Introduction to Stochastic Population Models

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Contents

1 Probability and Random Variables

The models that you have seen thus far are deterministic models. For any time t, there is a unique solution $X(t)$. On the other hand, stochastic models result in a distribution of possible values $X(t)$ at a time t. To understand the properties of stochastic models, we need to use the language of probability and random variables.

1.1 The Basic Ideas of Probability

1.1.1 Sample Spaces and Events

Probability: Probability is used to make inferences about populations.

Experiment: Some process whose outcome is not known with certainty.

Sample Space: The collection of all possible outcomes of an experiment or process; denoted $\mathcal{S}$.

Event: Any collection of possible outcomes of an experiment; denoted $A,\ B$, etc.

Relative Frequency Interpretation of Probability

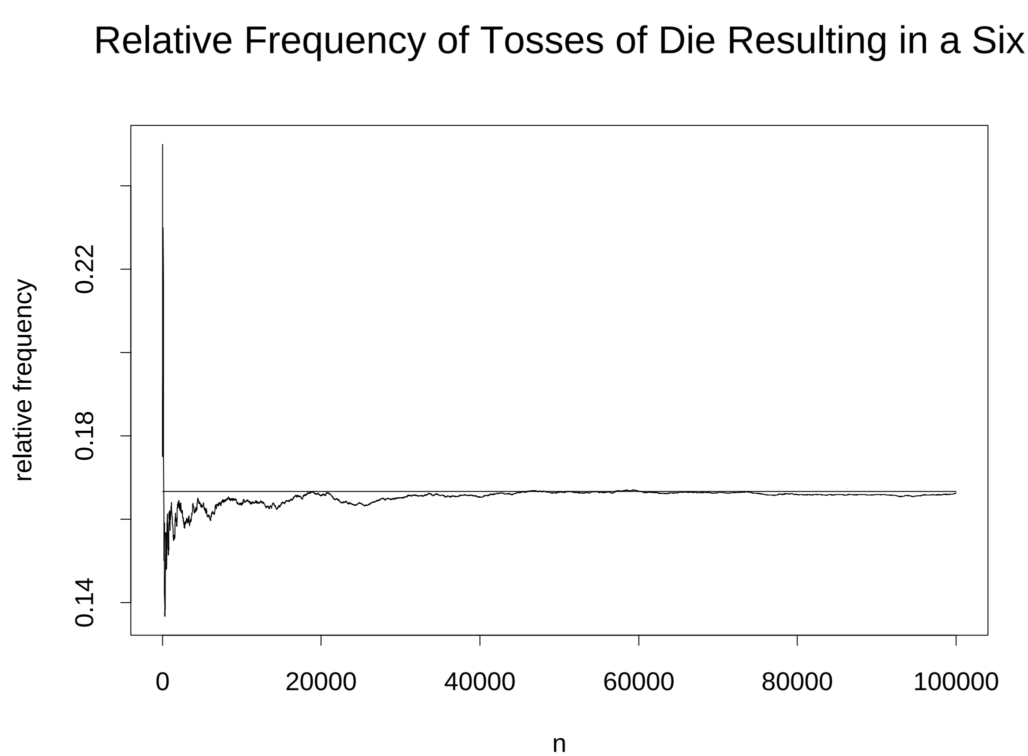
A random experiment is carried out a large number (n) of times and the number ($n(A)$) of times that event A occurs is recorded. Then the proportion of times that A occurs will tend to the probability of A:

$$\frac{n(A)}{n} \longrightarrow P(A)$$

Illustration of Long-Run Relative Frequency

Suppose a die is tossed repeatedly, and we count the number of times that the toss results in six spots. We then plot the proportion of times that the toss results in a six versus the number of tosses.

n	$n(A)$	$\frac{n(A)}{n}$
10	2	0.20000
100	23	0.23000
1000	160	0.16000
10000	1639	0.16390
100000	16618	0.16618



Axioms:

1. $P(A) > 0$ for any event A
2. $P(\mathcal{S}) = 1$
3. For any collection $A_1, A_2, \ldots$ of mutually exclusive events ($A_i \cap A_j = \emptyset$ for $i \neq j$),

$$P(A_1 \cup A_2 \cup \cdots) = \sum_{i=1}^{\infty} P(A_i)$$

Properties:

- $0 \leq P(A) \leq 1$
- $P(\emptyset) = 0$
- Probability an event does not occur: $P(A') = 1 - P(A)$.
- $P(A \cup B) = P(A) + P(B) - P(A \cap B)$
- If A and B are mutually exclusive,
  $P(A \cup B) = P(A) + P(B)$

1.1.2 Conditional Probability

For any two events A and B with $P(B) > 0$ the *conditional probability of A given that B has occurred*:

$$P(A|B) = \frac{P(A \cap B)}{P(B)}$$

The multiplication rule for $P(A \cap B)$ is:

$$\begin{aligned} P(A \cap B) &= P(A|B)P(B) \\ P(A \cap B) &= P(B|A)P(A) \end{aligned}$$

Law of Total Probability

Let $A_1, \ldots, A_n$ be mutually exclusive and exhaustive events. Exhaustive means that

$$A_1 \cup A_2 \cup \cdots \cup A_n = \mathcal{S}.$$

Assume also that $P(A_j) > 0$ for each j. Then for any event B,

$$P(B) = \sum_{j=1}^{n} P(B|A_j)P(A_j)$$

If $P(B) > 0$, this law implies **Bayes Theorem**:

$$P(A_k|B) = \frac{P(B|A_k)P(A_k)}{\sum_{j=1}^{n} P(B|A_j)P(A_j)}$$

Example: Diagnostic Testing.

Define the two events:

A= event that disease is present

B= event that diagnostic test is positive

We usually know the following:

- Prevalence of disease, say $P(A) = .001$
- Sensitivity of test, say $P(B|A) = 0.95$
- Specificity of test, say $P(B'|A') = 0.90$

We want to know, $P(A|B)$ or $P(A'|B')$

Solution:

$$\begin{aligned} P(A|B) &= \frac{P(B|A)P(A)}{P(B|A)P(A)+P(B|A')P(A')} \\ &= \frac{(0.95)(0.001)}{(0.95)(0.001)+(1-0.90)(1-0.001)} \\ &= 0.0094 \end{aligned}$$

$$\begin{aligned} P(A'|B') &= \frac{P(B'|A')P(A')}{P(B'|A')P(A')+P(B'|A)P(A)} \\ &= \frac{(0.90)(0.999)}{(0.90)(0.999)+(1-0.95)(0.001)} \\ &= 0.9999444 \end{aligned}$$

1.1.3 Independence

Two events A and B are **independent** if

$$P(A \cap B) = P(A)P(B).$$

They are **dependent** otherwise.

When $P(A) > 0$ and $P(B) > 0$, this definition is equivalent to

$$P(A|B) = P(A) \quad \text{and} \quad P(B|A) = P(B)$$

.

Extension of Independence to Several Events

We say that $A_1, A_2, \ldots, A_n$ are **mutually independent** if for every subset $\{i_1, \ldots, i_k\}$ $(k \geq 2)$, we have

$$P(A_{i_1} \cap A_{i_2} \cap \cdots \cap A_{i_k}) = P(A_{i_1})P(A_{i_2}) \cdots P(A_{i_k})$$

We say that $A_1, A_2, \ldots, A_n$ are **pairwise independent** if

$$P(A_i \cap A_j) = P(A_i)P(A_j)$$

for every pair $(i, j),\ i \neq j$.

Pairwise independence does not imply mutual independence.

1.2 Random Variables

Random variables help us to make a link between probability and numbers that we observe as data.

A **random variable (rv)** is a numerical valued function defined on a sample space. A random variable X “maps” an outcome in a sample space to a numerical value.

The probability that a rv X takes a value in the set A is given by

$$P[X \in A] = P[X^{-1}(A)].$$

We use capital letters such as X or Y to denote random variables.

Let s be an elementary outcome. A value, $X(s)$, of X is denoted x.

A random variable is **discrete** if it can take on a finite or countable number of values.

A **continuous** random variable takes on an uncountable number of values.

1.3 Probability Distributions of a Discrete R.V.

The probability distribution of a discrete r.v. is a list of the distinct values x of X together with the associated probabilities:

$$p(x) = P(X = x)$$

By $P(X = x)$, we mean $P(A_x)$ where

$$A_x = \{s \in \mathcal{S} : X(s) = x\}.$$

We can express $p(x)$ as a function or in a table:

x	x_1	x_2	x_3	$\ldots$	x_k
$p(x)$	$p(x_1)$	$p(x_2)$	$p(x_3)$	$\ldots$	$p(x_k)$

A function $p(x)$ or p_x is a **probability mass function (pmf)** of some random variable X if

- $p(x) \geq 0$ all x
- $\sum_{\text{all } x_i} p(x_i) = 1$

An alternative way to represent a probability distribution is by using **the cumulative distribution function (cdf)**:

$$F(x) = P(X \le x) = \sum_{y: y \le x} p(y), \qquad -\infty < x < \infty$$

For a discrete random variable taking values on $x_1 < x_2 < \cdots < x_k$,

$$p(x_j) = F(x_j) - F(x_{j-1}),\ j = 2, \ldots, k.$$

1.3.1 Parameters of Probability Distributions

Suppose that for each value of α, $p(x; \alpha)$ is a probability distribution for a random variable X. Then α is said to be a **parameter** of the distribution. The collection of distributions

$$\{p(x; \alpha) : \alpha \in \mathcal{A}\}$$

is called a **parametric family** of distributions.

1.3.2 Expected Values of Discrete RV

- Mean of a discrete RV

  The mean of a rv X is

  $$E[X] = \mu = \sum_{x \in \mathcal{D}} x \cdot p(x)$$

  where $\mathcal{D}$ is the set of possible values of X.

- Expected value of a function of X

  The expected value of a function $h(X)$ is:

  $$E[h(X)] = \mu_{h(X)} = \sum_{x \in \mathcal{D}} h(x) \cdot p(x)$$

  If $h(X)$ is a linear function of the form $aX + b$:

  $$E(aX + b) = aE(X) + b$$

- Variance of a discrete R.V.

  The variance of a discrete R.V. is

$$\begin{aligned} V(X) &= \sigma^2 \\ &= \sigma_X^2 \\ &= E[(X-\mu)^2] \end{aligned}$$

- The **standard deviation** of X is

$$\sigma = \sigma_X = \sqrt{V(X)} = \sqrt{\sigma^2} = \mathrm{SD}(X)$$

- The variance of a linear function $aX + b$ is

$$V(aX+b) = a^2 V(X) = a^2 \sigma^2$$

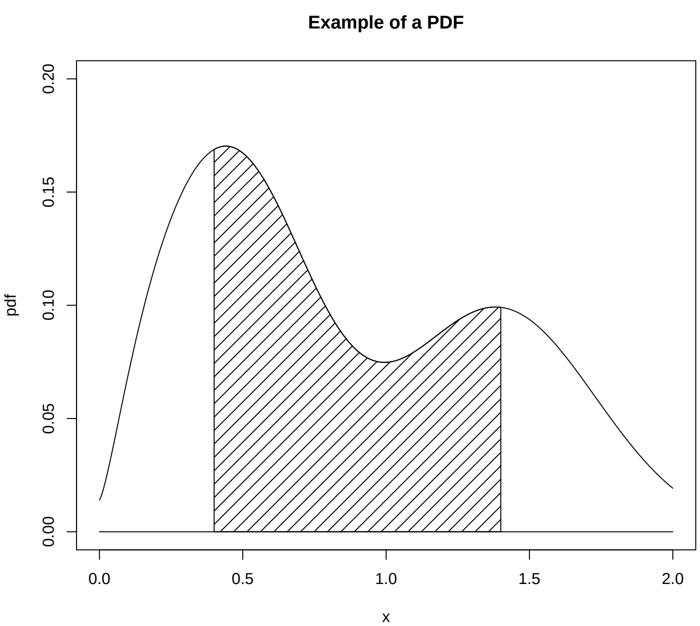
- **Implications:**
  - $V(aX) = a^2 V(X)$
  - $\mathrm{SD}(aX) = |a| \mathrm{SD}(X)$
  - $V(X+b) = V(X)$
  - $\mathrm{SD}(X+b) = \mathrm{SD}(X)$

1.4 Continuous Random Variables

A *continuous random variable* can assume any value in an interval on the real line. The distribution of a continuous random variable is determined by the probability density function (pdf). The pdf of X is a function $f(x)$ such that for any numbers a and b where $a < b$,

$$P(a \leq X \leq b) = \int_a^b f(x)dx$$

The graph of $f(x)$ is often called a density curve.

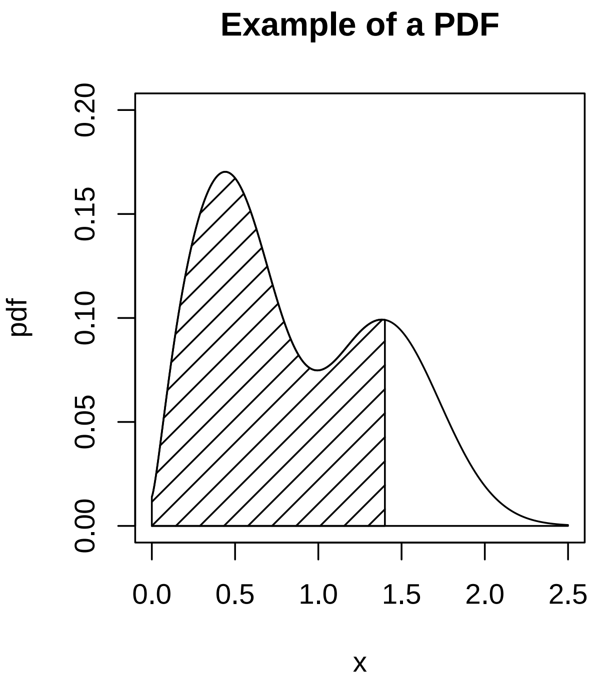


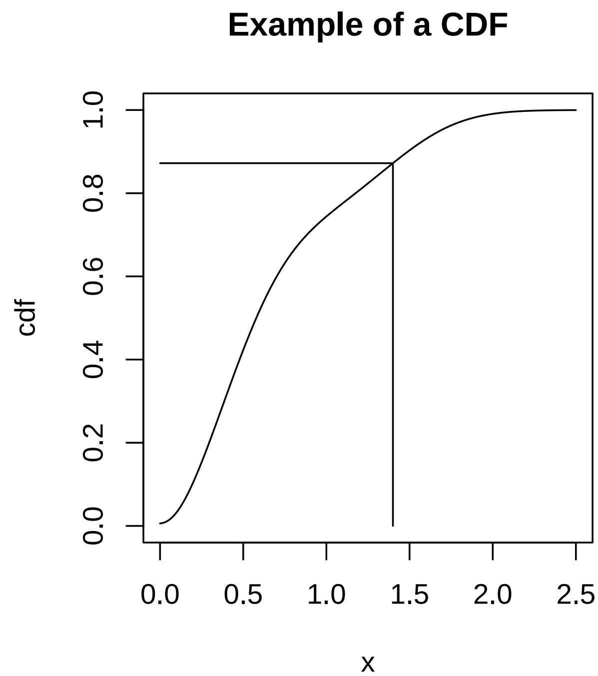
For $f(x)$ to be a pdf it must satisfy:

1. $f(x) \geq 0$ all x
2. $\int_{-\infty}^{\infty} f(x)dx = 1$ (area under curve is 1).

