{aligned} \quad (183)$$

Now we will expand the summations through the first term and combine terms to obtain the p.d.e. for this p.g.f.

$$\sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \frac{\beta\gamma}{\delta} j P_{i+1,j}(t) r^i s^j - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \frac{\beta\gamma}{\delta} j P_{i,j}(t) r^i s^j \quad (184)$$

by re-indexing

$$= \sum_{i=1}^{\infty} \sum_{j=0}^{\infty} \frac{\beta\gamma}{\delta} j P_{i,j}(t) r^{i-1} s^j - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \frac{\beta\gamma}{\delta} j P_{i,j}(t) r^i s^j \quad (185)$$

As you can see in the first summation of equation (185) $i=1$ after re-indexing. This is a problem, we need to have i start at zero, so we must add and subtract that extra term that is missing, so equation (185) becomes

$$\frac{\beta\gamma}{\delta}\left(\frac{1}{r}-1\right)s\sum_{i=1}^{\infty}\sum_{j=0}^{\infty}jP_{i,j}(t)r^i s^{j-1}+\sum_{j=0}^{\infty}jP_{0,j}(t)s^j-\sum_{j=0}^{\infty}jP_{0,j}(t)s^j. \quad (186)$$

That extra term that is being added, goes into the first two summations but we are left with an extra summation term which must be subtracted from the p.d.e, thus equation (186) is

$$\frac{\beta\gamma}{\delta}\left(\frac{1}{r}-1\right)s\frac{\partial\phi}{\partial s}-\frac{\beta\gamma}{\delta}\frac{1}{r}\sum_{j=0}^{\infty}jP_{0j}(t)s^j. \quad (187)$$

This process must be repeated with the next term, so

$$\begin{aligned} & \sum_{i=0}^{\infty}\sum_{j=0}^{\infty}\frac{\alpha\delta}{\beta}iP_{i,j-1}(t)r^i s^j-\frac{\alpha\delta}{\beta}iP_{i,j}(t)r^i s^j \\ = & \sum_{i=0}^{\infty}\sum_{j=0}^{\infty}\frac{\alpha\delta}{\beta}iP_{i,j}(t)r^i s^{j+1}-\frac{\alpha\delta}{\beta}iP_{i,j}(t)r^i s^j \\ = & \frac{\alpha\delta}{\beta}(s-1)r\sum_{i=0}^{\infty}\sum_{j=0}^{\infty}iP_{i,j}(t)r^{i-1} s^j \\ = & \frac{\alpha\delta}{\beta}(s-1)r\frac{\partial\phi}{\partial r}. \end{aligned} \quad (188)$$

We now have run into problems when trying to analyze this p.g.f. because we have this left over summation which we must include in our partial differential equation. Putting this together, we have

$$\frac{\partial\phi}{\partial t}=\frac{\beta\gamma}{\delta}\left(\frac{1}{r}-1\right)s\frac{\partial\phi}{\partial s}+\frac{\alpha\delta}{\beta}(s-1)r\frac{\partial\phi}{\partial r}-\frac{\beta\gamma}{\delta}\frac{1}{r}\sum_{j=0}^{\infty}jP_{0j}(t)s^j. \quad (189)$$

We want to calculate the expected values of each population so we must differentiate with respect to r and then s and evaluate each one at $r=1$ and $s=1$. Differentiating with respect to r gives us

$$\begin{aligned} \frac{\partial}{\partial t}\frac{\partial\phi}{\partial r} &= -\frac{\beta\gamma}{\delta}\frac{1}{r^2}s\frac{\partial\phi}{\partial s}+\frac{\beta\gamma}{\delta}\left(\frac{1}{r}-1\right)s\frac{\partial^2\phi}{\partial s\partial r}+\frac{\alpha\delta}{\beta}(s-1)\frac{\partial\phi}{\partial r} \\ &+ \frac{\alpha\delta}{\beta}(s-1)r\frac{\partial^2\phi}{\partial r^2}+\frac{\beta\gamma}{\delta}\frac{1}{r^2}\sum_{j=0}^{\infty}jP_{0j}(t)s^j \end{aligned} \quad (190)$$

$$\begin{aligned} \frac{\partial}{\partial t}\frac{\partial\phi}{\partial s} &= \frac{\beta\gamma}{\delta}\left(\frac{1}{r}-1\right)s\frac{\partial^2\phi}{\partial s^2}+\frac{\beta\gamma}{\delta}\left(\frac{1}{r}-1\right)\frac{\partial\phi}{\partial s}+\frac{\alpha\delta}{\beta}r\frac{\partial\phi}{\partial r} \\ &+ \frac{\alpha\delta}{\beta}(s-1)r\frac{\partial^2\phi}{\partial r\partial s}-\frac{\beta\gamma}{\delta}\frac{1}{r}\sum_{j=0}^{\infty}j^2P_{0j}(t)s^{j-1} \end{aligned} \quad (191)$$

After evaluating the partial at $r=1$ and $s=1$, we end up with the expected value of the U population and the expected value of the V population.

$$\frac{d}{dt}E[U(t)] = -\frac{\beta\gamma}{\delta}(E[V(t)] - \sum_{j=0}^{\infty} jP_{0j}(t)) \quad (192)$$

$$\frac{d}{dt}E[V(t)] = -\frac{\alpha\delta}{\beta}E[U(t)] - \frac{\beta\gamma}{\delta} \sum_{j=0}^{\infty} j^2 P_{0j}(t) \quad (193)$$

These expected values compare to the linearized predator-prey model, where we realize that each equation's growth rate is in respect to the other population. However we have two left over summations. Since

$$P_{0j}(t) = P(U(t) = 0, V(t) = j) \quad (194)$$

$$= P(V(t) = j | U(t) = 0) P(U(t) = 0) \quad (195)$$

If \bar{x} is not an integer, then $U(t) = X(t) - \bar{x}$ is an integer

$$P(U(t) = 0) = P(X(t) - \bar{x} = 0) = P(X(t) = \bar{x}) = 0. \quad (196)$$

For the expected value of the y population the argument for that left over summation is the same.

$$P_{0j}(t) = P(U^2(t) = 0, V^2(t) = j) \quad (197)$$

$$= P(V^2(t) = j | U^2(t) = 0) P(U^2(t) = 0) \quad (198)$$

If \bar{x} is not an integer then

$$P(U^2(t) = 0) = P((X(t) - \bar{x})^2 = 0) = P(X(t) = \bar{x}) = 0 \quad (199)$$

Simulation of a linearized predator prey process

A simulation of the time portrait, phase portrait and variance of the linearized predator-prey process can be found in Figure 11.

2.4 Classic Competing Hunters Model

Now we will consider a classical model describing the interaction between two similar species that compete for a common resource.

The model assumptions, simplifications, and notation.

1. There are two species interacting: a type 'A' species x and a type 'B' species y . For the purposes of this model no other species interact with these two.

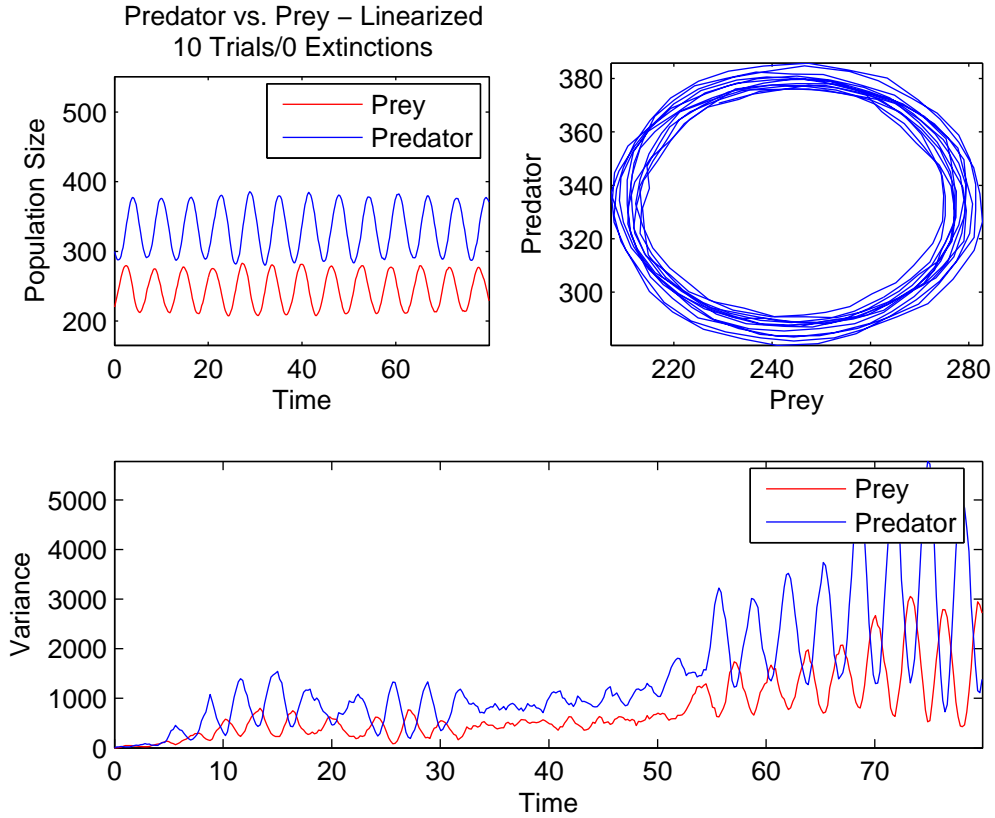


Figure 11: The initial populations are 220 for the prey population and 300 for the predator population. The growth rates are $\alpha = 1$, $\beta = .003$, $\gamma = 1$, and $\delta = .0041$.

2. In the absence of one of the species, the other exhibits pure exponential growth. In particular $\frac{dx}{dt} = \alpha x$ where $\alpha > 0$ and $\frac{dy}{dt} = \gamma y$ where $\gamma > 0$. Implicit in this assumption is that there is sufficient food and space to allow either species to grow indefinitely.
3. When the two species are in the presence of one other, each population will decrease at a rate proportional to the product of the two populations. Thus, extinction is certain for at least one of the populations.

$$\frac{dx}{dt} = \alpha x - \beta xy \tag{200}$$

$$\frac{dy}{dt} = \gamma y - \delta xy \tag{201}$$

where $\alpha, \beta, \gamma, \delta$ are growth rates.

Factoring gives

$$\begin{aligned} \frac{dx}{dt} &= x(\alpha - \beta y) \\ \frac{dy}{dt} &= y(\gamma - \delta x). \end{aligned}$$

Phase plane of competing hunters model

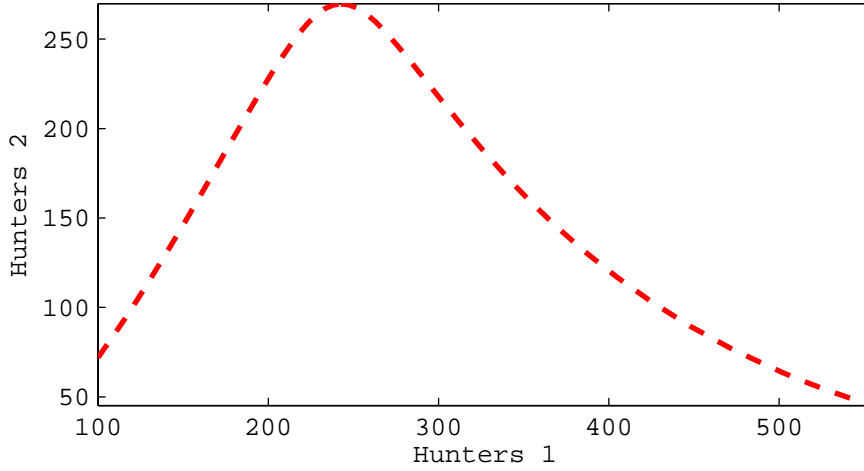


Figure 12: The initial populations are 100 for Hunters 1 population and 72 for Hunters 2 population. The growth rates are $\alpha = 1$, $\beta = .003$, $\gamma = 2.43$, and $\delta = .01$

The equilibrium points $(0, 0)$ and $(\gamma/\delta, \alpha/\beta)$ are the same as in our predator-prey model. A sample phase plane is shown in Figure 12. Naturally, we are not interested in the $(0, 0)$ solution. The $(\gamma/\delta, \alpha/\beta)$ solution has a saddle point of trajectories about it. Jacobian analysis determines this. To help in the analysis of this model we will have to linearize the competing hunters equations.

$$F(x, y) = \alpha x - \beta xy \quad (202)$$

$$G(x, y) = \gamma y - \delta xy \quad (203)$$

We will replace these functions with their Taylor series approximations. Here is the linearization of both populations at the critical point (\bar{x}, \bar{y})

$$F(x, y) = F(\bar{x}, \bar{y}) + \frac{\partial F}{\partial x}(\bar{x}, \bar{y})(x - \bar{x}) + \frac{\partial F}{\partial y}(\bar{x}, \bar{y})(y - \bar{y}) \quad (204)$$

$$G(x, y) = G(\bar{x}, \bar{y}) + \frac{\partial G}{\partial x}(\bar{x}, \bar{y})(x - \bar{x}) + \frac{\partial G}{\partial y}(\bar{x}, \bar{y})(y - \bar{y}). \quad (205)$$

Here u and v is the distance from x and y to the critical point, \bar{x} , \bar{y} that is

$$u = x - \bar{x} \quad (206)$$

$$v = y - \bar{y} \quad (207)$$

We use u and v to obtain new functions of the two populations for the linearized form

$$\frac{du}{dt} \approx + \frac{\partial F}{\partial x}(\bar{x}, \bar{y})u + \frac{\partial F}{\partial y}(\bar{x}, \bar{y})v \quad (208)$$

$$\frac{dv}{dt} \approx +\frac{\partial G}{\partial x}(\bar{x}, \bar{y})u + \frac{\partial G}{\partial y}(\bar{x}, \bar{y})v \quad (209)$$

The partials with respect to x and y for both functions are

$$\frac{\partial F}{\partial x} = \alpha - \beta y \quad (210)$$

$$\frac{\partial F}{\partial y} = -\beta x \quad (211)$$

$$\frac{\partial G}{\partial x} = -\delta y \quad (212)$$

$$\frac{\partial G}{\partial y} = \gamma - \delta x \quad (213)$$

The critical point is $(\frac{\gamma}{\delta}, \frac{\alpha}{\beta})$ and when we substitute this into the Jacobian we have

$$J\left(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}\right) = \begin{pmatrix} 0 & -\frac{\beta\gamma}{\delta} \\ -\frac{\alpha\delta}{\beta} & 0 \end{pmatrix} \quad (214)$$

After solving the Jacobian we end up with two differential equations, $u'(t)$ and $v'(t)$

$$\frac{du}{dt} = u' = -\frac{\beta\gamma}{\delta}v \quad (215)$$

$$\frac{dv}{dt} = v' = -\frac{\alpha\delta}{\beta}u \quad (216)$$

The chain rule from calculus implies that

$$\frac{du}{dv} = \frac{du}{dt} \frac{dt}{dv};$$

thus

$$\frac{du}{dv} = \frac{\gamma\beta^2 v}{\alpha\delta^2 u}.$$

so

$$\alpha\delta^2 u du = \gamma\beta^2 v dv.$$

Integrating both sides yields

$$\frac{\alpha\delta^2 u^2}{2} = \frac{\gamma\beta^2 v^2}{2} + C.$$

which upon rearrangement gives

$$\frac{\alpha\delta^2 u^2}{2} - \frac{\gamma\beta^2 v^2}{2} = C \quad \text{or} \quad \frac{u^2}{\beta^2\gamma} - \frac{v^2}{\alpha\delta^2} = C.$$

Substituting to get back our to our original variables yields

$$\frac{\left(x - \frac{\gamma}{\delta}\right)^2}{\beta^2\gamma} - \frac{\left(y - \frac{\alpha}{\beta}\right)^2}{\alpha\delta^2} = C.$$

This is, of course, the equation for an hyperbola centered at the fixed point. The implication is that close to the fixed point, the trajectories look like hyperbolas; which confirms our prior determination that the fixed point was a saddle. Indeed, close to the fixed point the trajectories are hyperbolas, further away they still bend about the fixed point, but with a less defined shape.

Competing hunters model

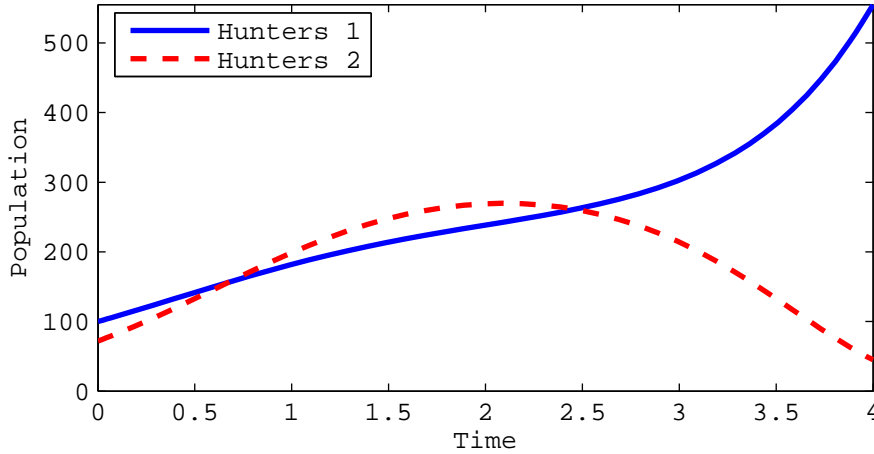


Figure 13: The initial populations are 100 for Hunters 1 population and 72 for Hunters 2 population. The growth rates are $\alpha = 1$, $\beta = .003$, $\gamma = 2.43$, and $\delta = .01$

2.5 Stochastic Competing Hunters Model

Let $X(t)$ be the size of one of the hunter's population at time t and $Y(t)$ be the size of the other at time t . In the model to be formulated, it is now assumed that instead of a (deterministic) rate of hunters births and deaths, there is a probability of a hunter birth or death. Thus $X(t)$ and $Y(t)$ are time dependent random variables.