An alternative method of expressing the distribution of a continuous random variable is using the cumulative distribution function (cdf). The cdf of a continuous RV is defined as:

$$F(x) = P(X \leq x) = \int_{-\infty}^{x} f(y)dy$$





Useful Properties:

- $P(a \leq X \leq b) = F(b) - F(a)$
- If X is a continuous RV with pdf $f(x)$ and cdf $F(x)$, then at every x at which $F'(x)$ exists:

$$F'(x) = f(x)$$

1.4.1 Percentiles

For $0 \leq p \leq 1$ the $(100p)^{th}$ percentile of the distribution of a continuous RV X is a value x_p such that $p = F(x_p)$

1.4.2 Expected Values, Mean and Variance

The expected value of a function $h(X)$ for a continuous rv is:

$$E[h(X)] = \int_{-\infty}^{\infty} h(x) \cdot f(x)dx$$

Some special cases:

Mean: $E[X] = \mu = \int_{-\infty}^{\infty} x \cdot f(x)dx$

Variance: $E[(X-\mu)^2] = \sigma^2 = \int_{-\infty}^{\infty} (x-\mu)^2 \cdot f(x)dx$

Remember: $E[(X-\mu)^2] = E[X^2] - (E[X])^2 = \sigma^2$

Note: The properties of expectation and variance of linear functions also hold in the continuous case.

1.5 Joint Probability Distributions

The joint cdf of two random variables X and Y is defined by

$$F(x, y) = P[X \leq x, Y \leq y].$$

We say that (X, Y) is discrete if

$$P[(X, Y) \in A] = \sum_{(x,y)\in A} p(x, y)$$

where $p(x, y) = P[X = x, Y = y]$ is the joint pmf of (X, Y).

We say that (X, Y) are jointly continuous rvs if there exists a function called the joint pdf such that

$$P[(X, Y) \in A] = \iint_A f(x, y)dxdy$$

The expectation of a function $h(X, Y)$ of (X, Y) is

$$E[h(X, Y)] = \begin{cases} \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} h(x, y)f(x, y)dxdy & \text{if } X, Y \text{ continuous} \\ \sum_x \sum_y h(x, y)p(x, y) & \text{if } X, Y \text{ discrete} \end{cases}$$

The random variables X and Y are *independent* if

$$P[X \in A, Y \in B] = P[X \in A] \times P[Y \in B]$$

for any events A and B. This is equivalent to

$$\begin{aligned} F(x, y) &= F_X(x)F_Y(y), && \text{for all } x, y \text{ for any rvs} \\ f(x, y) &= f_X(x)f_Y(y), && \text{for all } x, y \text{ for continuous rvs} \\ p(x, y) &= p_X(x)p_Y(y), && \text{for all } x, y \text{ for discrete rvs} \end{aligned}$$

1.5.1 Conditional Distributions

Conditional distributions are a basic tool in the description of stochastic processes.

The **conditional probability mass function** of Y given that $X = x_0$ is

$$f_{Y|x_0}(y) = \frac{f_{XY}(x_0, y)}{f_X(x_0)}, \qquad \text{for } f_X(x_0) > 0.$$

Similarly, the **conditional probability mass function** of X given that $Y = y_0$ is

$$f_{X|y_0}(x) = \frac{f_{XY}(x, y_0)}{f_Y(y_0)}, \qquad \text{for } f_Y(y_0) > 0.$$

Properties of the Conditional PMF

- $f_{Y|x_0}(y) > 0$
- $\sum_y f_{Y|x_0}(y) = 1$
- $P(Y = y|X = x_0) = f_{Y|x_0}(y)$
- We can find expectations using conditional pmfs.

Conditional Mean and Variance:

- $E(Y|x) = \mu_{Y|x} = \sum_y y f_{Y|x}(y)$
- $V(Y|x) = \sigma^2_{Y|x} = \sum_y (y - \mu)^2 f_{Y|x}(y)$

1.5.2 Conditional Distributions for Bivariate Continuous RVs

Given that (X, Y) are continuous rvs with pdf $f_{XY}(x, y)$, the conditional pdf of Y given that $X = x_0$ is

$$f_{y|x_0}(y) = \frac{f_{XY}(x_0, y)}{f_X(x_0)} \qquad \text{for } f_X(x_0) > 0.$$

Properties:

- $f_{y|x_0}(y) \geq 0$
- $\int_{-\infty}^{\infty} f_{y|x_0}(y)dy = 1$
- $P(Y \in B|X = x_0) = \int_B f_{y|x_0}(y)dy = 1$

Conditional Mean and Variance:

- $E(Y|X = x_0) = \mu_{Y|x_0} = \int_{-\infty}^{\infty} y f_{y|x_0}(y) dy$
- $V(Y|X = x_0) = \sigma^2_{Y|x_0} = \int_{-\infty}^{\infty} (y - \mu_{Y|x_0})^2 f_{y|x_0}(y) dy$

Remark: The conditional mean $E(Y|X = x_0)$ is known as the *regression function* of Y on x.

1.6 Some Special Cases

1.6.1 Poisson Distribution

Consider these random variables:

- Number of telephone calls received per hour.
- Number of days school is closed due to snow.
- Number of trees in an area of forest.
- Number of bacteria in a culture.

A random variable X, the number of events occurring during a given time interval or in a specified region, is called a *Poisson* random variable. The corresponding distribution:

$$X \sim \text{Poisson}(\lambda)$$

where λ is the rate per unit time or rate per unit area.

$$p(x;\lambda) = P(X = x) = \frac{e^{-\lambda}\lambda^x}{x!} \quad , \quad x = 0, 1, 2, \ldots, \; \lambda > 0$$

The mean and variance of a Poisson random variable are

$$\begin{aligned} E[X] = &\quad \mu &= \lambda \\ V[X] = &\quad \sigma^2 &= \lambda \end{aligned}$$

1.6.2 The Poisson Process

We will be examining various *stochastic processes* that correspond to some of the deterministic population models studied so far.

A *stochastic processes* $\{X(t), t \in T\}$ is an indexed collection of random variables. We are interested in several properties of a stochastic process:

- The distribution of $X(t)$ for a fixed time t.
- The joint distribution of $(X(t_1), X(t_2), \ldots, X(t_k))$ for any times $t_1, \ldots, t_k$.
- The appearance of a *sample path* or *realization* of the stochastic process: $\{X(t; s) : t \in T\}$.

We will show how the Poisson distribution arises in a stochastic process for which we make a few reasonable assumptions. We first define a counting process.

A stochastic process $\{X(t), t \geq 0\}$ is said to be a *counting process* if

1. $X(t) \geq 0$
2. $X(t)$ is integer valued
3. If $s < t$, then $X(s) \leq X(t)$.
4. For $s < t$, $X(t) - X(s)$ equals the number of events that have occurred in the interval $(s, t]$.

Let $\{X(t), t \geq 0\}$ be a counting process that satisfies

1. $X(0) = 0$
2. $X(s)$ is independent of $X(t+s) - X(s)$ for any $s, t > 0$ (independent increments).
3. The distribution of $X(t+s) - X(s)$ depends only on t for any $s, t > 0$ (stationary increments).
4. $P(X(t+h) - X(t) = 1) = \lambda h + o(h)$
5. $P(X(t+h) - X(t) \geq 2) = o(h)$

Then we can show that

$$P_x(t) = P(X(t) = x) = \frac{e^{-\lambda t}(\lambda t)^x}{x!},\ x = 0, 1, 2, \ldots$$

The process $\{X(t), t \geq 0\}$ is called a *Poisson process*.

Outline of Proof

Consider

$$P_0(t+h) = P_0(t)P_0(h) = P_0(t)(1 - \lambda h) + o(h).$$

Then

$$\frac{P_0(t+h) - P_0(t)}{h} = -\lambda P_0(t) + \frac{o(h)}{h}.$$

Let $h \to 0$ and obtain $P_0'(t) = -\lambda P_0(t)$. This implies that $P_0(t) = e^{\lambda t}$.

For $x \geq 1$,

$$\begin{aligned} P_x(t+h) &= P[X(t)=x, X(t+h)-X(t)=0] \\ &\quad + P[X(t)=x-1, X(t+h)-X(t)=1] \\ &\quad + P[X(t+h)=x, X(t+h)-X(t)\geq 2] \\ &= P_x(t)P_0(h) + P_{x-1}(t)P_1(h) + o(h) \\ &= (1-\lambda h)P_x(t) + \lambda h P_{x-1}(t) + o(h) \end{aligned}$$

Divide both sides by h and let $h \to 0$:

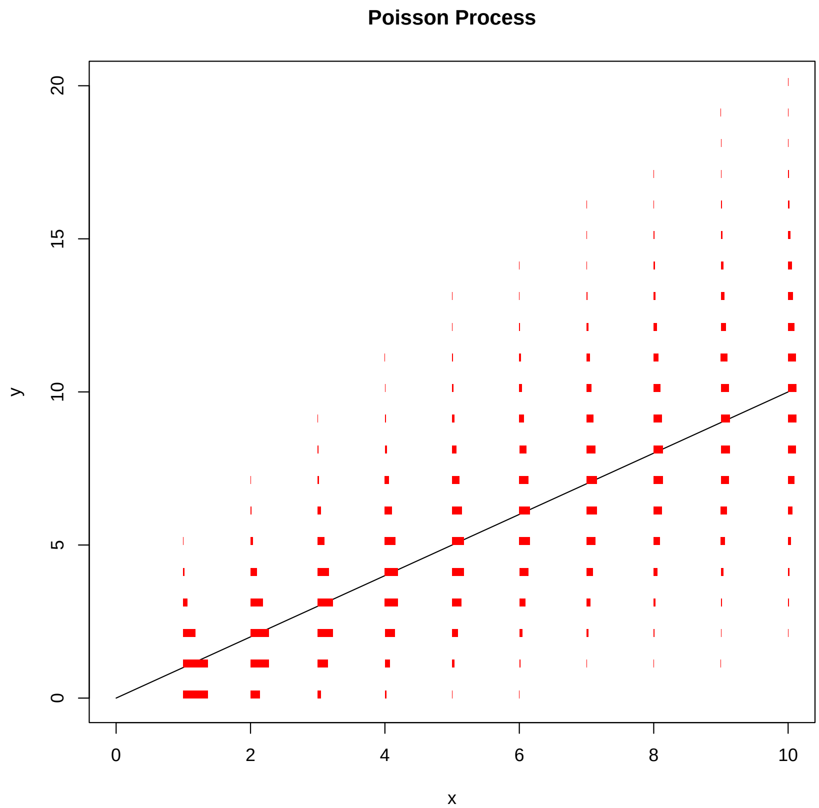
$$P_x'(t) = -\lambda P_x(t) + \lambda P_{x-1}(t),\ x = 1, 2, \ldots.$$

The solution to this system of differential equations is

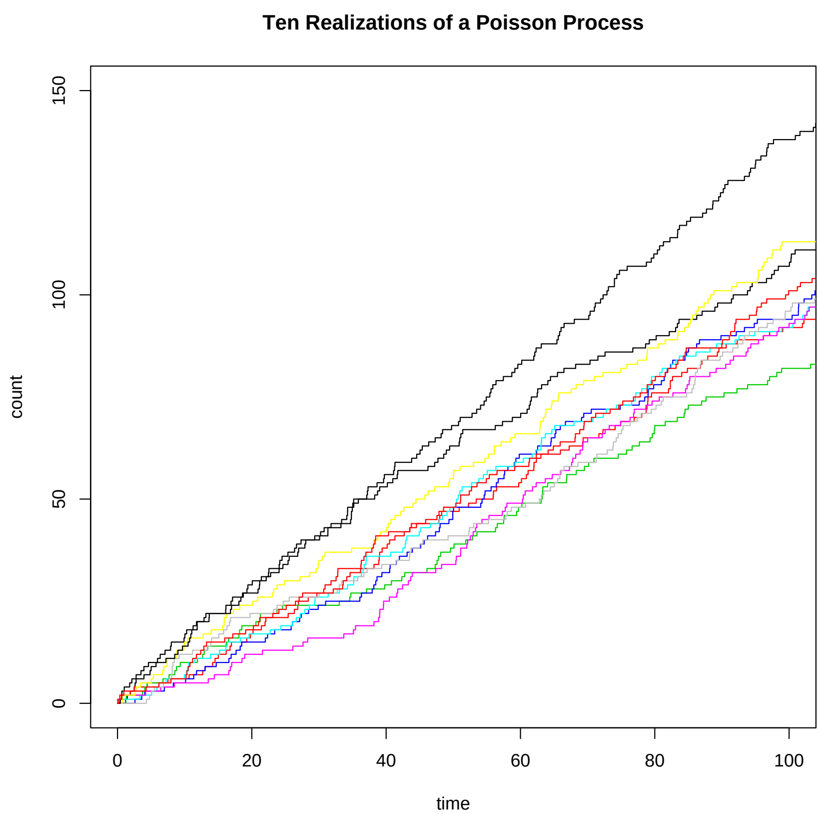
$$P_x(t) = \frac{e^{-\lambda t}(\lambda t)^x}{x!},\ x = 1, 2, \ldots.$$

Figures: The first figure on the next page illustrates the variation in a Poisson process with $\lambda = 1$ for various times. The red bars represent the pmf of the Poisson process at $t = 1, 2, \ldots, 10$.

The second figure depicts 10 realizations of a Poisson process with $\lambda = 1$.