Let the probability of there being i first hunters and j second hunters at time t be denoted by

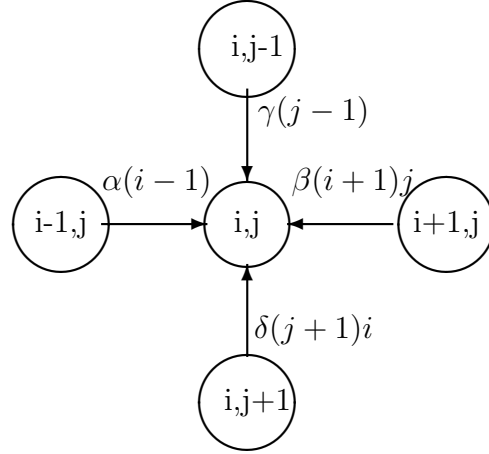
$$P_{i,j}(t) = P[X(t) = i, Y(t) = j], \text{ for } i = 0, 1, 2, \dots, j = 0, 1, 2, \dots$$

As we have done before, births and deaths in this process occur proportional to the population size. We assume that the infinitesimal probability of an individual birth in the first hunter population during the small time interval Δt is $\alpha i \Delta t + o(\Delta t)$, where $\alpha > 0$ is the birth rate of the first hunter. Similarly, we assume that the infinitesimal probability of an individual birth in the second hunter population during the small time interval Δt is $\gamma j \Delta t + o(\Delta t)$, where $\delta > 0$ is the death rate of the second hunter.

To mimic the deterministic model interaction term, we assume that the infinitesimal probability of a death in the first hunter's population occurring during Δt is $\beta ij \Delta t + o(\Delta t)$, where $\beta > 0$ is the death rate of the first hunter. Similarly, a death in the second hunter's population occurs during Δt with infinitesimal probability $\delta ij \Delta t + o(\Delta t)$, with $\gamma > 0$. These rates are summarized in the following table.

Transition	Rate
$(i, j) \rightarrow (i + 1, j)$	αi
$(i, j) \rightarrow (i - 1, j)$	$\beta i j$
$(i, j) \rightarrow (i, j + 1)$	γj
$(i, j) \rightarrow (i, j - 1)$	$\delta i j$

These transitions occur on the nonnegative integer lattice and can be visualized in the following way:



The standard argument using the forward Kolmogorov equations is used to obtain $P_{i,j}(t)$, by considering the probability $P_{i,j}(t + \Delta t)$. This probability is obtained as the sum of the probabilities of the following mutually exclusive events:

- a) There are i first hunters and j second hunters by time t and no birth or deaths of either species occur in $(t, t + \Delta t)$.
- b) There are $i - 1$ first hunters and j second hunters by time t and a birth occurs in the first hunters population in $(t, t + \Delta t)$.
- c) There are i first hunter and $j - 1$ second hunters by time t and a birth occurs in the second hunters population in $(t, t + \Delta t)$.
- d) There are $i + 1$ first hunters and j second hunters by time t and a death occurs in the first hunters population in $(t, t + \Delta t)$.
- e) There are i first hunters and $j + 1$ second hunters and a death occurs in the second hunters population in $(t, t + \Delta t)$. This gives

$$\begin{aligned}
 P'_{ij}(t) = & \alpha(i-1)P_{i-1j}(t) + \beta(i+1)jP_{i+1j}(t) + \gamma(j-1)P_{ij-1}(t) \\
 & + \delta(j+1)iP_{ij+1}(t) - (\alpha i + \beta i j + \gamma j + \delta i j)P_{ij}(t)
 \end{aligned} \tag{217}$$

Just as in the stochastic predator prey model, this doubly infinite system of differential equations is not easily solved and in fact, it appears to be an open problem to obtain its closed form solution. Letting, as always,

$$\phi(r, s, t) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_{i,j}(t) r^i s^j \quad (218)$$

be the probability generating function for this system. We do not have $P_{ij}(t)$ but we do have $P'_{ij}(t)$ so we plug that into the p.g.f.

$$\frac{\partial \phi}{\partial t}(r, s, t) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P'_{i,j}(t) r^i s^j \quad (219)$$

By plugging in equation(217) into equation (219) we then have

$$\begin{aligned} \frac{\partial \phi}{\partial t} = & - \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} (\alpha i + \beta i j - \gamma j + \delta i j) P_{i,j}(t) r^i s^j \\ & + \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \alpha (i-1) P_{i-1,j}(t) r^i s^j \\ & + \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \beta (i+1) j P_{i+1,j}(t) r^i s^j \\ & + \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \gamma (j-1) P_{i,j-1}(t) r^i s^j \\ & + \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \delta (j+1) i P_{i,j+1}(t) r^i s^j \end{aligned} \quad (220)$$

We expand each of these sums as we did in the stochastic predator-prey model. The analysis is virtually identical here and will be omitted.

We obtain

$$\frac{\partial \phi}{\partial t} = \alpha(r-1)r \frac{\partial \phi}{\partial r} + \gamma(s-1)s \frac{\partial \phi}{\partial s} + (r\delta(s-1) + (r-1)s\beta) \frac{\partial \phi}{\partial s \partial r}. \quad (221)$$

The expected size of the Hunter 'A' population is given by

$$\begin{aligned} \left. \frac{\partial \phi}{\partial r} \right|_{r=s=1} &= \alpha \frac{\partial \phi}{\partial r} - \beta \frac{\partial^2 \phi}{\partial r \partial s} \\ &= \alpha E[X(t)] - \beta E[X(t)Y(t)]. \end{aligned} \quad (222)$$

Similarly, the Hunter 'B' population is

$$\begin{aligned} \left. \frac{\partial \phi}{\partial s} \right|_{r=s=1} &= \gamma \frac{\partial \phi}{\partial s} - \delta \frac{\partial^2 \phi}{\partial r \partial s} \\ &= \gamma E[Y(t)] - \delta E[X(t)Y(t)]. \end{aligned} \quad (223)$$

As we can see the equations of the expected values correspond to the differential equations for the deterministic competing hunters model.

Simulation of a competing hunters process

A simulation of the time portrait, phase portrait and variance of the competing hunters process can be found in Figure 14.

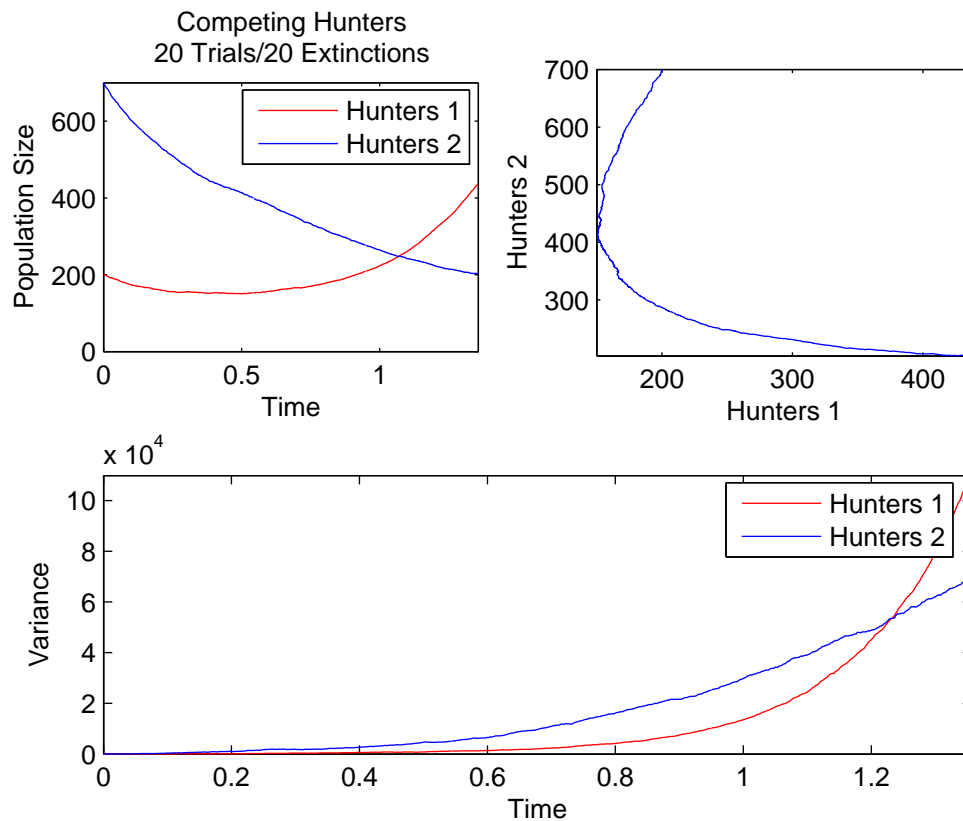


Figure 14: The initial populations are 200 for Hunters 1 population and 700 for Hunters 2 population. The growth rates are $\alpha = 2.55$, $\beta = .006$, $\gamma = 2.2$, and $\delta = .02$.

2.6 Linearized Competing Hunters Model

Since the partial differential equation is not readily solved we will consider a stochastic version of the linearized competing hunters model. To linearize the Competing Hunters model we take the same approach as the predator-prey model. It may be easier to work with the linearize version. We will look at the behavior of the linearized competing hunters model and compare it to the non linearized stochastic model. The linearize competing hunters of the previous section is given here as

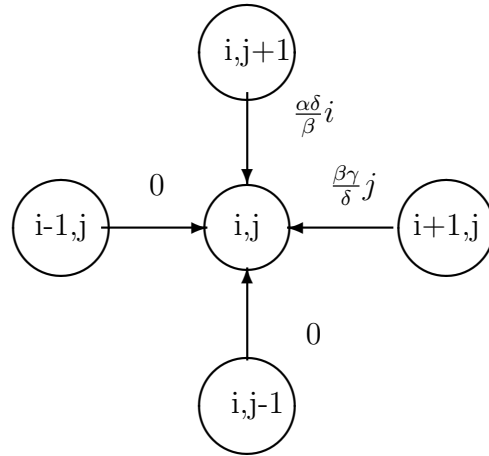
$$u'(t) = - \frac{\beta\gamma}{\delta}v \quad (224)$$

$$v'(t) = - \frac{\alpha\delta}{\beta}u \quad (225)$$

Letting $(U(t),V(t))$ be a bivariate nonnegative integer valued process, then we can mimic the growth rates in this linearized model as in the following table

Transition	Rate
$(i, j) \rightarrow (i + 1, j)$	0
$(i, j) \rightarrow (i - 1, j)$	$\frac{\beta\gamma}{\delta}j$
$(i, j) \rightarrow (i, j + 1)$	0
$(i, j) \rightarrow (i, j - 1)$	$\frac{\alpha\delta}{\beta}i$

Now we can visualize these transitions



We use these transition rates and can write the probability as we have before.

$$P'_{ij}(t) = \frac{\beta\gamma}{\delta}jP_{i+1,j}(t) + \frac{\alpha\delta}{\beta}iP_{i,j+1}(t) - \left(\frac{\beta\gamma}{\delta}j + \frac{\alpha\delta}{\beta}i\right)P_{i,j}(t). \quad (226)$$

The p.d.e. of the p.g.f is

$$\begin{aligned} \frac{\partial\phi}{\partial t} &= \frac{\delta\alpha}{\beta}r\left(\frac{1}{s} - 1\right)\frac{\partial\phi}{\partial r} - \frac{\delta\alpha}{\beta}\frac{1}{s}\sum_{i=0}^{\infty} iP_{i,0}(t)r^i \\ &+ \frac{\beta\gamma}{\delta}\left(\frac{1}{r} - 1\right)s\frac{\partial\phi}{\partial s} - \frac{\beta\gamma}{\delta}\frac{1}{r}\sum_{j=0}^{\infty} P_{0,j}(t)s^j \end{aligned} \quad (227)$$

After re-indexing and solving for the p.d.e. we are left with two left over terms in this linearized version. We still want the expected values for both populations so we must differentiate the p.d.e. with respect to r and then s.

Differentiating (227) with respect to r we end up with

$$\begin{aligned}
\frac{\partial}{\partial r} \frac{\partial}{\partial t} &= \frac{\delta\alpha}{\beta} \left(\frac{1}{s} - 1\right) \frac{\partial\phi}{\partial r} - \frac{\delta\alpha}{\beta} \frac{1}{s} \sum_{i=0}^{\infty} iP_{i,0}(t)r^{i-1} - \frac{\beta\gamma}{\delta} \frac{s}{r^2} \frac{\partial\phi}{\partial s} \\
&+ \frac{\beta\gamma}{\delta} \frac{1}{r^2} \sum_{j=0}^{\infty} jP_{0,j}(t)s^j + \frac{\delta\alpha}{\beta} r \left(\frac{1}{s} - 1\right) \frac{\partial^2\phi}{\partial r^2} \\
&+ \frac{\beta\gamma}{\delta} \left(\frac{1}{r} - 1\right) s \frac{\partial^2\phi}{\partial r \partial s}
\end{aligned} \tag{228}$$

Differentiating (227) with respect to s we end up with

$$\begin{aligned}
\frac{\partial}{\partial s} \frac{\partial}{\partial t} &= - \frac{\delta\alpha}{\beta} \frac{r}{s^2} \frac{\partial\phi}{\partial r} + \frac{\delta\alpha}{\beta} \frac{1}{s^2} \sum_{i=0}^{\infty} iP_{i,0}(t)r^i + \frac{\beta\gamma}{\delta} \left(\frac{1}{r} - 1\right) \frac{\partial\phi}{\partial s} \\
&- \frac{\beta\gamma}{\delta} \frac{1}{r} \sum_{j=0}^{\infty} jP_{0,j}(t)s^{j-1} + \frac{\beta\gamma}{\delta} \left(\frac{1}{r} - 1\right) s \frac{\partial^2\phi}{\partial s^2} \\
&+ \frac{\delta\alpha}{\beta} r \left(\frac{1}{s} - 1\right) \frac{\partial^2\phi}{\partial r \partial s}
\end{aligned} \tag{229}$$

We evaluate each partial at r=1 and s=1 in order to get the expected value of each population

$$\left. \frac{\partial}{\partial r} \frac{\partial\phi}{\partial t} \right|_{r=s=1} = -\frac{\delta\alpha}{\beta} \sum_{i=0}^{\infty} iP_{i,0}(t) - \frac{\beta\gamma}{\delta} \frac{\partial\phi}{\partial s} + \frac{\beta\gamma}{\delta} \sum_{j=0}^{\infty} jP_{0,j}(t) \tag{230}$$

$$\left. \frac{\partial}{\partial s} \frac{\partial\phi}{\partial t} \right|_{r=s=1} = -\frac{\delta\alpha}{\beta} \frac{\partial\phi}{\partial r} + \frac{\delta\alpha}{\beta} \sum_{i=0}^{\infty} iP_{i,0}(t) - \frac{\beta\gamma}{\delta} \sum_{j=0}^{\infty} jP_{0,j}(t) \tag{231}$$

The expected values for both populations are

$$\frac{d}{dt} E[U(t)] = -\frac{\beta\gamma}{\delta} E[V(t)] - \frac{\delta\alpha}{\beta} \sum_{i=0}^{\infty} iP_{i,0}(t) + \frac{\beta\gamma}{\delta} \sum_{j=0}^{\infty} jP_{0,j}(t) \tag{232}$$

$$\frac{d}{dt} E[V(t)] = -\frac{\delta\alpha}{\beta} E[U(t)] + \frac{\delta\alpha}{\beta} \sum_{i=0}^{\infty} iP_{i,0}(t) - \frac{\beta\gamma}{\delta} \sum_{j=0}^{\infty} jP_{0,j}(t) \tag{233}$$

For the expected values of both populations we have four left over summations, which we have assume equal zero. We will use the same argument as before for the predator-prey

model.

$$P_{i0}(t) = P(V(t) = 0, U(t) = i) \quad (234)$$

$$= P(U(t) = i | V(t) = 0) P(V(t) = 0) \quad (235)$$

If \bar{y} is not an integer then

$$P(V(t) = 0) = P(Y(t) - \bar{y} = 0) = P(Y(t) = \bar{y}) = 0 \quad (236)$$

$$P_{0j}(t) = P(U(t) = 0, V(t) = j) \quad (237)$$

$$= P(V(t) = j | U(t) = 0) P(U(t) = 0) \quad (238)$$

If \bar{x} is not an integer then

$$P(U(t) = 0) = P(X(t) - \bar{x} = 0) = P(X(t) = \bar{x}) = 0 \quad (239)$$

Using this argument we can ignore each of these summations, and see that each expected value is in respect to the other population.

Simulation of a linearized competing hunters process

A simulation of the time portrait, phase portrait and variance of the linearized competing hunters process can be found in Figure 15.