Poisson Process
y
0
5
10
15
20
x
0
2
4
6
8
10



Ten Realizations of a Poisson Process
count
0
50
100
150
time
0
20
40
60
80
100

1.6.3 Normal Distribution

The **normal** or **Gaussian** distribution has the pdf:

$$f(x;\mu,\sigma) = \frac{1}{\sqrt{2\pi}\,\sigma} e^{-(x-\mu)^2/2\sigma^2} \qquad -\infty < x < \infty$$

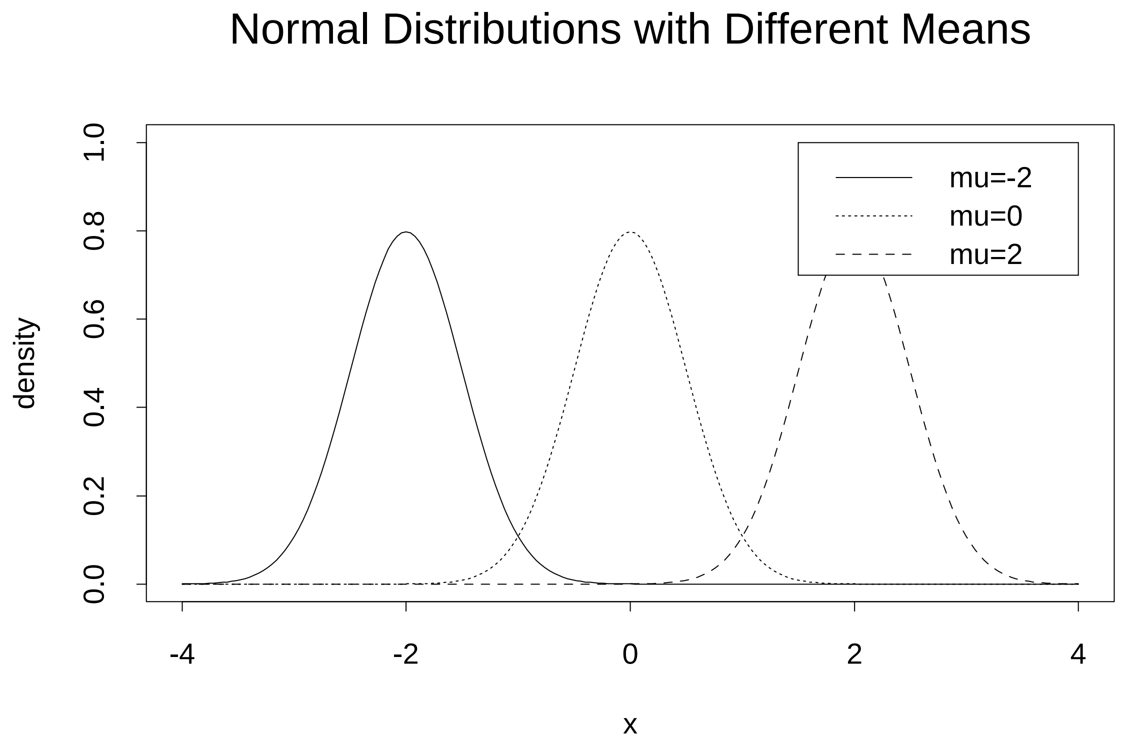
The mean and variance are

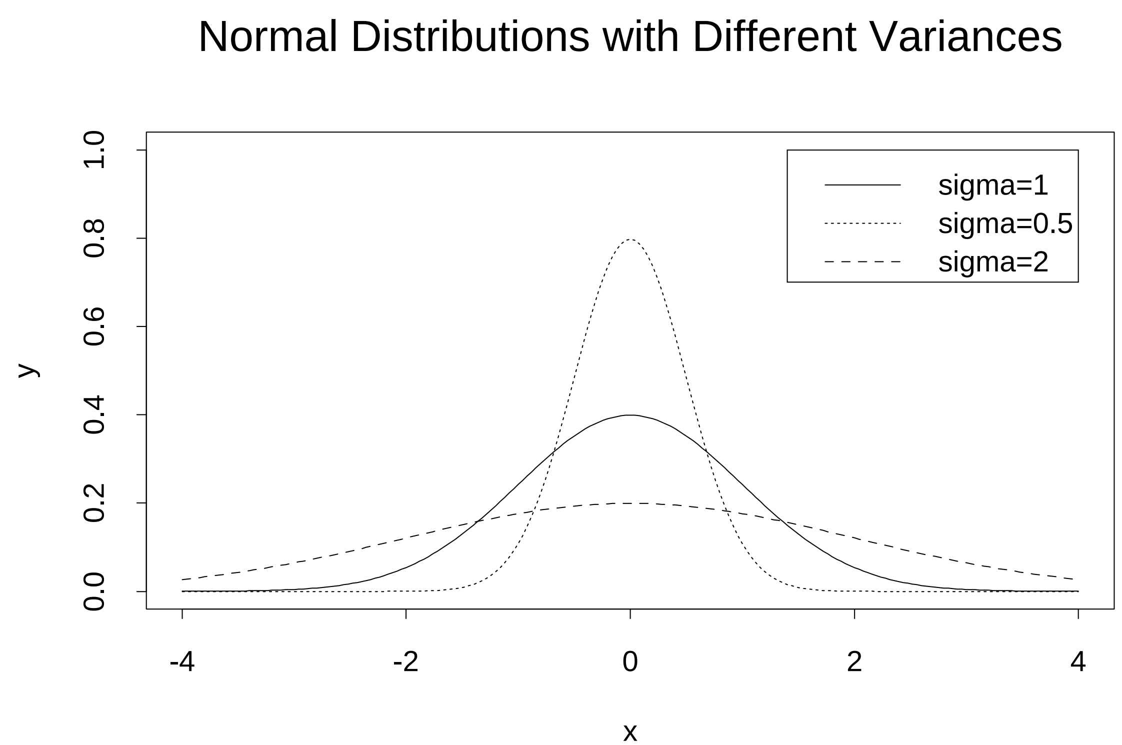
$$\begin{aligned} E(X) &= \mu \\ V(X) &= \sigma^2 \end{aligned}$$

The shorthand for this family of distributions as:

$$X \sim N(\mu, \sigma^2)$$

Some Normal Distributions


Normal Distributions with Different Means
density
1.0
0.8
0.6
0.4
0.2
0.0
-4
-2
0
2
4
x
mu=-2
mu=0
mu=2


Normal Distributions with Different Variances
y
1.0
0.8
0.6
0.4
0.2
0.0
-4
-2
0
2
4
x
sigma=1
sigma=0.5
sigma=2

1.7 Gamma Distribution

The gamma distribution is a family of distributions that yields a wide variety of skewed distributions. It is often used to model the lifetime length of manufactured items.

Central to the gamma distribution is the gamma function:

$$\Gamma(\alpha) = \int_0^\infty x^{\alpha-1} e^{-x} dx \qquad \alpha > 0$$

Some properties of the gamma function:

1. $\alpha > 1, \quad \Gamma(\alpha) = (\alpha - 1)\Gamma(\alpha - 1)$.
2. If n is positive integer: $\Gamma(n) = (n-1)!$
3. $\Gamma(\frac{1}{2}) = \sqrt{\pi}$.

Using the properties of the gamma function, we obtain the pdf of the gamma (α, β) distribution:

$$f(x;\alpha,\beta) = \frac{1}{\beta^\alpha \Gamma(\alpha)} x^{\alpha-1} e^{-x/\beta} \qquad x \geq 0,\ \alpha > 0,\ \beta > 0$$

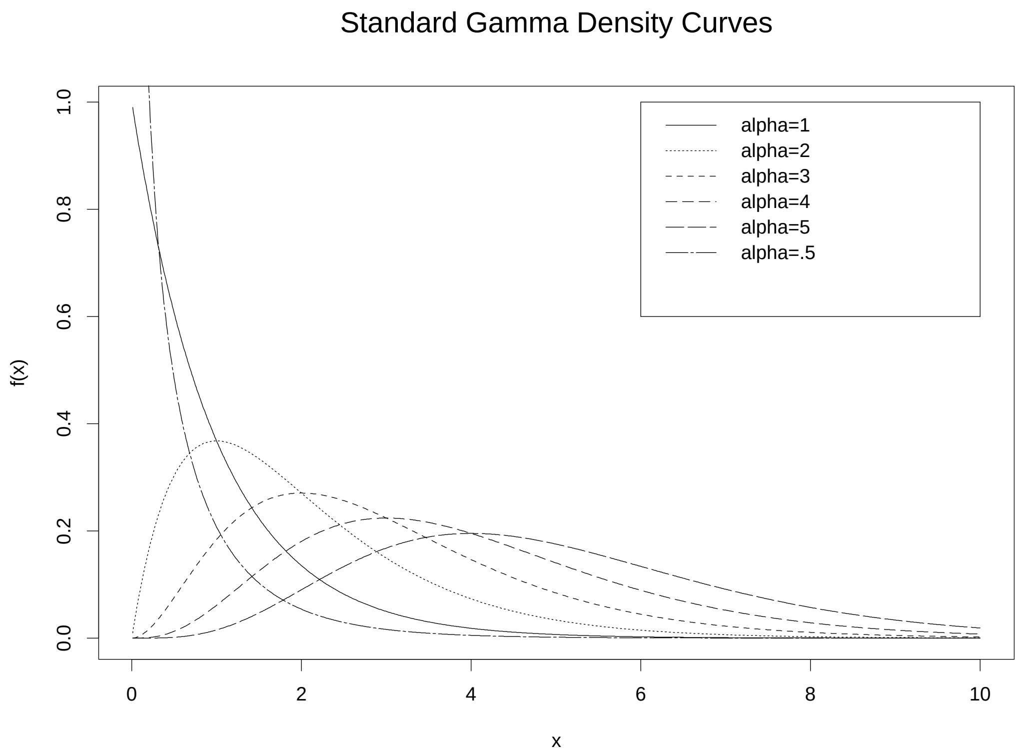
The mean and variance of the gamma distribution are:

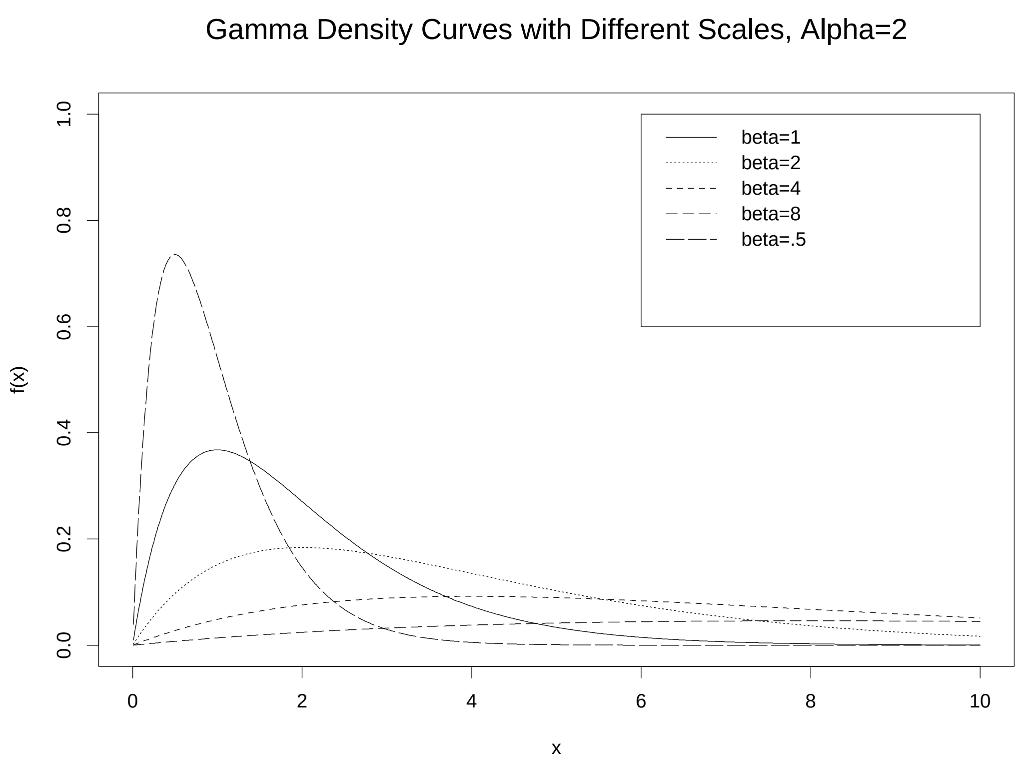
$$\begin{aligned} E(X) &= \alpha\beta \\ V(X) &= \alpha\beta^2 \end{aligned}$$

- α is the shape parameter and β is the scale parameter.

- If $\beta = 1$ then we call this the *standard gamma distribution*.
- If $\alpha = 1$, the distribution is the *exponential distribution*. Letting $\lambda = 1/\beta$, the pdf of the exponential distribution is given by

$$f(x;\lambda) = \lambda e^{-\lambda x} \qquad x \geq 0, \lambda > 0$$


Standard Gamma Density Curves
alpha=1
alpha=2
alpha=3
alpha=4
alpha=5
alpha=.5
f(x)
x
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
10


Gamma Density Curves with Different Scales, Alpha=2
beta=1
beta=2
beta=4
beta=8
beta=.5
f(x)
x
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
10

1.7.1 Distribution of Elapsed Time in the Poisson Process

Recall the Poisson distribution and how it is used to calculate probabilities for certain events in time or space:

Let T_1 denote the time of the first event and $T_n,\ n = 2, 3, \ldots$ be the time between the $(n-1)^{st}$ and n^{th} events. Then $(T_1, T_2, \ldots)$ are independent and identically distributed (iid) exponential(λ) random variables.

Let $S_n = T_1 + \cdots + T_n$. Then S_n has a gamma$(1/\lambda, n)$ distribution.

This can be noted by the fact that

$$S_n \leq t \Leftrightarrow X(t) \geq n.$$

Hence,

$$P[S_n \leq t] = P[X(t) \geq n] = \sum_{j=n}^{\infty} e^{-\lambda t} \frac{(\lambda t)^j}{j!}.$$

We differentiate this to get the pdf of S_n:

$$f(t) = \frac{\lambda^n}{(n-1)!} t^{n-1} e^{-\lambda t},\ t > 0.$$

2 An Introduction to Stochastic Population Models

References

[1] J. H. Matis and T. R. Kiffe. *Stochastic Population Models, a Compartmental Perspective.* Springer-Verlag, New York, 2000.

[2] E. Renshaw. *Modelling Biological Populations in Space and Time*. Cambridge University Press, Cambridge, 1991.

2.1 Some Ecological Examples

1. Spread of muskrats in the Netherlands

2. Invasion by Africanized honey bee

3. Infestations of honey bees by varroa mites

2.2 A Quick Contrast Between Deterministic and Stochastic Models

We consider the linear birth-death model where each individual gives birth at rate a_1 and dies at rate a_2. We let $X(t)$ be the number of individuals in the population at time t.

2.2.1 Deterministic Model

The differential equation for the deterministic model is

$$\frac{dX(t)}{dt} = (a_1 - a_2)X(t),$$

with solution

$$X(t) = X(0)e^{(a_1 - a_t)t}.$$

The deterministic model results in either exponential growth or exponential decay of the population.

2.2.2 Stochastic Model

For the stochastic model, we make assumptions concerning events in a small time interval of $(t, t+\Delta t)$ of length Δt. We suppose that each individual gives birth with probability $a_1\Delta t$ and dies with probability $a_2\Delta t$. This leads to the assumptions:

$$\begin{aligned} P(X(t+\Delta t) = x+1 | X(t) = x) &= a_1 x\Delta t + o(\Delta t) \\ P(X(t+\Delta t) = x-1 | X(t) = x) &= a_2 x\Delta t + o(\Delta t) \\ P(X(t+\Delta t) = x | X(t) = x) &= 1 - (a_1 + a_2)x\Delta t + o(\Delta t) \end{aligned}$$

We let $p_x(t) = P[X(t) = x]$. The above assumptions imply that

$$\begin{aligned} p_x(t+\Delta t) &= p_x(t)[1-(a_1+a_2)x\Delta t] + p_{x-1}(t)(x-1)a_1\Delta t \\ &\quad + p_{x+1}(t)(x+1)a_2\Delta t \end{aligned}$$

since $X(t) = x$ can be reached from $X(t) = x-1, x, x+1$ in a small time interval. Letting $\Delta t \to 0$, we obtain the system of differential equations, called the Kolmogorov forward equations, for $p_x(t)$:

$$\dot{p}_x(t) = a_1(x-1)p_{x-1}(t) - [(a_1+a_2)x]p_x(t) + a_2(x+1)p_{x+1}(t)$$

for $x > 0$ and

$$\dot{p}_0(t) = a_2 p_1(t)$$

The solution to these equations can be solved using standard differential equation techniques. We now focus on the stochastic aspects.

Since the individuals behave independently, we can view the population as comprising X_0 separate populations, each of size 1. When $X_0 = 1$, the population size $X(t)$ follows a geometric distribution with pmf

$$\begin{aligned} p_0(t) &= \alpha(t) \\ p_x(t) &= [1-\alpha(t)][1-\beta(t)][\beta(t)]^{x-1}, \quad x = 1, 2, \ldots \end{aligned}$$

where

$$\begin{aligned} \alpha(t) &= \frac{a_2(e^{(a_1-a_2)t}-1)}{a_1 e^{(a_1-a_2)t}-a_2} \\ \beta(t) &= \frac{a_1(e^{(a_1-a_2)t}-1)}{a_1 e^{(a_1-a_2)t}-a_2} \end{aligned}$$

Standard results for the geometric distribution yield the mean and variance functions for the population size:

$$\begin{aligned} E[X(t)] &= X_0 e^{(a_1-a_2)t} \\ V[X(t)] &= X_0 \left[\frac{a_1+a_2}{a_1-a_2}\right] e^{(a_1-a_2)t}(e^{(a_1-a_2)t} - 1) \end{aligned}$$

- The mean function agrees with the deterministic model, however the variance function depends on the magnitudes of the birth and death rates as well as on their difference.