2.7 Polynomial - Two populations

We can now generalize the proceeding sections by considering populations that are described by the differential equations

$$\frac{dx}{dt} = a(x, n_a)b(x, n_b) - c(x, n_c)d(x, n_d) \quad (240)$$

$$\frac{dy}{dt} = e(x, n_e)f(x, n_f) - g(x, n_g)h(x, n_h) \quad (241)$$

Let $X(t)$ and $Y(t)$ be nonnegative, integer valued processes with transition described in the following table

Transition	Rate
$i, j \rightarrow i + 1, j$	$a(i, n_a)b(j, n_b)$
$i, j \rightarrow i - 1, j$	$c(i, n_c)d(j, n_d)$
$i, j \rightarrow i, j + 1$	$e(i, n_e)f(j, n_f)$
$i, j \rightarrow i, j - 1$	$g(i, n_g)h(j, n_h)$

We must assume there is no emigration rate in either populations so that $c_0 = 0 = h_0$
Then if

$$P_{i,j}(t) = P[X(t) = i, Y(t) = j | X(0) = 0] \quad (242)$$

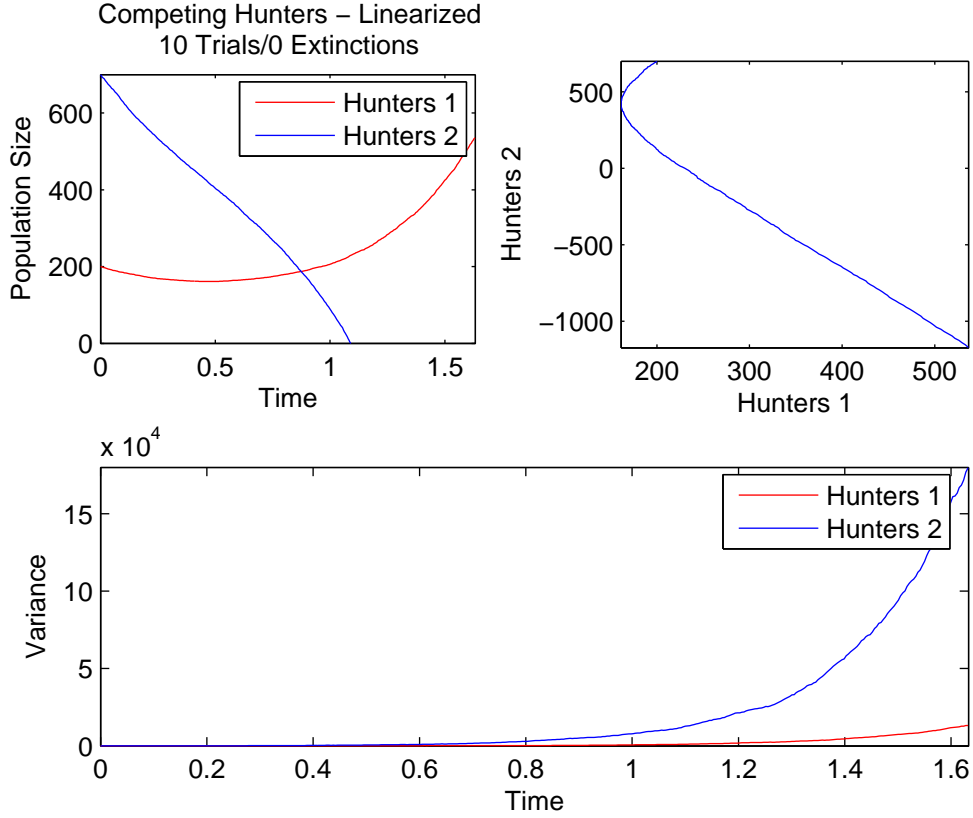


Figure 15: The initial populations are 200 for the Hunters 1 population and 700 for the Hunters 2 population. The growth rates are $\alpha = 2.55$, $\beta = .0061$, $\gamma = 2.2$, and $\delta = .021$.

we can derive the forward Kolmogorov equations in the usual manner specifically,

$$\begin{aligned}
P'_{i,j}(t) &= a(i-1, n_a) b(j, n_b) P_{i-1,j}(t) + c(i+1, n_c) d(j, n_d) P_{i+1,j}(t) \\
&+ e(i, n_e) f(j-1, n_f) P_{i,j-1}(t) + g(i, n_g) h(j+1, n_h) P_{i,j+1}(t) \\
&- (a(i, n_a) b(j, n_b) + c(i, n_c) d(j, n_d) \\
&+ e(i, n_e) f(j, n_f) + g(i, n_g) h(j, n_h)) P_{i,j}(t)
\end{aligned} \tag{243}$$

Letting

$$\phi(r, s, t) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_{i,j}(t) r^i s^j \tag{244}$$

be the probability generating function, we have

$$\begin{aligned}
\frac{\partial \phi}{\partial t} &= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P'_{i,j}(t) r^i s^j \\
&= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} a(i-1, n_a) b(j, n_b) P_{i-1,j}(t) r^i s^j \\
&+ \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} c(i+1, n_c) d(j, n_d) P_{i+1,j}(t) r^i s^j \\
&+ \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} e(i, n_e) f(j-1, n_f) P_{i,j-1}(t) r^i s^j \\
&+ \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} g(i, n_g) h(j+1, n_h) P_{i,j+1}(t) r^i s^j \\
&- \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} (a(i, n_a) b(j, n_b) + c(i, n_c) d(j, n_d) \\
&+ e(i, n_e) f(j, n_f) + g(i, n_g) h(j, n_h)) P_{i,j}(t) r^i s^j. \tag{245}
\end{aligned}$$

To simplify this expression for $\frac{\partial \phi}{\partial t}$ we need to evaluate series of the form

$$\sum_{i=0}^{\infty} \sum_{j=0}^{\infty} i^n j^m P_{i,j}(t) r^i s^j \tag{246}$$

in terms of the p.g.f. $\phi(r, s, t)$. Using equation (80), we can write the sum in equation as

$$\begin{aligned}
\sum_{i=0}^{\infty} \sum_{j=0}^{\infty} i^n j^m P_{i,j}(t) r^i s^j &= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \sum_{k=0}^n \sum_{l=0}^m S_2(n, k) [i]_k S_2(m, l) [j]_l P_{i,j}(t) r^i s^j \\
&= \sum_{k=0}^n r^k \sum_{l=0}^m s^l \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} S_2(n, k) [i]_k S_2(m, l) [j]_l P_{i,j}(t) r^{i-k} s^{j-l} \\
&= \sum_{k=0}^n r^k S_2(n, k) \sum_{l=0}^m s^l S_2(m, l) \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} [i]_k [j]_l P_{i,j}(t) r^{i-k} s^{j-l} \\
&= \sum_{k=0}^n r^k S_2(n, k) \sum_{l=0}^m s^l S_2(m, l) \frac{\partial^{k+l} \phi}{\partial r^k \partial s^l} r^k s^l \\
&= \sum_{k=0}^n \sum_{l=0}^m r^k s^l S_2(m, l) S_2(n, k) \frac{\partial^{k+l} \phi}{\partial r^k \partial s^l} r^k s^l \tag{247}
\end{aligned}$$

So, using this expression, we can write the birth rate term of the prey as

$$\begin{aligned}
\sum_{i=0}^{\infty} \sum_{j=0}^{\infty} a(i-1, n_a) b(j, n_b) P_{i-1, j}(t) r^i s^j &= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \sum_{k=0}^n \sum_{l=0}^m a_k (i-1)^k b_l j^l P_{i-1, j}(t) r^i s^j \\
&= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \sum_{k=0}^n \sum_{l=0}^m a_k i^k b_l j^l P_{i, j}(t) r^{i+1} s^j \\
&= r \sum_{k=0}^n \sum_{l=0}^m a_k b_l \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} i^k j^l P_{i, j}(t) r^i s^j \\
&= r \sum_{k=0}^n \sum_{l=0}^m a_k b_l \sum_{i=0}^k \sum_{j=0}^l S_2(k, i) S_2(l, j) \frac{\partial^{i+j} \phi}{\partial r^i \partial s^j} r^i s^j.
\end{aligned} \tag{248}$$

Similarly the death rate terms is

$$\begin{aligned}
\sum_{i=0}^{\infty} \sum_{j=0}^{\infty} c(i+1, n_c) d(j, n_d) P_{i+1, j}(t) r^i s^j &= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \sum_{k=0}^n \sum_{l=0}^m c_k (i+1)^k d_l j^l P_{i+1, j}(t) r^i s^j \\
&= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} \sum_{k=0}^n \sum_{l=0}^m c_k i^k d_l j^l P_{i, j}(t) r^{i-1} s^j \\
&= \frac{1}{r} \sum_{k=0}^n \sum_{l=0}^m c_k d_l \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} i^k j^l P_{i, j}(t) r^i s^j \\
&= \frac{1}{r} \sum_{k=0}^n \sum_{l=0}^m c_k d_l \sum_{i=0}^k \sum_{j=0}^l S_2(k, i) S_2(l, j) \frac{\partial^{i+j} \phi}{\partial r^i \partial s^j} r^i s^j
\end{aligned} \tag{249}$$

In a very similar manner we do this same procedure for the next six terms. Combining all

of these expressions in the representation for $\frac{\partial\phi}{\partial t}$ gives

$$\begin{aligned}
\frac{\partial\phi}{\partial t} &= (r-1) \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} a(i, n_a) b(j, n_b) P_{i,j}(t) r^i s^j \\
&+ \left(\frac{1}{r} - 1\right) \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} c(i, n_c) d(j, n_d) P_{i,j}(t) r^i s^j \\
&+ (s-1) \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} e(i, n_e) f(j, n_f) P_{i,j}(t) r^i s^j \\
&+ \left(\frac{1}{s} - 1\right) \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} g(i, n_g) h(j, n_h) P_{i,j}(t) r^i s^j \\
&= (r-1) \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_a, h) S_2(n_b, k) \frac{\partial^{h+k}\phi}{\partial r^h \partial s^k} r^h s^k \\
&+ \left(\frac{1}{r} - 1\right) \sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_c, h) S_2(n_d, k) \frac{\partial^{h+k}\phi}{\partial r^h \partial s^k} r^h s^k \\
&+ (s-1) \sum_{i=0}^{n_e} \sum_{j=0}^{n_f} e_i f_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_e, h) S_2(n_f, k) \frac{\partial^{h+k}\phi}{\partial r^h \partial s^k} r^h s^k \\
&+ \left(\frac{1}{s} - 1\right) \sum_{i=0}^{n_g} \sum_{j=0}^{n_h} g_i h_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_g, h) S_2(n_h, k) \frac{\partial^{h+k}\phi}{\partial r^h \partial s^k} r^h s^k
\end{aligned} \tag{250}$$

Using this expression we can, however obtain some useful information. We can find the

expected population sizes, we take the partial with respect to r, we obtain

$$\begin{aligned}
\frac{\partial}{\partial r} \frac{\partial \phi}{\partial t} &= \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_a, h) S_2(n_b, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \\
&+ (r-1) \frac{\partial}{\partial r} \left[\sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_a, h) S_2(n_b, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \right] \\
&- \frac{1}{r^2} \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} c_i d_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_c, h) S_2(n_d, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \\
&+ \left(\frac{1}{r} - 1 \right) \frac{\partial}{\partial r} \left[\sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_c, h) S_2(n_d, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \right] \\
&+ (s-1) \frac{\partial}{\partial r} \left[\sum_{i=0}^{n_e} \sum_{j=0}^{n_f} e_i f_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_e, h) S_2(n_f, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \right] \\
&+ \left(\frac{1}{s} - 1 \right) \frac{\partial}{\partial r} \left[\sum_{i=0}^{n_g} \sum_{j=0}^{n_h} g_i h_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_g, h) S_2(n_h, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \right]. \quad (251)
\end{aligned}$$

Interchanging the order of the derivatives and evaluating this expression at r=s=1 we have

$$\begin{aligned}
\frac{d}{dt} E[X(t)] &= \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j \sum_{h=0}^i \sum_{k=0}^j S_2(i, h) S_2(j, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} \Big|_{r=s=1} \\
&- \sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j \sum_{h=0}^i \sum_{k=0}^j S_2(i, h) S_2(j, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} \Big|_{r=s=1}. \quad (252)
\end{aligned}$$

Using the relation in equation (89) we have

$$\begin{aligned}
&x(x-1)(x-2)\dots(x-n+1)(y)(y-1)(y-2)\dots(y-m+1) \\
&= \sum_{r=0}^n \sum_{s=0}^m S_1(n, r) S_1(m, s) X^r Y^s. \quad (253)
\end{aligned}$$

Recall that ϕ is a p.g.f. so the partial derivative at r=1 and s=1 becomes

$$\begin{aligned}
\frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} &= E[X(X-1)(X-2)\dots(X-n+1)(Y)(Y-1)(Y-2)\dots(Y-m+1)] \\
&= E \left[\sum_{r=0}^n \sum_{s=0}^m S_1(n, r) S_1(m, s) X^r Y^s \right] \quad (254)
\end{aligned}$$

Substituting equation (254) into equation (252) gives us

$$\begin{aligned} \frac{\partial}{\partial t} \frac{\partial \phi}{\partial r} \Big|_{r=s=1} &= \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j \sum_{h=0}^i \sum_{k=0}^j S_2(i, h) S_2(j, k) E \left[\sum_{h'=0}^h \sum_{k'=0}^k S_1(h, h') S_1(k, k') X^{h'} Y^{k'} \right] \\ &- \sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j \sum_{h=0}^i \sum_{k=0}^j S_2(i, h) S_2(j, k) E \left[\sum_{h'=0}^h \sum_{k'=0}^k S_1(h, h') S_1(k, k') X^{h'} Y^{k'} \right] \end{aligned} \quad (255)$$

Since the stirling numbers of the first kind $S_1(h, h')$ and $S_1(k, k')$ are just constants, we are able to pull them out of the expected value so now this becomes

$$\begin{aligned} \frac{\partial}{\partial t} \frac{\partial \phi}{\partial r} \Big|_{r=s=1} &= \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j \sum_{h=0}^i \sum_{k=0}^j S_2(i, h) S_2(j, k) \sum_{h'=0}^h \sum_{k'=0}^k S_1(h, h') S_1(k, k') E \left[X^{h'} Y^{k'} \right] \\ &- \sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j \sum_{h=0}^i \sum_{k=0}^j S_2(i, h) S_2(j, k) \sum_{h'=0}^h \sum_{k'=0}^k S_1(h, h') S_1(k, k') E \left[X^{h'} Y^{k'} \right] \end{aligned} \quad (256)$$

We are able to reduce this expression because there is a very useful orthogonal relation between Stirling numbers of the first kind and second kind. Using the relation in equation (95) we are able to combine Stirling numbers of the first kind and second kind

$$\begin{aligned} &= \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j \sum_{h=0}^i \sum_{h'=0}^h S_2(i, h) S_1(h, h') \sum_{k=0}^j \sum_{k'=0}^k S_2(j, k) S_1(k, k') E \left[X^{h'} Y^{k'} \right] \\ &- \sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j \sum_{h=0}^i \sum_{h'=0}^h S_2(i, h) S_1(h, h') \sum_{k=0}^j \sum_{k'=0}^k S_2(j, k) S_1(k, k') E \left[X^{h'} Y^{k'} \right] \end{aligned} \quad (257)$$

After combining them, the equation reduces to

$$= \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j E \left[X^i Y^j \right] - \sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j E \left[X^i Y^j \right] \quad (258)$$

This process can also be applied to verify the expected value of the prey term by differentiating with respect to s . This will result in

$$= \sum_{i=0}^{n_e} \sum_{j=0}^{n_f} e_i f_j E \left[X^i Y^j \right] - \sum_{i=0}^{n_g} \sum_{j=0}^{n_h} g_i h_j E \left[X^i Y^j \right] \quad (259)$$

These two equations correspond with the deterministic model.

We can summarize the preceding as the following Theorem:

Theorem 2.1. Let $X(t)$ and $Y(t)$ be nonnegative, integer valued processes with transition described in the following table

Transition	Rate
$i, j \rightarrow i + 1, j$	$a(i, n_a)b(j, n_b)$
$i, j \rightarrow i - 1, j$	$c(i, n_c)d(j, n_d)$
$i, j \rightarrow i, j + 1$	$e(i, n_e)f(j, n_f)$
$i, j \rightarrow i, j - 1$	$g(i, n_g)h(j, n_h)$

we must assume there is no emigration from either populations $c_0 = 0 = h_0$

if

$$P_{i,j}(t) = P[X(t) = i, Y(t) = j | X(0) = 0] \quad (260)$$

and

$$\phi(r, s, t) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_{i,j}(t) r^i s^j \quad (261)$$

Then

$$\begin{aligned} \frac{\partial \phi}{\partial t} &= (r-1) \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_a, h) S_2(n_b, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \\ &+ \left(\frac{1}{r} - 1\right) \sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_c, h) S_2(n_d, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \\ &+ (s-1) \sum_{i=0}^{n_e} \sum_{j=0}^{n_f} e_i f_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_e, h) S_2(n_f, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \\ &+ \left(\frac{1}{s} - 1\right) \sum_{i=0}^{n_g} \sum_{j=0}^{n_h} g_i h_j \sum_{h=0}^i \sum_{k=0}^j S_2(n_g, h) S_2(n_h, k) \frac{\partial^{h+k} \phi}{\partial r^h \partial s^k} r^h s^k \end{aligned} \quad (262)$$

where $S_2(n_a, h)$ and $S_2(n_b, k)$ are Stirling numbers of the second kind and using this relation

$$\begin{aligned} &x(x-1)(x-2)\dots(x-n+1)(y)(y-1)(y-2)\dots(y-m+1) \\ &= \sum_{r=0}^n \sum_{s=0}^m S_1(n, r) S_1(m, s) X^r Y^s \end{aligned} \quad (263)$$

it becomes

$$\begin{aligned}
&= \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j \sum_{h=0}^i \sum_{h'=0}^h S_2(i, h) S_1(h, h') \sum_{k=0}^j \sum_{k'=0}^k S_2(j, k) S_1(k, k') E \left[X^{h'} Y^{k'} \right] \\
&- \sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j \sum_{h=0}^i \sum_{h'=0}^h S_2(i, h) S_1(h, h') \sum_{k=0}^j \sum_{k'=0}^k S_2(j, k) S_1(k, k') E \left[X^{h'} Y^{k'} \right]
\end{aligned} \tag{264}$$

The expected value $E[X(t)]$ of the integer valued processes of $X(t)$ and $Y(t)$ satisfies the differential equation

$$= \sum_{i=0}^{n_a} \sum_{j=0}^{n_b} a_i b_j E \left[X^i Y^j \right] - \sum_{i=0}^{n_c} \sum_{j=0}^{n_d} c_i d_j E \left[X^i Y^j \right] \tag{265}$$

$$= \sum_{i=0}^{n_e} \sum_{j=0}^{n_f} e_i f_j E \left[X^i Y^j \right] - \sum_{i=0}^{n_g} \sum_{j=0}^{n_h} g_i h_j E \left[X^i Y^j \right] \tag{266}$$

3 Future Goals

We briefly explored a plethora of avenues related to stochastic processes. Given a great deal more time, these are a few of the things we would like to dissect.