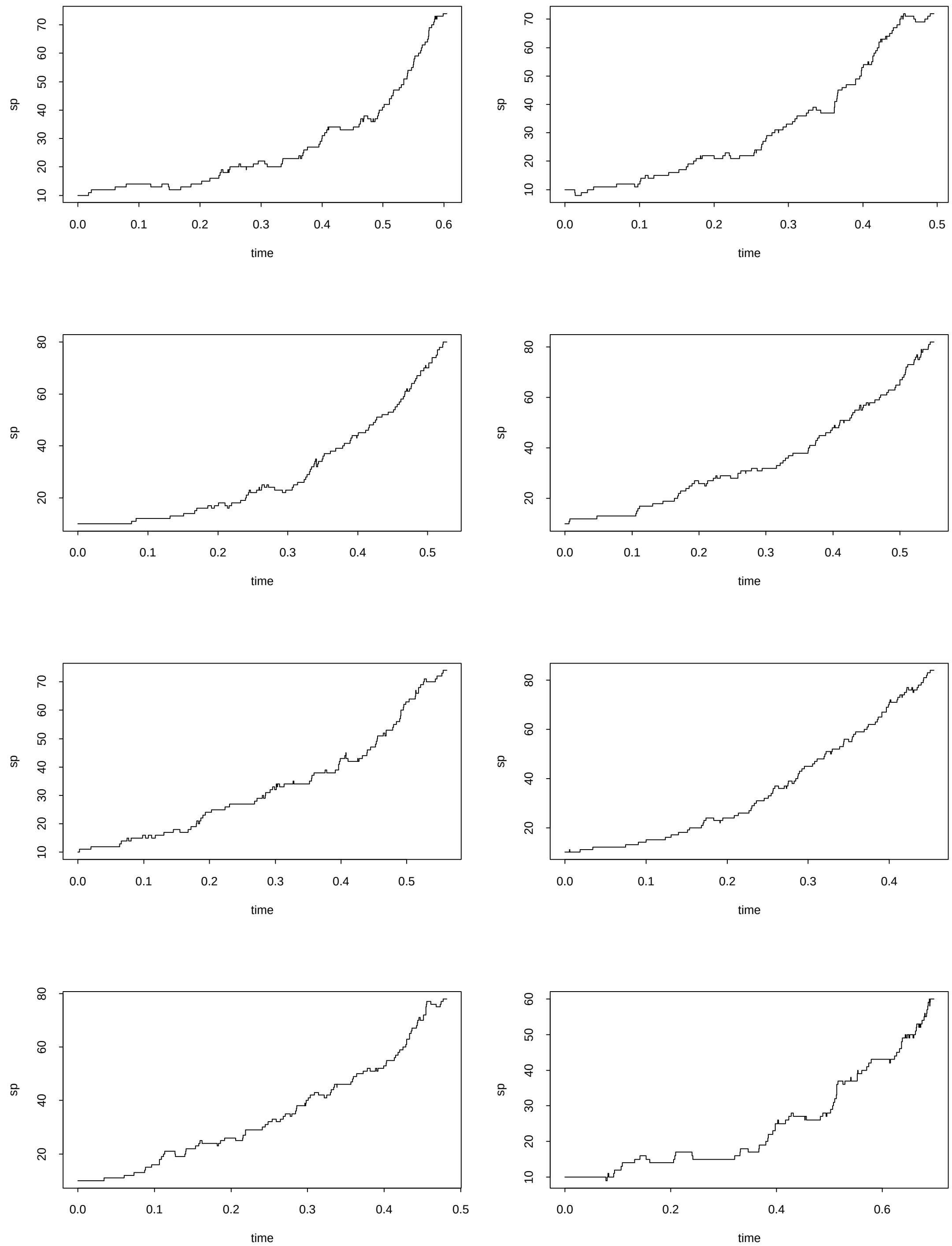
- For the deterministic model, there is exponential growth if the birth rate exceeds the death rate. However, for the stochastic model, there is a probability of extinction even in this case:

$$p_0(t) = \alpha(t)^{X_0}$$

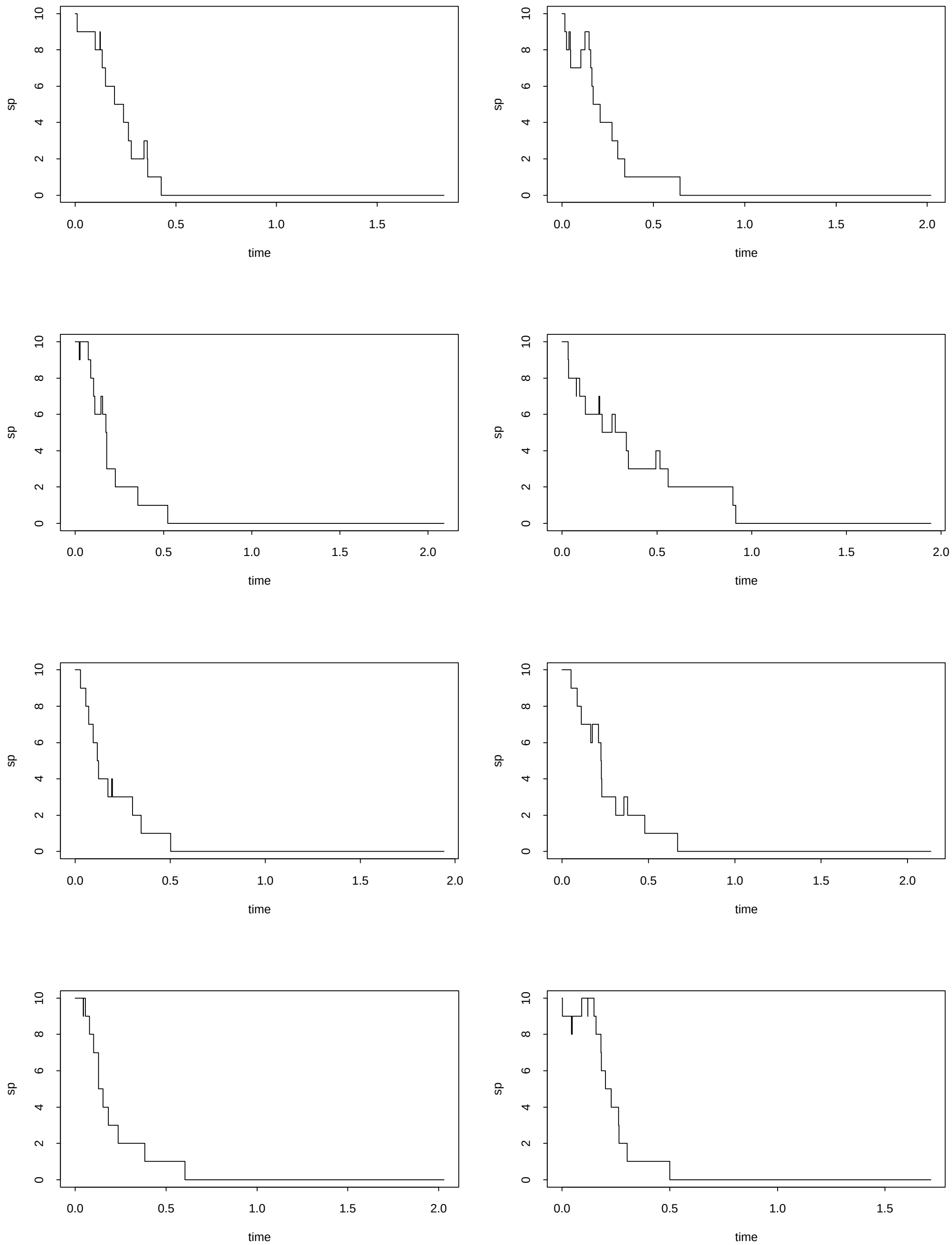
- We now look at the probability of ultimate extinction:
  - If $a_1 < a_2, p_0(\infty) = 1$
  - If $a_1 > a_2, p_0(\infty) = (a_2/a_1)^{X_0}$.
  - If $a_1 = a_2, p_0(t) = [a_2 t/(1 + a_2 t)]^{X_0} \to 1$ as $t \to \infty$.

- It is easy to simulate the stochastic model. By examining sample paths, one can see how single realizations of a process can give misleading results.
  - One can show that the time between events is exponentially distributed with parameter $R(X) = (a_1 + a_2)X(t)$.
  - A birth occurs at this time with probability $a_1/(a_1 + b_1)$.
  - Otherwise, a death occurs.

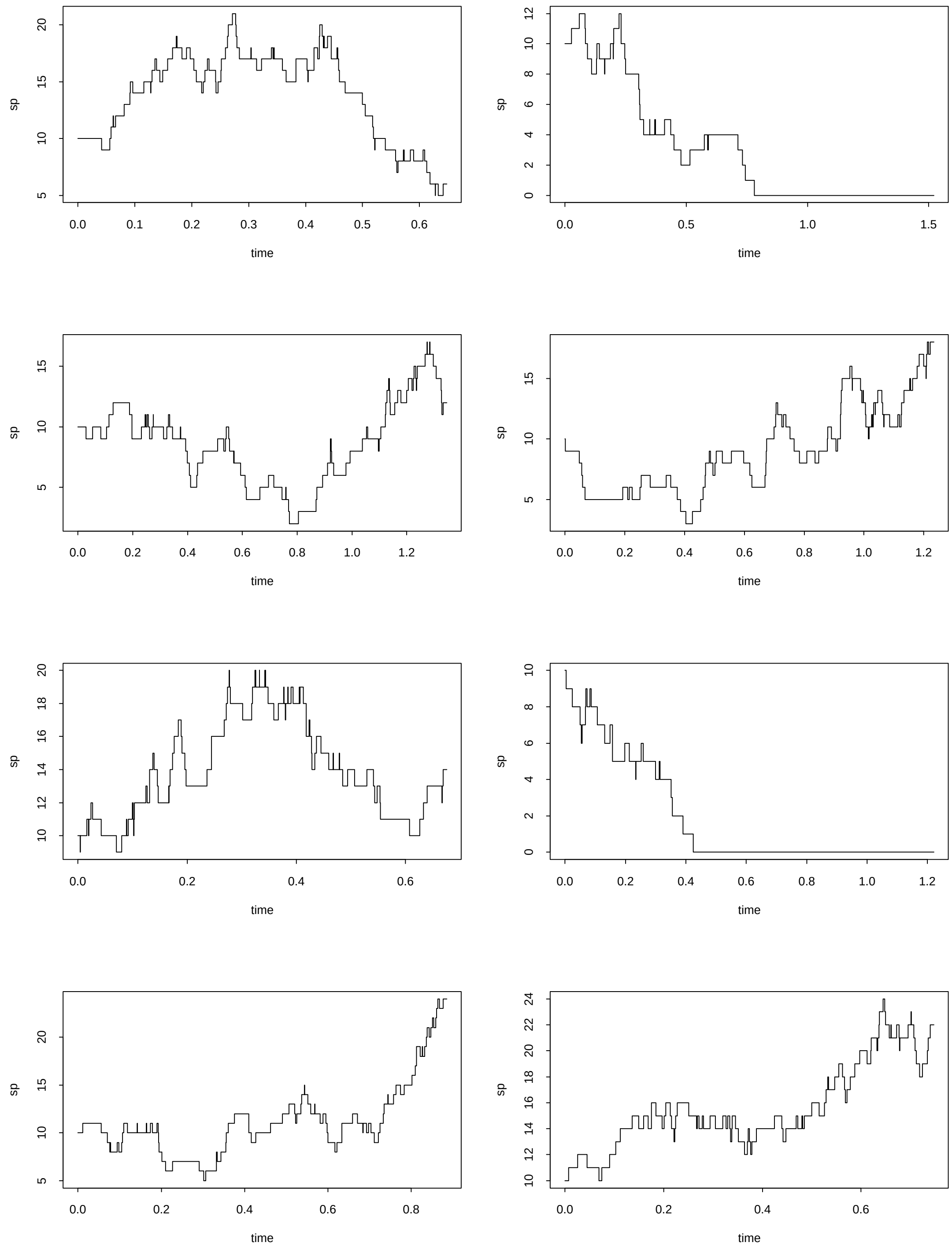
- Simulation with $a_1 = 5,\ a_2 = 1,\ X_0 = 10$



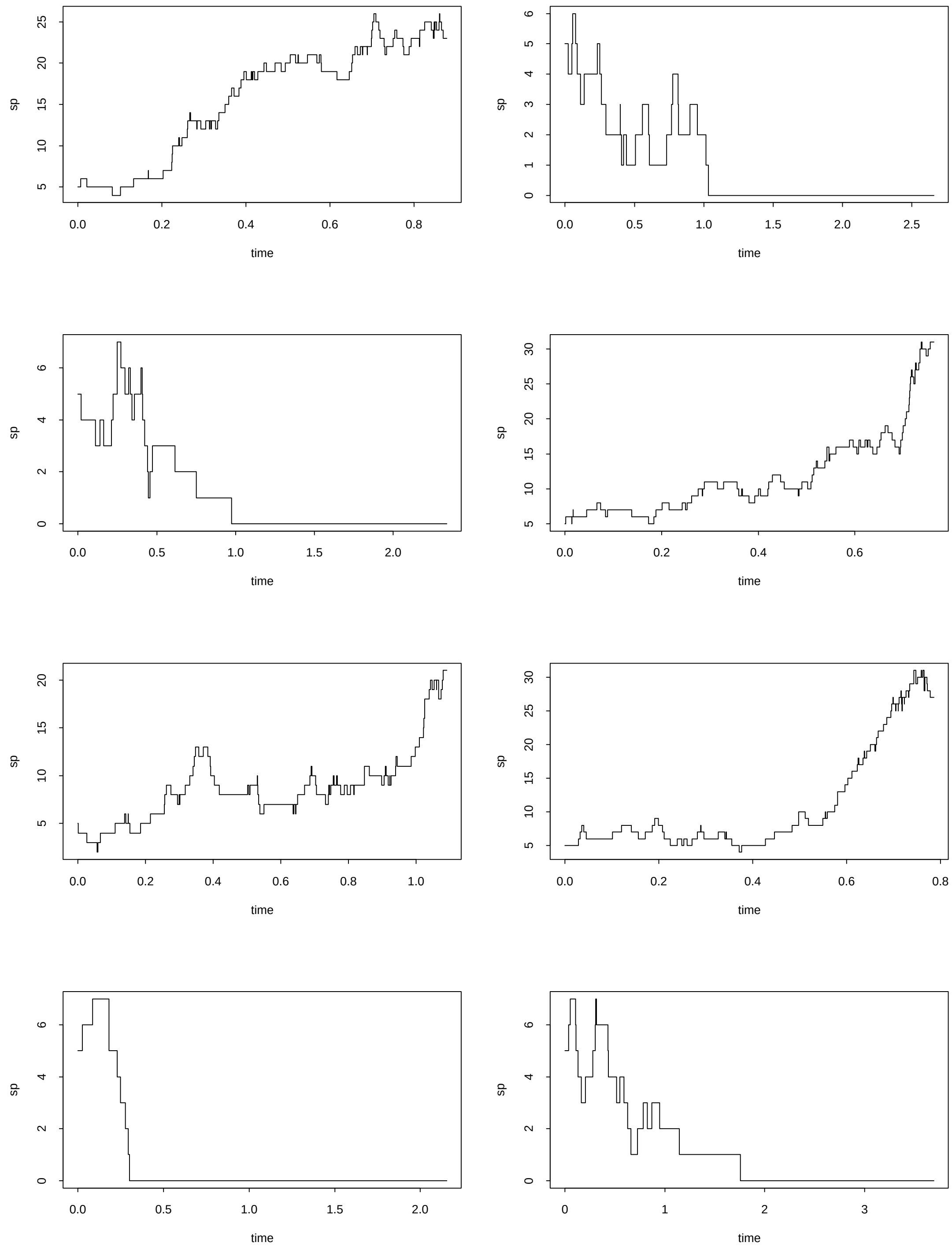
- Simulation with $a_1 = 1,\ a_2 = 5,\ X_0 = 10$



- Simulation with $a_1 = 5,\ a_2 = 5,\ X_0 = 10$



- Simulation with $a_1 = 5,\ a_2 = 4,\ X_0 = 5$



3 Basic Methods for Single Population Models

Basic notation:

- $X(t) =$ the random population size at time t
- $p_x(t) =$ Prob$[X(t) = x]$, the probability that the random population size equals x at time t
- $\boldsymbol{p}(t) = [p_0(t), p_1(t), \ldots, p_x(t), \ldots]$, the probability distribution of $X(t)$

Goal: Solve for $\boldsymbol{p}(t)$ for any $t > 0$ based on simple assumptions concerning $X(t)$.

Once we know $\boldsymbol{p}(t)$, we (in theory) know all the properties of $X(t)$.

Example: Immigration-Death Model

$X(t) =$ the number of insects in a field at a given time

Assume $X(0) = 0$.

1. $P\{X$ will increase by 1 unit due to immigration$\} = I\Delta t$
2. $P\{X$ will decrease by 1 unit due to death$\} = \mu_X \Delta t$ where the death rate is linear, $\mu_X = aX$.

We will show later that this results in $X(t)$ being a Poisson random variable with parameter

$$\lambda(t) = (1 - e^{-at})I/a.$$

The Corresponding Deterministic Model:

Letting the derivative of $X(t)$ be $\dot{X}(t)$, the model is

$$\dot{X}(t) = I - aX(t).$$

This has solution

$$X(t) = (1 - e^{-at})I/a$$

3.1 Moments of $X(t)$

Moments are means of powers of $X(t)$.

The mean or first moment of $X(t)$ is

$$\mu_1(t) = E[X(t)] = \sum_{x=0}^{\infty} x p_x(t)$$

The i^{th} moment of $X(t)$ is

$$\mu_i(t) = E[(X(t))^i] = \sum_{x=0}^{\infty} x^i p_x(t)$$

Special Case: A Poisson random variable X has probability mass function

$$p(x;\lambda) = P(X = x) = \frac{e^{-\lambda}\lambda^x}{x!} \quad , \quad x = 0, 1, 2, \ldots, \ \lambda > 0$$

$$\begin{aligned} E[X] &= \textstyle\sum_{x=0}^{\infty} x \frac{e^{-\lambda}\lambda^x}{x!} &&= \textstyle\sum_{x=1}^{\infty} x \frac{e^{-\lambda}\lambda^x}{x!} \\ &= \textstyle\sum_{x=1}^{\infty} \frac{x}{x} \frac{e^{-\lambda}\lambda\lambda^{x-1}}{(x-1)!} &&= \lambda \textstyle\sum_{x=1}^{\infty} \frac{e^{-\lambda}\lambda^{x-1}}{(x-1)!} \\ &= \lambda \textstyle\sum_{y=0}^{\infty} \frac{e^{-\lambda}\lambda^y}{y!} &&= \lambda \end{aligned}$$

3.2 Simulation of the Stochastic Process

- It is easy to simulate these basic stochastic processes by using a random number generator to obtain random variables representing the times between arrivals and the times between deaths.

- The times between arrivals will have an exponential distribution with parameter I (mean $1/I$).

- The times between deaths will have an exponential distribution with parameter $\mu_X = aX(t)$.

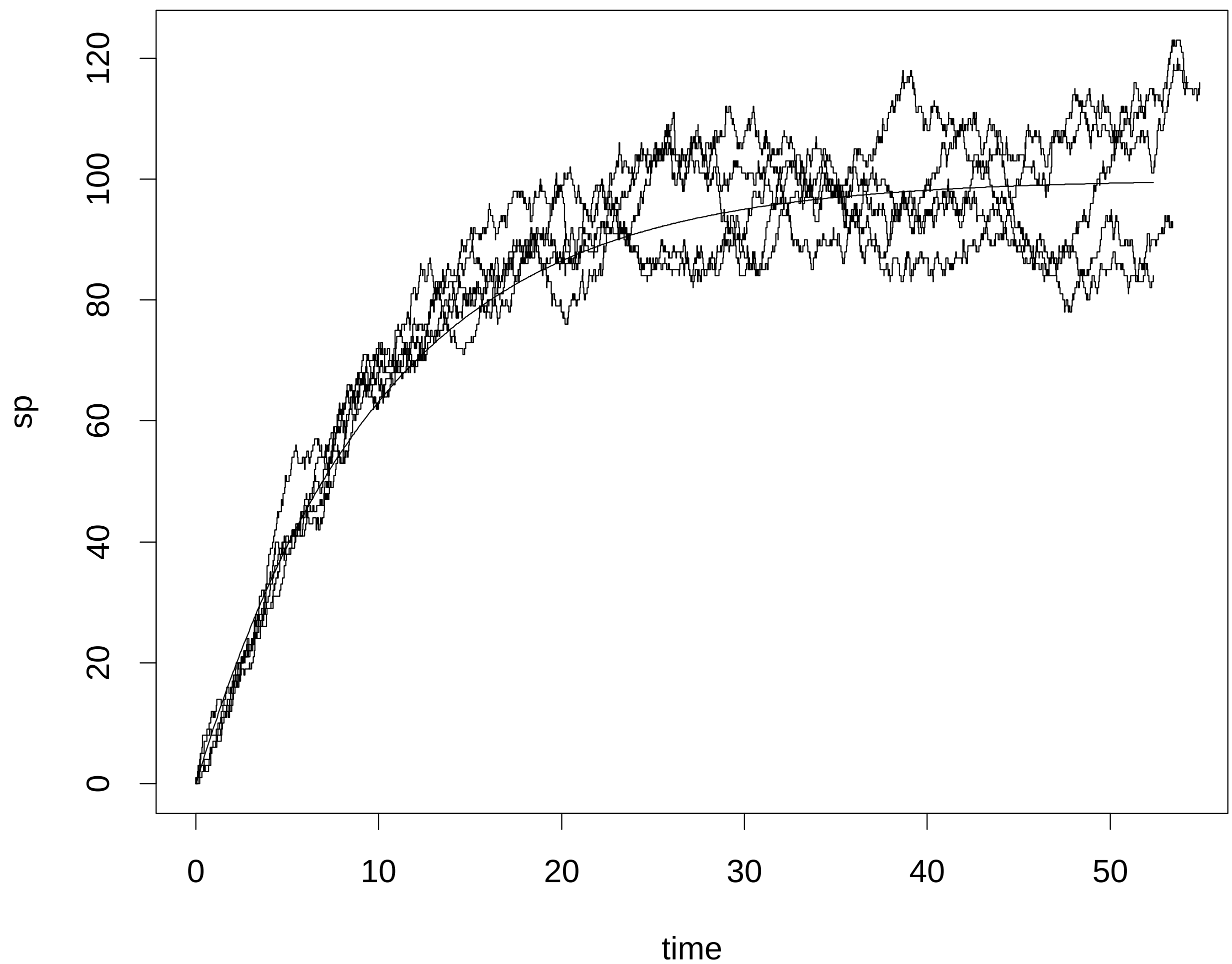
- An algorithm for simulation of the process can be summarized as follows:

  1. Set $X(0) = 0$.
  2. Generate t_1 from an $\exp(I)$ distribution. Set $X(t_1) = 1$.
  3. If $X(t_i) = 0$, generate t_I from an $\exp(I)$ distribution. Set $t_i = t_{i-1} + t_I$ and $X(t_i) = 1$.
  4. Otherwise, generate t_I from an $\exp(I)$ distribution and t_D from $\exp(aX(t_i))$ distribution.
     - If $t_I < t_D$ set $t_i = t_{i-1} + t_I$ and $X(t_i) = X(t_{i-1}) + 1$.
     - If $t_I > t_D$ set $t_i = t_{i-1} + t_D$ and $X(t_i) = X(t_{i-1}) - 1$.
  5. Return to Step 3.

A simpler algorithm is the following:

1. Generate t^* from an $\exp(I + aX(t))$ distribution. Set $t_i = t_{i-1} + t^*$.
2. Generate U from a Uniform$(0, 1)$ distribution.
   - If $U < I/(I + aX(t))$, set $X(t_i) = X(t_{i-1}) + 1$.
   - Otherwise, set $X(t_i) = X(t_{i-1}) - 1$.

Example: Let $X(t)$ denote the number of corn earworms in a field at time t. The immigration rate is $I = 10$ insects per day and the departure (death) rate is $\mu_X = 0.1X$ per day. The process was generated four times using these parameters. The solid line is the mean function (or deterministic curve).



3.3 Kolmogorov Differential Equations for Probability Functions

A standard approach to solving for $\boldsymbol{p}(t)$ is using the Kolmogorov differential equations. This approach makes use of assumptions concerning the probabilities of various events occuring in a small interval of length Δt.

Suppose that $X(t+\Delta t) = x$. There are the following possibilities for the way this could occur starting at time t:

1. $X(t) = x$ with no change from t to $t + \Delta t$
2. $X(t) = x - 1$ with only a single immigration in Δt
3. $X(t) = x + 1$ with only a single death in Δt
4. Other possibilities involving two or more independent changes in Δt

These assumptions yield the expression for the probability that $X(t+\Delta t) = x$:

$$\begin{aligned}
p_x(t+\Delta t) = \quad & P[X(t+\Delta t)=x|X(t)=x]P[X(t)=x] \\
& + P[X(t+\Delta t)=x|X(t)=x+1]P[X(t)=x+1] \\
& + P[X(t+\Delta t)=x|X(t)=x-1]P[X(t)=x-1] \\
& + P[X(t+\Delta t)=x|X(t)\neq x, x-1, x+1] \\
& \quad \times P[X(t)\neq x, x-1, x+1] \\
= \quad & p_x(t)[1 - I\Delta t - ax\Delta t] + p_{x+1}(t)[a(x+1)\Delta t] \\
& + p_{x-1}(t)[I\Delta t] + o(\Delta t)
\end{aligned}$$

We subtract $p_x(t)$, divide by Δt, and then take the limit as $\Delta t \to 0$:

$$\dot{p}_x(t) = I p_{x-1}(t) - (I + ax) p_x(t) + a(x+1) p_{x+1}(t) \text{ for } x > 0$$

and

$$\dot{p}_0(t) = -I p_0(t) + a p_1(t)$$

The solution to this set of differential equations is the Poisson distribution with mean $\lambda(t) = (1 - e^{-at}) I/a$.

In matrix form, the Kolmogorov equations can be written in the form

$$\dot{\boldsymbol{p}}(t) = \boldsymbol{p}(t)\boldsymbol{R},$$

where $\boldsymbol{R}$ is a tridiagonal matrix. For our immigration-death model, the $\boldsymbol{R}$ matrix is infinite with elements for $i, j \geq 0$

$$r_{i,j} = \begin{cases} r_{i,i+1} = I & \\ r_{i,i-1} = ai & \\ r_{i,i} = -(ai + I) & \\ r_{i,j} = 0 & \text{for } |i - j| > 1. \end{cases}$$

3.4 Generating Functions

Generating functions are useful tools for finding the population size distribution and moments of this distribution.

Suppose that $X(t)$ is a discrete random variable with probability mass function $p_x(t),\ x = 0, 1, 2, \ldots$.

- The *probability generating function* (pgf) is defined as

  $$P(s,t) = \sum_{x=0}^{\infty} s^x p_x(t).$$

  Probabilities can be obtained by differentiating $P(s,t)$.

- The *moment generating function* (mgf) of $X(t)$ is defined as

  $$M(\theta,t) = \sum_{x=0}^{\infty} e^{\theta x} p_x(t).$$

  One can show that

  $$M(\theta,t) = \sum_{i=0}^{\infty} \mu_i(t)\theta^i / i!$$

  Thus, one can find the i^{th} moment of $X(t)$ by differentiating the mgf with respect to θ.

- The *cumulant generating function* (cgf) is

$$K(\theta, t) = \log(M(\theta, t))$$

with power series expansion

$$K(\theta, t) = \sum_{i=0}^{\infty} \kappa_i(t)\theta^i / i!$$

The quantity $\kappa_i(t)$ is called the i^{th} *cumulant* of $X(t)$. Cumulants can be obtain by differentiating the cgf.

The cumulants are related to the moments:

$$\begin{aligned}
\kappa_1(t) &= E(X(t)) = \mu_1(t) \\
\kappa_2(t) &= E[(X(t) - \mu_1(t))^2] = V(X(t)) = \mu_2(t) - [\mu_1(t)]^2 \\
\kappa_3(t) &= E[(X(t) - \mu_1(t))^3] = \mu_3(t) - 3\mu_2(t)\mu_1(t) - 2\mu_1(t)^2 \\
\vdots &\quad \vdots
\end{aligned}$$

Example: The population size random variable has the Poisson distribution with parameter $\lambda(t)$.

The pmf is

$$p_x(t) = \frac{e^{-\lambda(t)}\lambda(t)^x}{x!} \qquad , \quad x = 0, 1, 2, \ldots$$

- The pgf is

$$P(s,t) = \sum_{x=0}^{\infty} s^x \frac{e^{-\lambda(t)}\lambda(t)^x}{x!} = e^{-\lambda(t)} \sum_{x=0}^{\infty} \frac{[s\lambda(t)]^x}{x!} = e^{(s-1)\lambda(t)}$$

- The mgf is

$$M(\theta,t) = P(e^\theta,t) = e^{(e^\theta-1)\lambda(t)}$$

- The cgf is

$$K(\theta,t) = \log(M(\theta,t)) = (e^\theta - 1)\lambda(t)$$

- The cumulants can be found by differentiation to be

$$\kappa_i(t) = \lambda(t), \text{ for all } i$$

3.5 PDEs for Cumulant Generating Functions

For many models it is more practical to form a system of PDEs for the generating functions rather than for the probabilities. We multiply the expression for $\dot{p}_x(t)$ by s^x and sum over x:

$$\sum s^x \dot{p}_x = I \sum s^x p_{x-1} - \sum (I+ax) s^x p_x + a \sum (x+1) s^x p_{x+1}$$

The left hand side is $\partial P(s,t)/\partial t$. Using the additional result that

$$\frac{\partial P(s,t)}{\partial s} = \sum x s^{x-1} p_x(t)$$

we obtain

$$\frac{\partial P(s,t)}{\partial t} = I(s-1)P(s,t) + a(1-s)\partial P(s,t)/\partial s$$

The initial condition corresponding to $X(0) = 0$ is $P(s,0) = 1$. The solution to this linear PDE is

$$P(s,t) = \exp\{(s-1)(1-e^{-at})I/a\}$$

The "random variable technique" in Bailey's classic book on stochastic processes enables one to directly write down the PDEs for the generating functions for birth-death-migration models.