Linearized Models

We would like to further explore the effects of linearizing population models. A generalized look at the error between linearized stochastic models and linearized deterministic models with the triangle inequality has been examined, but could bear a more detailed scrutiny.

K Populations with Polynomial Growth Rates

After a brief analysis, we are certain the polynomial growth rates can be extended to an arbitrary number of populations all interacting. Given more time and lots of paper, this belief will be realized.

Taylor Expansion of Transcendental Functions

Not all growth models are in the form of polynomials, some of them contain natural logs – such as the well-known Gompertz growth model. Taylor expansions of these functions would present these functions as polynomials. A detailed analysis

Time to Extinction

Some time was dedicated to generalizing the time to extinction theorem to arbitrary polynomial growth rates. Immediate results were unclear but worth another more intensive look.

Steady State of Predator Prey

Similar to *Time to Extinction*, some hard time was dedicated to solving the bivariate recurrence relationship of predator-prey steady state probabilities resulting in another repulsive, though ordered, relationship.

Models Expected to Go Extinct Drop Below Deterministic

There is a proof in Allen's book that the stochastic logistic process is equal to or less than the deterministic. Though the approach used did not lend itself well to proving the same for an Allee model, we feel that stochastic processes of even powers could use a similar approach to state that their expectations cannot be more than their respective deterministic models.

Spatial Predator-Prey Modeling

The most entertaining of the competing models is certainly the curious oscillations of the predator-prey model. Some brief simulations of two interacting predator-prey models yielded some enticingly colorful graphs. Armed with a general formula for K interacting populations, we will be able to crack this wide open.

Variance of Stochastic Processes

The variance is well defined for the more simple stochastic processes – Birth, Death, Birth-Death and Birth-Death-Immigration. Simulations showed some well-behaved activity with a great deal of data. We would like to devote more time and computer cycles to exploring the variance.

A MATLAB Code

Some of the code we used in generating our results has been included for your perusal. Included are three chunks of code that will simulate a single population with polynomial birth and death rates, a predator-prey process, and a linearized competing hunters process.

Single Population Stochastic

```
% Stochastic Process of Single Population with Polynomial Growth Rate
% AMSSI 2005 - Team NERJ
% Public Domain. Mess with this as much as you want.
% poly2str function thanks to http://home.online.no/~pjacklam/
%
% birth    = Birth polynomial with powers in descending order
% death    = Death polynomial with powers in descending order
% initPop  = Initial population
%
% Run as:
```



```

% singlepop([coeff of birth poly],[coeff of death poly],initial pop, # trials

function singlepop(b,d,initPop,trials) global birth death birth = b;
death = d;

maxSteps = 700;           % Maximum steps for simulation
numSteps = 60;           % Number of graph points to quantize to
numPaths = 3;            % Number of sample paths to plot with average

% First we generate the population growths and times in their own cell
fprintf('Generating %d trials', trials);
tic;                      % Start timer
A=cell(1,trials);        % Cell array to avoid a sparse matrix
for i = 1:trials
    pop = zeros(1,maxSteps); % Initialize population and time vectors
    t = zeros(1,maxSteps);
    pop(1) = initPop;      % Fill in initial population and time
    t(1) = 0;
    j = 1;                % j = Step counter for current simulation
    while (pop(j) > 0 & j < maxSteps)
        % Evaluate birth and death polynomials with current population
        popB = polyval(birth,pop(j));
        total = popB+polyval(death,pop(j));
        % Figure out which window we're in and adjust population
        if (rand < popB/total)
            pop(j+1) = pop(j) + 1;
        else
            pop(j+1) = pop(j) - 1;
        end
        % Generate new time step and add to current time
        t(j+1) = -log(rand)/total + t(j);
        j = j+1;
    end
    A{i}=[pop(1:j) ; t(1:j)]; % Save pop and time vectors in a cell
    if (mod(i,fix(trials/10))==0)
        fprintf('.') ; % Print out progress dot
    end
end

% Keep track of the lengths of runs and num steps
timeLen = zeros(1,trials); % Make a time length vector
stepLen = zeros(1,trials); % Make a step length vector
for i=1:trials
    timeLen(i) = A{i}(2,end);
    stepLen(i) = length(A{i});
end

```

```

end

% We look at the trials up until the first one to maxSteps ran out of time.
maxStepLens=find(stepLen==max(stepLen));
maxTime=min(timeLen(maxStepLens));
numExtinct=trials; % First assume everything went extinct
if (max(stepLen) == maxSteps) % Check how many made it to maxSteps
    numExtinct = trials-length(maxStepLens);
end
fprintf('%.2f secs\n',toc); % Log time of the most intensive part

% Now we quantize the data into a discrete time interval
plotTime = linspace(0,maxTime,numSteps); % Time vector to plot
plotPop = zeros(trials,numSteps); % Pop vector to plot
plotPop(:,1) = initPop; % Initialize Pop vector

fprintf('Quantizing');
for i = 1:trials % i = Current trial
    j = 2; % j = Current quantized step
    k=1; % k = Current time step of actual data
    while (k < length(A{i}) & j <= numSteps)
        % If next actual time > quantized step
        if (A{i}(2,k+1) >= plotTime(j))
            plotPop(i,j) = A{i}(1,k); % Record population as current
            j = j+1;
        else
            k = k+1;
        end
    end % End trial
    if (mod(i,fix(trials/10))==0)
        fprintf(' '); % Print out progress dot
    end
end % End quantizing

% We take non-zero population entries and find average and variance
fprintf('\nFinding Mean and Variance');
varPop=zeros(1,numSteps); % Initialize variance and average vectors
avgPop=zeros(1,numSteps); for i=1:numSteps
    w = plotPop(:,i); % w = Use every population run
    avgPop(i)=mean(w); % Average non-zero values
    varPop(i)=var(w); % Variance of non-zero values
    if (mod(i,fix(numSteps/10))==0)
        fprintf(' '); % Print out progress dot
    end
end
end

```

```

% Plot the graphs and label 'em proper
fprintf('\nPlotting.\n');
idxPaths = 1:ceil(trials/numPaths):trials; % Indices of paths to show
plotPaths = plotPop(idxPaths,:); % Sample paths to plot
maxPop = max([max(plotPaths) avgPop]); % Max population for y axis
maxTime = max(plotTime); figure('Position',[100 100 500 500]);

subplot(2,1,1); hold off
plot(plotTime,avgPop,'k','LineWidth',2); % Plot the average
hold on
[t,Y]=ode45(@diffpop,plotTime,initPop); % Plot deterministic
plot(t,Y,'r--','LineWidth',2);
stairs(plotTime,plotPaths',''); % Plot the sample paths
axis([0 maxTime 0 maxPop]); % Set axes and labels
set(gca,'FontName','Courier New'); xlabel('Time','FontName','Courier
New'); ylabel('Population','FontName','Courier New');
legend('Average Stochastic','Deterministic','Sample Paths',...
'Location','NorthWest');
title(sprintf('Single Population\n%d Trials\nx'' = %s - (%s)',...
trials,poly2str(birth),poly2str(death)));

subplot(2,1,2);
plot(plotTime,varPop,'k','LineWidth',2); % Plot variance
axis([0 maxTime 0 max(varPop)]); set(gca,'FontName','Courier New');
xlabel('Time','FontName','Courier New');
ylabel('Variance','FontName','Courier New');

fprintf('Took %.2f secs\n',toc); % Log time

function dydx = diffpop(t,x) global birth death dydx =
polyval(birth,x)-polyval(death,x);

```

Predator Prey Process

```

% Stochastic Process of Predator Prey
% AMSSI 2005 - Team NERJ
% Public Domain. Mess with this as much as you want.
% This is not as well documented or coded as singlepop.m, enjoy!
%
% birth = Birth polynomial with powers in descending order
% death = Death polynomial with powers in descending order
% initPop = Initial population

```

```

function predprey(trials)

maxSteps = 80000;
numSteps = 1000;           % Number of steps

% x' = alpha*x - beta*x*y    Prey
initprey = 220;            % Initial population for prey
alpha    = 1;              % Birth rate
beta     = .003;          % Interaction (death)

% y' = -gamma*y + delta*x*y  Predators
initpred = 300;           % Initial population for predators
gamma    = 1;             % Starvation rate
delta    = .004;         % Hunting rate

fprintf('Starting %d trials...', trials);
tic;    % Start timer
last = 0; A=cell(1,trials); for b = 1:trials
    prey = zeros(1,maxSteps);    % Initialize vectors
    pred = zeros(1,maxSteps);
    t = zeros(1,maxSteps);
    prey(1) = initprey;          % Initialize populations and time
    pred(1) = initpred;
    t(1) = 0;
    a = 1;
    while (prey(a) > 0 && pred(a) > 0 && a < maxSteps)
        preyB = alpha*prey(a);
        preyD = beta*prey(a)*pred(a);
        predB = delta*pred(a)*prey(a);
        predD = gamma*pred(a);
        total = preyB+preyD+predB+predD;

        r1 = rand;
        r2 = rand;
        % Figure out which window we're in.
        if (r1 < preyB/total)
            pred(a+1) = pred(a);
            prey(a+1) = prey(a) + 1;
        elseif (r1 >= preyB/total && r1 < (preyB + preyD)/total)
            pred(a+1) = pred(a);
            prey(a+1) = prey(a) - 1;
        elseif (r1 >= (preyB + preyD + predB)/total)
            pred(a+1) = pred(a) - 1;
            prey(a+1) = prey(a);
        else