Let the possible changes in population size $X(t)$ from t to $t+\Delta t$ be denoted as

$$P[X(t) \text{ changes by } j \text{ units}] = f_j(X)\Delta t + o(\Delta t)$$

For our immigration death model, the possible changes (or intensity functions) are

$$f_1 = I \text{ and } f_{-1} = ax$$

For intensity functions of the form

$$f(x) = \sum a_k x^k$$

we define the operator notation:

$$\begin{aligned} f\left(s\frac{\partial}{\partial s}\right)P &= \sum a_k s^k \frac{\partial^k P}{\partial s^k} \text{ and} \\ f\left(\frac{\partial}{\partial \theta}\right)M &= \sum a_k \frac{\partial^k M}{\partial \theta^k} \end{aligned}$$

Bailey provides the following operator equations for the pgf and mgf:

$$\begin{aligned} \frac{\partial P}{\partial t} &= \sum_{j\neq 0}(s^j - 1)\, f_j\left(s\frac{\partial}{\partial s}\right)P(s,t) \\ \frac{\partial M}{\partial t} &= \sum_{j\neq 0}(e^{j\theta} - 1)\, f_j\left(\frac{\partial}{\partial \theta}\right)M(\theta,t) \end{aligned}$$

Example: Immigration-Death Process

For our immigration death model, the possible changes (or intensity functions) are

$$f_1 = I \text{ and } f_{-1} = ax$$

Thus,

$$f_1\left(s\frac{\partial}{\partial s}\right)P(s,t) = Is^0\frac{\partial^0 P}{\partial s^0} = IP(s,t)$$
$$f_{-1}\left(s\frac{\partial}{\partial s}\right)P(s,t) = as\frac{\partial P}{\partial s}$$

Hence,

$$\frac{\partial P(s,t)}{\partial t} = I(s-1)P(s,t) + (s^{-1}-1)as\frac{\partial P(s,t)}{\partial s}$$

Also,

$$f_1\left(\frac{\partial}{\partial \theta}\right)M(\theta,t) = I\frac{\partial^0 M}{\partial \theta^0} = IM(\theta,t)$$
$$f_{-1}\left(\frac{\partial}{\partial \theta}\right)M(\theta,t) = a\frac{\partial M}{\partial \theta}$$

We end up with

$$\frac{\partial M}{\partial t} = I(e^{\theta}-1)M + a(e^{-\theta}-1)\frac{\partial M}{\partial \theta}.$$

With the boundary condition $M(\theta,0)=1$, the solution is

$$M(\theta,t) = \exp\{(e^{\theta}-1)(1-e^{-at})I/a\}$$

We can often find simpler PDEs for the cgf and use this to find ODEs for the cumulants:

$$K(\theta, t) = \log M(\theta, t).$$

Thus, for this model

$$\frac{\partial K}{\partial t} = I(e^{\theta} - 1) + a(e^{-\theta} - 1)\frac{\partial K}{\partial \theta}.$$

Using the series expansion of K and equating powers of θ, we obtain

$$\begin{aligned}
\dot{\kappa}_1(t) &= I - a\kappa_1(t) \\
\dot{\kappa}_2(t) &= I + a\kappa_1(t) - 2a\kappa_2(t) \\
\dot{\kappa}_3(t) &= I - a\kappa_1(t) + 3a\kappa_2(t) - 3a\kappa_3(t)
\end{aligned}$$

With the initial conditions $\kappa_1(0) = \kappa_2(0) = \kappa_3(0) = 0$, the solution is

$$\kappa_1(t) = \kappa_2(t) = \kappa_3(t) = (1 - e^{-at})I/a$$

This approach will prove useful for more complex models. We summarize it as follows:

1. Use model assumptions to formulate intensity functions f_j.
2. Use the operator equations to obtain the PDEs for the moment generating function.
3. Transform these to PDEs for the cumulant generating function.
4. Use a series expansion to obtain differential equations for the cumulants.
5. Solve the differential equations for the cumulants.

4 Some Linear One-Population Models

4.1 Linear Immigration-Death Models

We consider models for a population of size $X(t)$ with linear death rate

$$\mu_X = aX$$

and immigration rate I. We will relax the assumption on initial population size.

4.1.1 Deterministic Model

The deterministic model is

$$\dot{X}(t) = -aX + I.$$

The solution with initial value $X(0) = X_0$ is

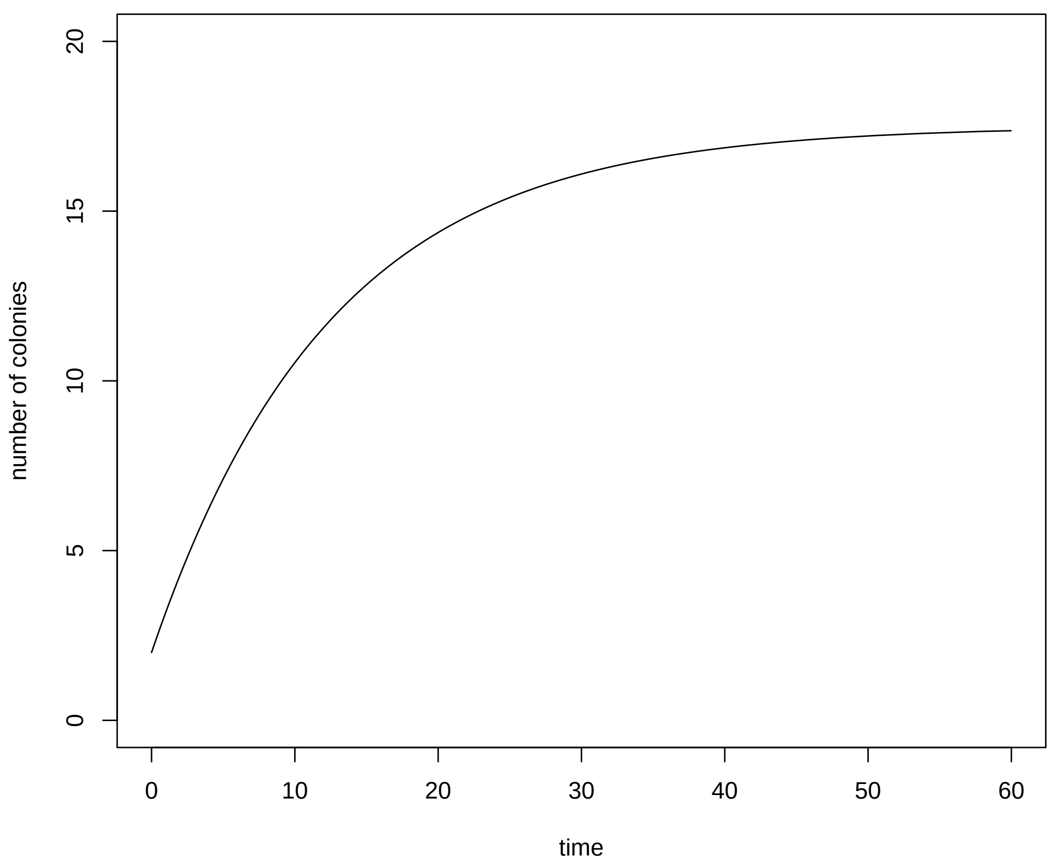
$$X(t) = X_0 e^{-at} + (1 - e^{-at})I/a.$$

Example: Let $X(t) =$ the number of Africanized honey bee (AHB) colonies at time t in a given region. Suppose the following assumed parameters:

$$\begin{aligned} I &= 1.4 \text{ colonies/time} \\ a &= 0.08 \text{ (time}^{-1}) \\ X(0) &= 2 \text{ colonies} \end{aligned}$$

The deterministic solution is

$$X(t) = 17.5 - 15.5e^{-0.08t}.$$



4.1.2 Stochastic Model

Earlier we found the PDE for the pgf

$$\frac{\partial P(s,t)}{\partial t} = I(s-1)P(s,t) + a(1-s)\frac{\partial P(s,t)}{\partial s}$$

The solution corresponding to $X(0) = X_0$ is

$$P(s,t) = [1 + (s-1)e^{-at}]^{X_0} \exp\{(s-1)(1-e^{-at})I/a\}$$

The pgf (or mgf) can be used to determine various properties of the probability distribution of $X(t)$.

- Consider the limiting distribution of the equilibrium population size X^* as $t \to \infty$. Since $a > 0$, the pgf of X^* is

  $$P(s,\infty) = \exp\{(s-1)I/a\}.$$

  This is the pgf of the Poisson distribution with parameter $\lambda = I/a$. The limiting distribution is independent of the initial population size, X_0.

- Note that the pgf is the product of two factors.
  - The first factor is the pgf of a binomial distribution with $n = X_0$ and $p = e^{-at}$.
  - The second factor is the pgf of a Poisson distribution with parameter $\lambda = (1 - e^{-at})I/a$.
- This implies that we can write

$$X(t) = X_1(t) + X_2(t)$$

  where $X_1(t)$ and $X_2(t)$ are independent random variables with the above binomial and Poisson distributions, respectively.

- The moment generating function is

$$M(\theta, t) = P(e^\theta, t)$$

  The cumulant generating function then is

$$K(\theta, t) = (e^\theta - 1)(1 - e^{-at})I/a + X_0 \log[1 + (e^\theta - 1)e^{-at}]$$

  The first three cumulants are

$$\begin{aligned}
\mu(t) &= X_0 e^{-at} + (1 - e^{-at})I/a \\
\sigma^2(t) &= \mu(t) - X_0 e^{-2at} \\
\kappa_3(t) &= \sigma^2(t) - 2X_0 e^{-2at}(1 - e^{-at})
\end{aligned}$$

4.1.3 Application to the AHB Population Dynamics

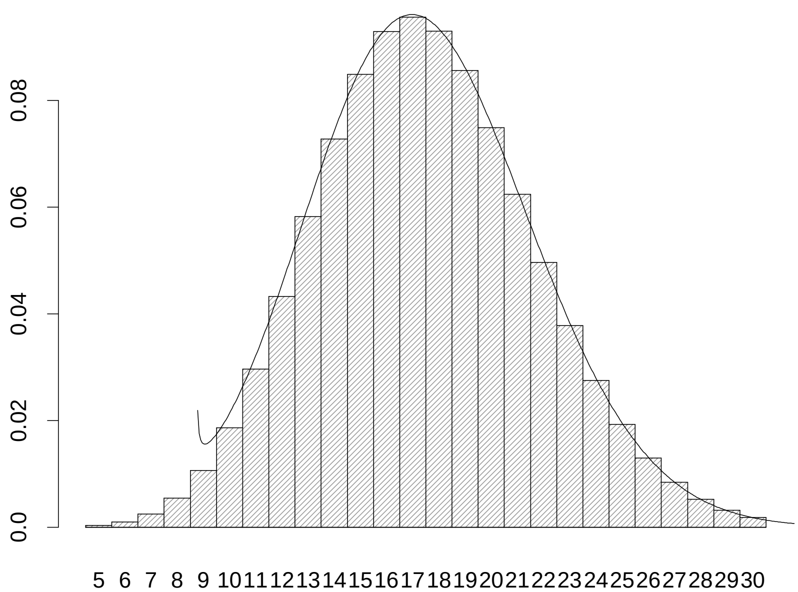
We return to the AHB population dynamics example with

$$\begin{aligned} I &= 1.4 \text{ colonies/time} \\ a &= 0.08 \text{ (time}^{-1}) \\ X(0) &= 2 \text{ colonies} \end{aligned}$$

The deterministic solution is

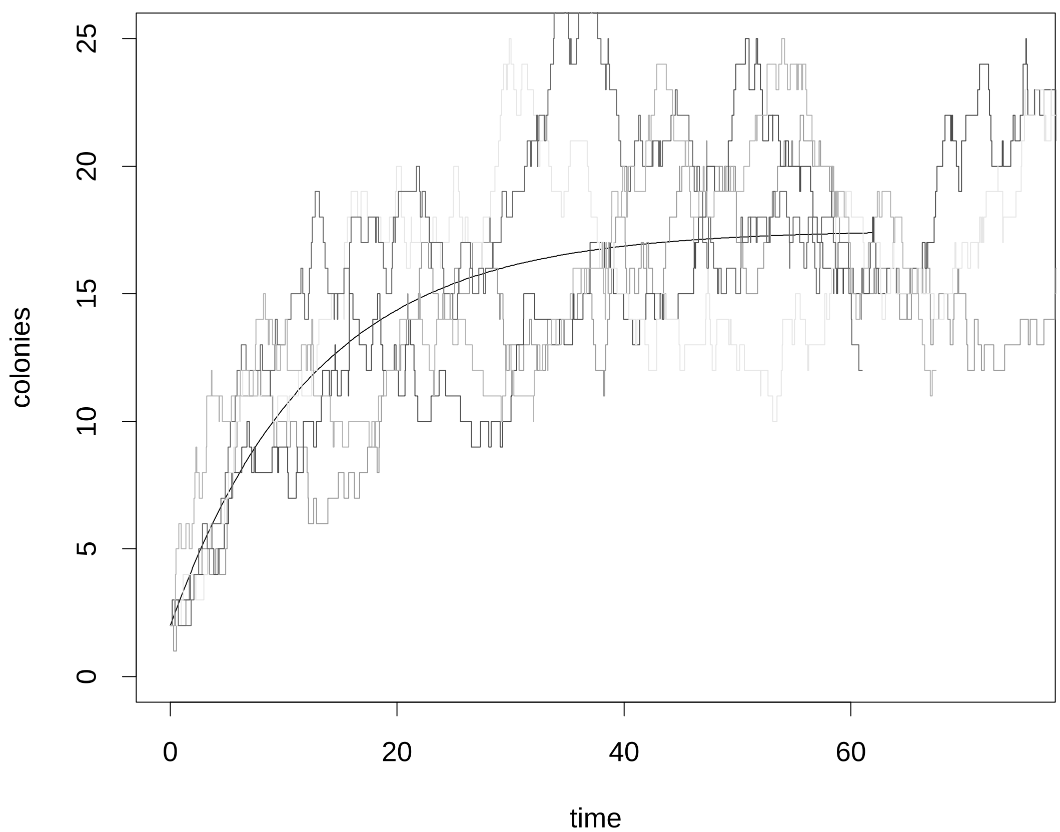
$$X(t) = 17.5 - 15.5e^{-0.08t}.$$

- The equilibrium solution is $X^* = 17.5$. For the stochastic model, the equilibrium solution X^* is now a Poisson random variable with parameter $I/a = 17.5$. The probability distribution and its saddlepoint approximation appear in the figure:

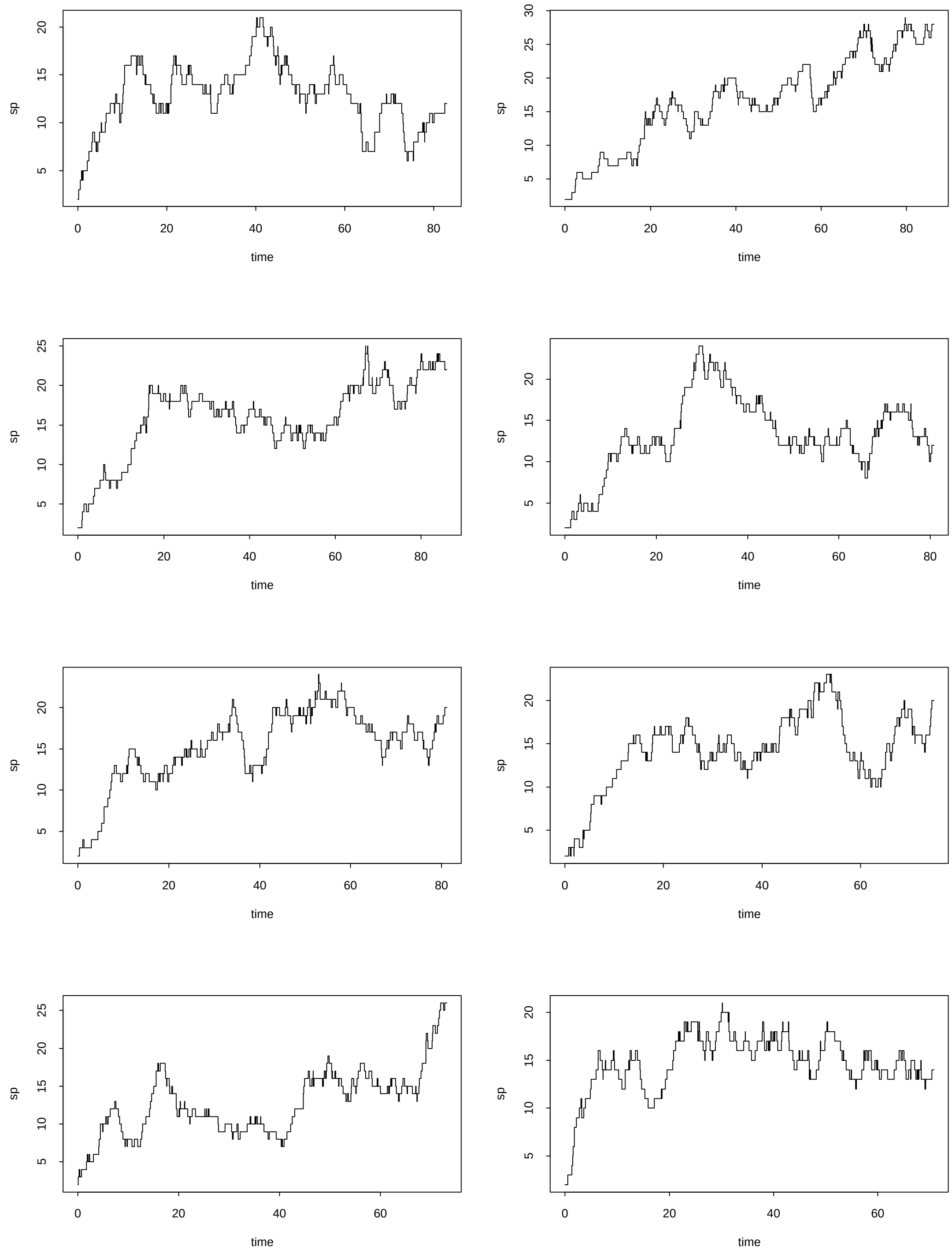


- The transient probability distributions are also of interest. They could be obtained directly from the pgf or mgf. To illustrate the variation in the AHB model, we will simulate the process several times using the assumed parameters. Notice the large amount of variation about the mean function.

Simulations of AHB Population Dynamics



- Several more sample paths with the same parameter values:



4.2 Linear Birth-Immigration-Death Models

We now consider a process that has a linear birth rate in addition to the linear death rate:

$$\lambda_X = a_1 X \text{ and } \mu_X = a_2 X$$

The immigration rate is assumed to equal I.

4.2.1 Solution to the Deterministic Model

The deterministic model can be written as

$$\dot{X}(t) = aX(t) + I \text{ where } a = a_1 - a_2.$$

The solution is

$$X(t) = X_0 e^{at} + (e^{at} - 1)I/a.$$

If $a < 0$, the equilibrium value is $-I/a$.

4.2.2 Probability Distributions for the Stochastic Model

The Kolmogorov forward equations are

$$\dot{p}_x(t) = [I+a_1(x-1)]p_{x-1}(t) - [I+(a_1+a_2)x]p_x(t) + a_2(x+1)p_{x+1}(t)$$

for $x > 0$ and

$$\dot{p}_0(t) = -Ip_0(t) + a_2 p_1(t)$$

The $\boldsymbol{R}$ matrix is tridiagonal with elements

$$r_{i,j} = \begin{cases} r_{i,i+1} = I + ia_1 & \\ r_{i,i-1} = ia_2 & \\ r_{i,i} = -I - i(a_1 + a_2) & \\ r_{i,j} = 0 & \text{for } |i-j| > 1. \end{cases}$$

The equilibrium distribution can be derived from the Kolmogorov equations by setting $\dot{\boldsymbol{p}}(t) = \mathbf{0}$. Letting $\pi_i = p_i(\infty)$, we get

$$\begin{aligned} \pi_1 &= \pi_0(I/a_1) \\ \pi_2 &= \pi_0 I(I + a_1)/2a_2^2 \\ \vdots & \quad \vdots \\ \pi_i &= \pi_0(a_1/a_2)^i \tbinom{i-1+(I/a_1)}{i} \end{aligned}$$

If $a_1 < a_2$, we can solve for π_0 by summing and setting the sum equal to 1:

$$\pi_0 = (-a/a_2)^{i/a_1}$$

We find that the distribution of X^* is the negative binomial distribution with pmf

$$\pi_i = \binom{k-1+i}{i} p^k (1-p)^i$$

where $k = I/a_1$ and $p = -a/a_2$.

4.2.3 Generating Functions

The intensity functions are

$$f_1 = I + a_1 x \text{ and } f_{-1} = a_2 x.$$

The resulting PDE is

$$\frac{\partial P}{\partial t} = I(s-1)P(s,t) + [a_1 s(1-s) + a_2(1-s)\partial P(s,t)/\partial s.$$

The analytical solution is

$$P(s,t) = \frac{a^{I/a_1}\{a_2(e^{at}-1) - (a_2 e^{at} - a_1)s\}^{X_0}}{\{(a_1 e^{at} - a_2) - a_1 s(e^{at}-1)\}^{X_0 + I/a_1}}$$

It would be difficult to solve for the transition probabilities by successive differentiation. However,

$$p_0(t) = P(0,t) = a^{I/a_1}(a_2 e^{at} - a_2)^{X_0}(a_1 e^{at} - a_2)^{-X_0 - I/a_1}.$$

The cumulant generating function is given by

$$\frac{\partial K}{\partial t} = I(e^{\theta} - 1) + \left\{a_1(e^{-\theta} - 1) + a_2(e^{-\theta} - 1)\right\}\frac{\partial K}{\partial \theta}.$$

Using a series expansion, we obtain ODEs for the first three cumulants:

$$\begin{aligned}
\dot{\kappa}_1(t) &= I + a\kappa_1 \\
\dot{\kappa}_2(t) &= I + c\kappa_1 + 2a\kappa_2 \\
\dot{\kappa}_3(t) &= I + a\kappa_1 + 3c\kappa_2 + 3a\kappa_3
\end{aligned}$$

These can be solved recursively when $X(0) = X_0$:

$$\begin{aligned}
\kappa_1(t) &= X_0 e^{at} + (e^{at} - 1)I/a \\
\kappa_2(t) &= X_0 c e^{at}(e^{at} - 1)/a + I(e^{at} - 1)(a_1 e^{at} - a_2)/a^2 \\
\kappa_3(t) &= X_0 e^{at}\left[3c^2(e^{at} - 1)^2 + a^2(e^{2at} - 1)\right]/2a^2 \\
&\quad + \left[-2ca_2 + (3c^2 - a^2)e^{at} - 6a_1 c e^{2at} + 4a_1^2 e^{3at}\right]/2a^3
\end{aligned}$$

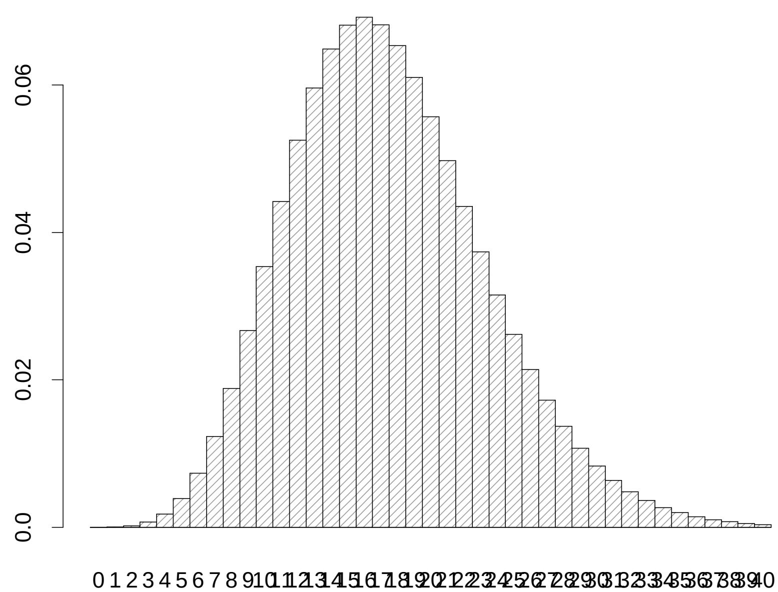
4.2.4 Application to AHB

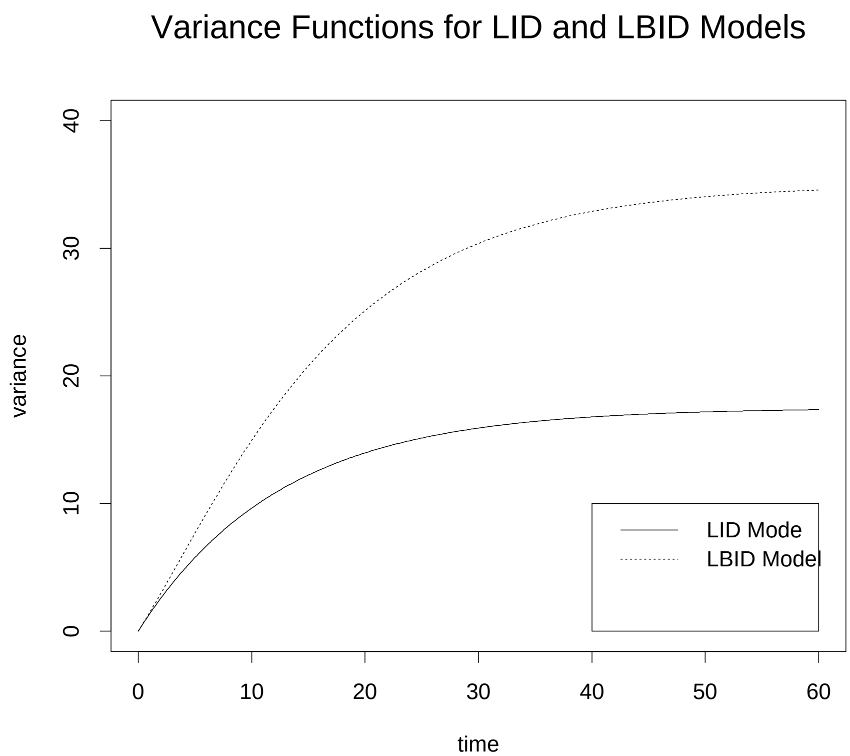
Consider the linear birth-death-immigration model with parameters;

$$\begin{aligned} I &= 1.4 & a_1 &= 0.08 \\ X(0) &= 2 & a_2 &= 0.16 \end{aligned}$$

Since the negative net growth rate is $a = -0.08$, the solution to the deterministic model is the same as the linear death-immigration process with the same death rate.

However, there is a large difference between the stochastic models in the two situations. We saw earlier that the equilibrium distribution of X^* was Poisson with mean 17.5 for the LID process. For the LBID model, the equilibrium distribution is negative binomial with $k = 17.5$ and $p = 0.5$. The LBID has much greater variance.



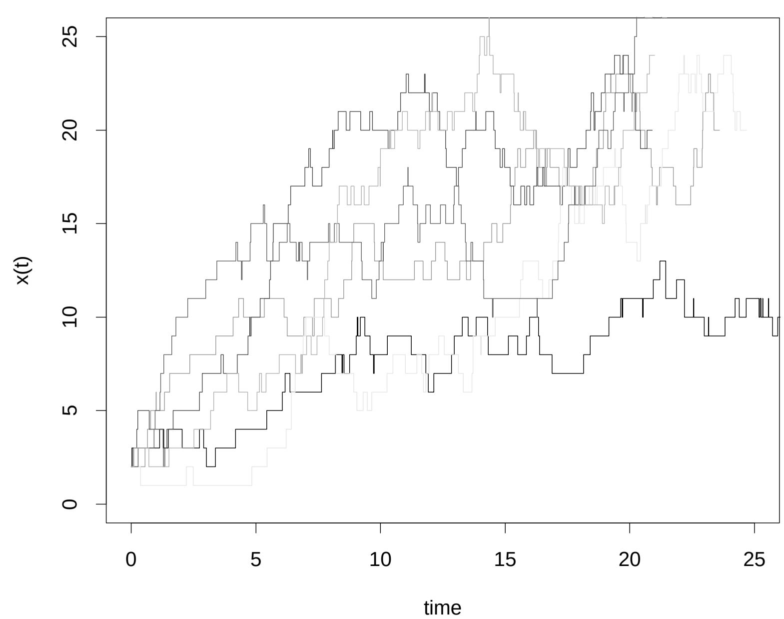


4.2.5 Simulation of the LBID Process

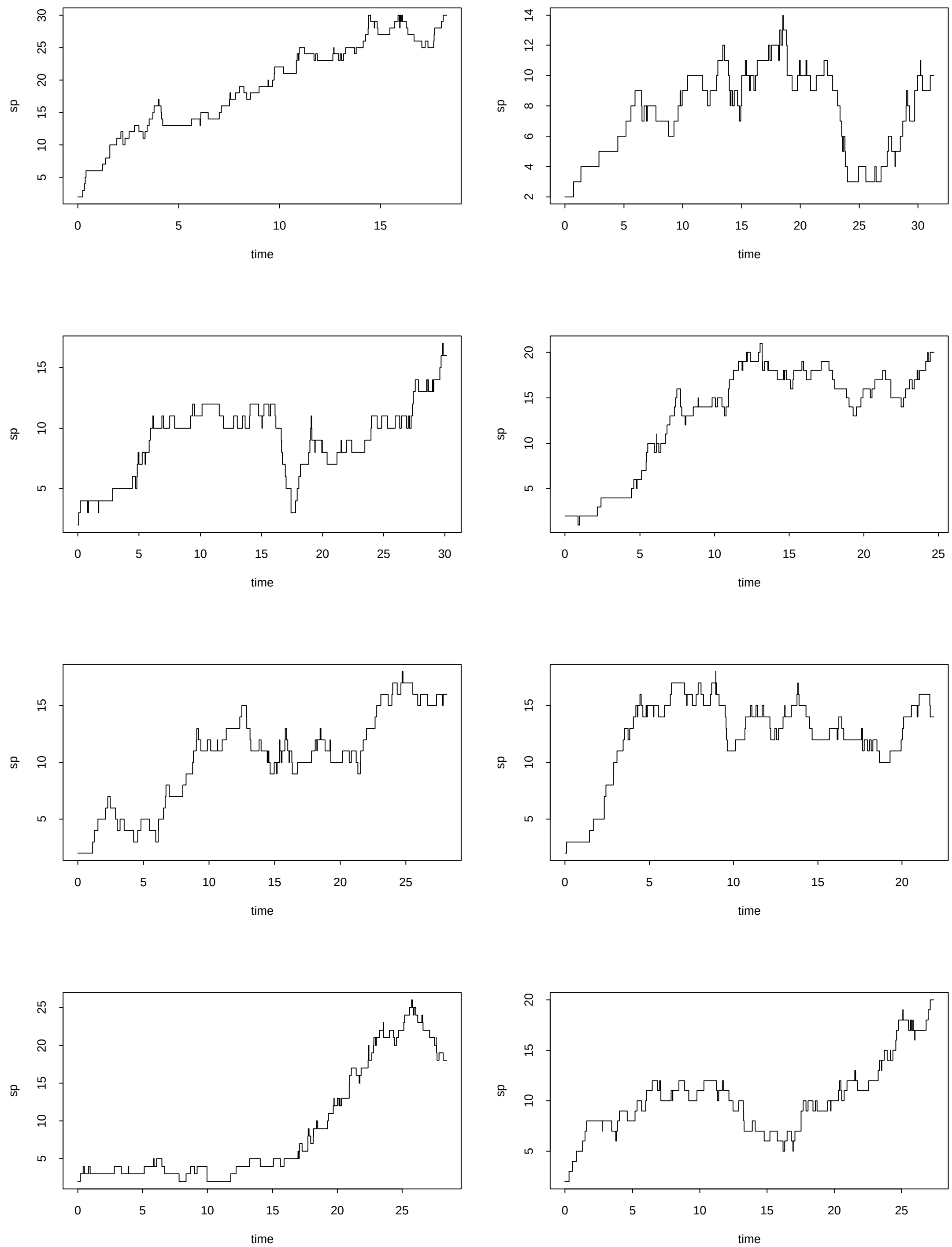
- The times between arrivals due to immigration will have an exponential distribution with parameter I (mean $1/I$).
- The times until the next death or birth will have an exponential distribution with parameter $\mu_X = aX(t)$ where $a = a_1 + a_2$.
- The next event will be a birth with probability $a1/a$ and a death with probability a_2/a.