```

```

        pred(a+1) = pred(a) + 1;
        prey(a+1) = prey(a);
    end
    t(a+1) = -log(r2)/total + t(a);
    a = a+1;
end
A{b}=[prey(1:a) ; pred(1:a) ; t(1:a)];      % Save in a cell
end

timeLen = zeros(1,trials);          % Make a time length vector
stepLen = zeros(1,trials);          % Make a step length vector
for i=1:trials
    timeLen(i) = A{i}(3,end);
    stepLen(i) = length(A{i});
end

% We look at the trials up until the first one to maxSteps ran out of time.
maxStepLens=find(stepLen==max(stepLen));
maxTime=min(timeLen(maxStepLens));
numExtinct=trials;                  % First assume everything went extinct
if (max(stepLen) == maxSteps)        % Check how many made it to maxSteps
    numExtinct = trials-length(maxStepLens);
end
fprintf('%.2f secs\n',toc);          % Log time of the most intensive part

t    = linspace(0,maxTime,numSteps); % time vector
prey = zeros(trials,numSteps);       % prey vector
pred = zeros(trials,numSteps);       % pred vector
prey(:,1) = initprey; pred(:,1) = initpred;
% Now we quantize the data into a discrete time interval
fprintf('Quantizing...\n');
for i = 1:trials                      % i = current trial
    j = 2;                             % j = current quantized time step
    k=1;                               % k = current time step of actual data
    trialSteps = length(A{i});
    while (k < trialSteps & j <= numSteps)
        % If next actual time > quantized step
        if (A{i}(3,k+1) >= t(j))
            prey(i,j) = A{i}(1,k);      % Record population as current
            pred(i,j) = A{i}(2,k);
            j = j+1;
        else
            k = k+1;
        end
    end
end                                     % end trial

```

```

end                                % end quantizing

% We take population entries and find average and variance
fprintf('Finding Mean and Variance...\n');
varprey=zeros(1,numSteps); varpred=zeros(1,numSteps); for
a=1:numSteps
    w=prey(:,a);
    avgprey(a)=mean(w);
    varprey(a)=var(w);
    v=pred(:,a);
    avgpred(a)=mean(v);
    varpred(a)=var(v);
end

fprintf('Plotting.\n'); maxvar=max(max(varprey),max(varpred));
maxavg=max(max(avgprey),max(avgpred));

subplot(2,2,1); hold off
plot(t,avgprey,'r',t,avgpred,'b');      % Time vs. populations
axis([0,max(t),0,maxavg]); xlabel('Time'); ylabel('Population
Size'); legend('Prey','Predator');

subplot(2,2,2);                        % Population phase plane
hold off plot(avgprey,avgpred);
axis([min(avgprey),max(avgprey),min(avgpred),max(avgpred)]);
xlabel('Prey'); ylabel('Predator');

subplot(2,1,2);                        % Variance
hold off plot(t,varprey,'r',t,varpred,'b');
axis([0,max(t),0,maxvar]); xlabel('Time'); ylabel('Variance');
legend('Prey','Predator');

subplot(2,2,1);                        % Print time taken
title(sprintf('Predator vs. Prey\n%d Trials/%d Extinctions',...
    trials,numExtinct));

```

Linearized Competing Hunters Process

```

% Stochastic Process of Linearized Competing Hunters
% AMSSI 2005 - Team NERJ
% Public Domain. Mess with this as much as you want.
% This is not as well documented or coded as singlepop.m, enjoy!
%

```

```

% birth = Birth polynomial with powers in descending order
% death = Death polynomial with powers in descending order
% initPop = Initial population
function comphuntlinear(trials)

maxSteps = 3000;
numSteps = 400; % Number of steps

% x' = alpha*x - beta*x*y Hunters 1
inithunt1 = 200; % Initial population for hunters 1
alpha = 2.55; % Birth rate
beta = .0061; % Interaction (death)

% y' = gamma*y - delta*x*y Hunters 2
inithunt2 = 700; % Initial population for hunters 2
gamma = 2.2; % Starvation rate
delta = .021; % Hunting rate

crithunt1 = gamma/delta; crithunt2 = alpha/beta; inithunt1 =
inithunt1 - crithunt1; inithunt2 = inithunt2 - crithunt2;

fprintf('Starting %d trials...', trials);
tic; % Start timer
last = 0; A=cell(1,trials); for b = 1:trials
    hunt1 = zeros(1,maxSteps); % Initialize vectors
    hunt2 = zeros(1,maxSteps);
    t = zeros(1,maxSteps);
    hunt1(1) = inithunt1; % Initialize populations and time
    hunt2(1) = inithunt2;
    t(1) = 0;
    a = 1;
    while (hunt1(a) ~= 0 && hunt2(a) ~= 0 && a < maxSteps)
        hunt1D = beta*gamma/delta*abs(hunt2(a));
        hunt2B = alpha*delta/beta*abs(hunt1(a));
        total = hunt1D+hunt2B;

        r1 = rand;
        r2 = rand;
        % Figure out which window we're in.
        if (r1 < hunt1D/total)
            if (hunt2(a) > 0)
                hunt2(a+1) = hunt2(a);
                hunt1(a+1) = hunt1(a) - 1;
            else
                hunt2(a+1) = hunt2(a);

```

```

        hunt1(a+1) = hunt1(a) + 1;
    end
else
    if (hunt1(a) > 0)
        hunt2(a+1) = hunt2(a) - 1;
        hunt1(a+1) = hunt1(a);
    else
        hunt2(a+1) = hunt2(a) + 1;
        hunt1(a+1) = hunt1(a);
    end
end
t(a+1) = -log(r2)/total + t(a);
a = a+1;
end
hunt1 = hunt1 + crithunt1;
hunt2 = hunt2 + crithunt2;
A{b}=[hunt1(1:a) ; hunt2(1:a) ; t(1:a)];      % Save in a cell
end

timeLen = zeros(1,trials);      % Make a time length vector
stepLen = zeros(1,trials);      % Make a step length vector
for i=1:trials
    timeLen(i) = A{i}(3,end);
    stepLen(i) = length(A{i});
end

% We look at the trials up until the first one to maxSteps ran out of time.
maxStepLens=find(stepLen==max(stepLen)); maxTime=min(timeLen);
numExtinct=trials;              % First assume everything went extinct
if (max(stepLen) == maxSteps)    % Check how many made it to maxSteps
    numExtinct = trials-length(maxStepLens);
end
fprintf('%.2f secs\n',toc);      % Log time of the most intensive part

t    = linspace(0,maxTime,numSteps);      % time vector
hunt1 = zeros(trials,numSteps);          % hunt1 vector
hunt2 = zeros(trials,numSteps);          % hunt2 vector
hunt1(:,1) = inithunt1+crithunt1; hunt2(:,1) = inithunt2+crithunt2;

% Now we quantize the data into a discrete time interval
fprintf('Quantizing...\n');
for i = 1:trials                      % i = current trial
    j = 2;                             % j = current quantized time step
    k=1;                                 % k = current time step of actual data
    trialSteps = length(A{i});

```



```

while (k < trialSteps & j <= numSteps)
    % If next actual time > quantized step
    if (A{i}(3,k+1) >= t(j))
        hunt1(i,j) = A{i}(1,k);      % Record population as current
        hunt2(i,j) = A{i}(2,k);
        j = j+1;
    else
        k = k+1;
    end
end
end          % end trial
end          % end quantizing

% We take population entries and find average and variance
fprintf('Finding Mean and Variance...\n');
varhunt1=zeros(1,numSteps); varhunt2=zeros(1,numSteps); for
a=1:numSteps
    w=hunt1(:,a);
    avghunt1(a)=mean(w);
    varhunt1(a)=var(w);
    v=hunt2(:,a);
    avghunt2(a)=mean(v);
    varhunt2(a)=var(v);
end

fprintf('Plotting.\n'); maxvar=max(max(varhunt1),max(varhunt2));
maxavg=max(max(avghunt1),max(avghunt2));

subplot(2,2,1); hold off
plot(t,avghunt1,'r',t,avghunt2,'b');      % Time vs. populations
axis([0,max(t),0,maxavg]); xlabel('Time'); ylabel('Population
Size'); legend('Hunters 1','Hunters 2');

subplot(2,2,2);                          % Population phase plane
hold off plot(avghunt1,avghunt2);
axis([min(avghunt1),max(avghunt1),min(avghunt2),max(avghunt2)]);
xlabel('Hunters 1'); ylabel('Hunters 2');

subplot(2,1,2);                          % Variance
hold off plot(t,varhunt1,'r',t,varhunt2,'b');
axis([0,max(t),0,maxvar]); xlabel('Time'); ylabel('Variance');
legend('Hunters 1','Hunters 2');

subplot(2,2,1);                          % Print time taken
title(sprintf('Competing Hunters - Linearized\n%d Trials/%d Extinctions',...
    trials,numExtinct));

```

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