- The algorithm for simulation the process can be summarized as follows:
  1. Set $X(0) = X_0$.
  2. If $X(t_i) = 0$, generate t_I from exp(I) distribution. Set $t_i = t_{i-1} + t_I$ and $X(t_i) = 1$.
  3. Otherwise, generate t_I from exp(I) distribution and t_D from exp($aX(t_i)$) distribution.
     (a) If $t_I < t_D$ set $t_i = t_{i-1} + t_I$ and $X(t_i) = X(t_{i-1}) + 1$.
     (b) If $t_I > t_D$, generate $U =$ a uniform(0,1) variable.
        i. If $U < a_1/a$ set $t_i = t_{i-1} + t_D$ and $X(t_i) = X(t_{i-1}) + 1$.
        ii. If $U > a_1/a$, set $t_i = t_{i-1} + t_D$ and $X(t_i) = X(t_{i-1}) - 1$.
  4. Return to Step 3.

Several Realizations of LBID Process



- Several More Realizations with the Same Parameter Values:



5 Some Nonlinear One-Population Models

5.1 Nonlinear Birth–Death Models

We now look at population models with nonlinear death rates. Consider the model with population rates

$$\lambda_X = \begin{cases} a_1 X - b_1 X^{s+1} & \text{for } X < (a_1/b_1)^{1/s} \\ 0 & \text{otherwise} \end{cases}$$

$$\mu_X = a_2 X + b_2 X^{s+1}$$

We call $a_1,\ a_2$ the intrinsic rates, and $b_1,\ b_2$ are the crowding coefficients that add density dependence to the model. We will look at the special case with $s = 1$ which leads to the logistic model.

5.1.1 Deterministic Model

We can write the deterministic model as

$$\dot{X}(t) = aX - bX^{s+1}$$

where $a = a1 - a_2$ and $b = b_1 - b_2$. This has solution

$$X(t) = \frac{K}{[1 + m\exp(-ast)]^{1/s}}$$

with

$$K = (a/b)^{1/s} \text{ and } m = (K/K_0)^s - 1$$

5.1.2 Probability Distributions for the Stochastic Model

Assume that $u = (a_1/b_1)^{1/s}$ is an integer. We can obtain the system of $u + 1$ Kolmogorov differential equations for the probabilities:

$$\begin{aligned}
\dot{p}_0(t) &= \mu_1 p_1(t) \\
\dot{p}_1(t) &= -(\lambda_1 + \mu_1) p_1(t) + \mu_2(t) p_2(t) \\
\dot{p}_x(t) &= \lambda_{x-1} p_{x-1}(t) - (\lambda_x + \mu_x) p_x(t) + \mu_{x+1} p_{x+1}(t), \\
& \qquad \text{for } x = 2, \ldots, u-1 \\
\dot{p}_u(t) &= \lambda_{u-1} p_{u-1}(t) - \mu_u p_u(t)
\end{aligned}$$

- Since there are only a finite number of equations, one can obtain numerical solutions.
- Since u is finite, a population size of 0 is an absorbing state and ultimate extinction is certain, i.e., $p_0(\infty) = 1$.
- A process is said to be *ecologically stable* if the extinction does not occur within a realizable time interval. A quantity of interest is the expected time until extinction, E_x.
- The quasi-equilibrium distribution is based on the idea that the population in equilibrium would not drift. The probabilities would satisfy the relationship

$$\mu_x p_x(t) = \lambda_{x-1} p_{x-1}(t) \text{ for } x = 2, \ldots, u$$

5.1.3 Generating Functions and Cumulants

The intensity functions are

$$\begin{aligned} f_1 &= a_1 x - b_1 x^{s+1} \\ f_{-1} &= a_2 x + b_2 x^{s+1} \end{aligned}$$

The PDE for the pgf has the form

$$\frac{\partial P}{\partial t} = (s-1)(a_1 s - a_2)\partial P(s,t)/\partial s + s(s-1)(b_1 s + b_2)\frac{\partial^2 P}{\partial s^2}.$$

This equation is analytically intractible. By substituting e^θ for s we get the PDE for the mgf, $M(\theta, t)$. Letting $K \log M$, we obtain the equation for the cgf:

$$\begin{aligned} \frac{\partial K}{\partial t} &= \left[(e^\theta - 1)a_1 + (e^{-\theta} - 1)a_2\right] \frac{\partial K}{\partial \theta} \\ &\quad + \left[(e^\theta - 1)(-b_1) + (e^{-\theta} - 1)b_2\right] \left[\frac{\partial^2 K}{\partial \theta^2} + \left(\frac{\partial K}{\partial \theta}\right)^2\right] \end{aligned}$$

Again, we can obtain differential equations for the cumulants. For $s = 1$, the first cumulant is

$$\dot{\kappa}_1(t) = (a - b\kappa_1)\kappa_1 - b\kappa_2$$

- The differential equation for the j^{th} cumulant depends on cumulants up to order $j + s$. This rules out finding exact solutions.

- One proposed approach is to set all cumulants above a certain order equal to zero and then solve the resulting finite system.

5.1.4 Application to AHB Population Dynamics

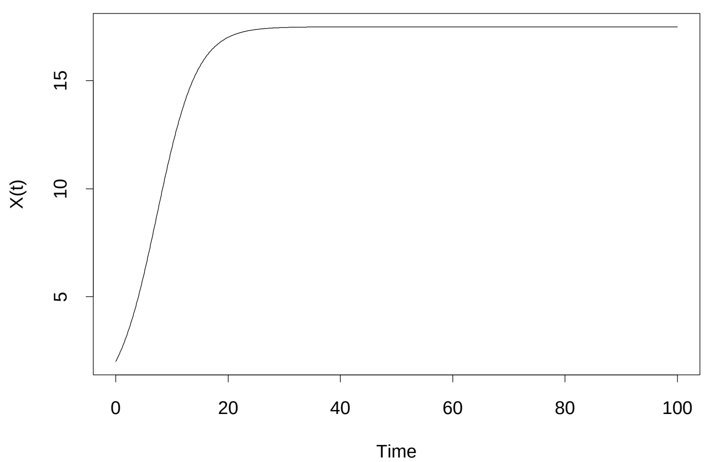
The nonlinear birth-death model with similar mean properties to the earlier models for AHB population dynamics has parameter values:

$$a_1 = 0.30 \qquad a_2 = 0.02$$
$$b_1 = 0.015 \qquad b_2 = 0.001.$$

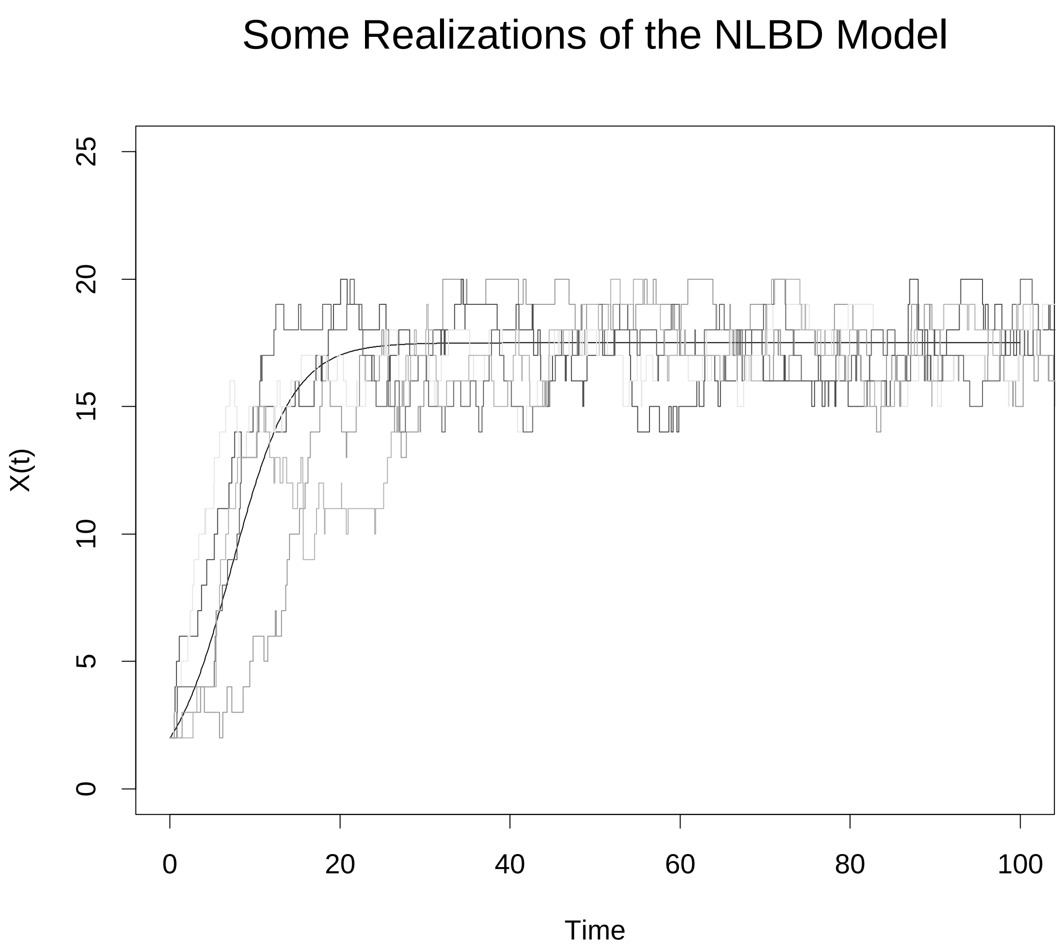
The solution to the deterministic model is

$$X(t) = \frac{17.5}{1 + 7.75e^{-0.28t}}.$$

Deterministic Solution of NLBD Model



- Simulation of the NLBD Model
  1. Compute the birth and death rates: $b(x) = a_1 x - b_1 x^2$ for $x < (a_1/b_1)$ and $d(x) = a_2 x + b_2 x^2$.
  2. Compute the time to the next event as exponential($b(x) + d(x)$) random variable.
  3. Generate a uniform(0,1) random variable U. If $U < b(x)/(b(x) + d(x))$, then the next event is a birth. Otherwise, it is a death.
- Some realizations of the NLBD model:



5.2 Nonlinear Birth-Immigration-Death Models

In addition to the assumptions of nonlinear birth and death rates, we assume that there is a constant immigration rate I.

5.2.1 Deterministic Model

The deterministic model is

$$\dot{X}(t) = I + aX - bX^{s+1}$$

where $a = a1 - a_2$ and $b = b_1 - b_2$. This has solution for $s = 1$:

$$X(t) = \left\{ a + \beta \left[\frac{1 - \delta e^{-\beta t}}{1 + \delta e^{-\beta t}} \right] \right\} / 2b$$

where

$$\begin{aligned} \beta &= (a^2 + 4bI)^{1/2} \\ \gamma &= (2bX_0 - a)/\beta \\ \delta &= (1 - \gamma)/(1 + \gamma) \end{aligned}$$

The carrying capacity is

$$K = (a + \beta)/2b$$

5.2.2 Simulation of the Stochastic Model

- The analysis of the stochastic model can be carried out by numerically solving the differential equations for the cumulants.
- However, the simulation of this model is still quite simple.
- Replace the birth rate in the simulation procedure for the NLBD model with $b(x) = I + a_1 x - b_1 x^2$. Steps 2 and 3 are the same as before. The one care that needs to be taken is to check whether the value of $X(t)$ is above the carrying capacity.

5.2.3 Application to AHB Population Dynamics

The parameter values for the NLBID model keeping the same carrying capacity as before are:

$$\begin{aligned} a_1 &= 0.30 & a_2 &= 0.02 \\ b_1 &= 0.012 & b_2 &= 0.004816. \\ I &= 0.25. \end{aligned}$$

The solution to the deterministic model with $X(0) = 2$ is

$$X(t) = 8.3254 + 0.1749 \left[\frac{1 - \delta e^{-\beta t}}{1 + \delta e^{-\beta t}} \right]$$

where $\delta = 5.4364$ and $\beta = 0.308571$.

5.2.4 Summary of Single Population Models

Properties	Model		
	LBID	NBD	NBID
Deterministic solution	easy	easy	difficult
Stochastic model	exact distribution exact cumulants	exact numerical solutions easy cumulant approximations true equilibrium dist. does not exist	approx. numerical solutions easy cumulant approx accurate for low I true equilibrium dist. exists
Advantages	widely used mechanistic basis	also widely used density-dependent growth	includes subtle but important immigration effect
Limitation	for initial period only	no immigration	challenging estimation for immigration

6 Models for Multiple Populations

6.1 Compartmental Models

Compartmental models are widely used in the modeling of drug flow. We will start by describing a deterministic model for the flow between various compartments. Define the following quantities:

- $X_i(t) =$ amount of substance in compartment i at time t
- $f_{ij}(t) =$ flow rate of substance from j to i at time t. Compartment 0 refers to the system exterior.
- $k_{ij}(t) = f_{ij}(t)/X_j(t) =$ proportional turnover rate from j to i at time t.
- $I_i(t) = f_{i0}(t)/X_j(t) =$ flow rate to i from the exterior
- $\mu_j(t) = f_{0j}(t)/X_j(t) =$ turnover rate from j to the exterior

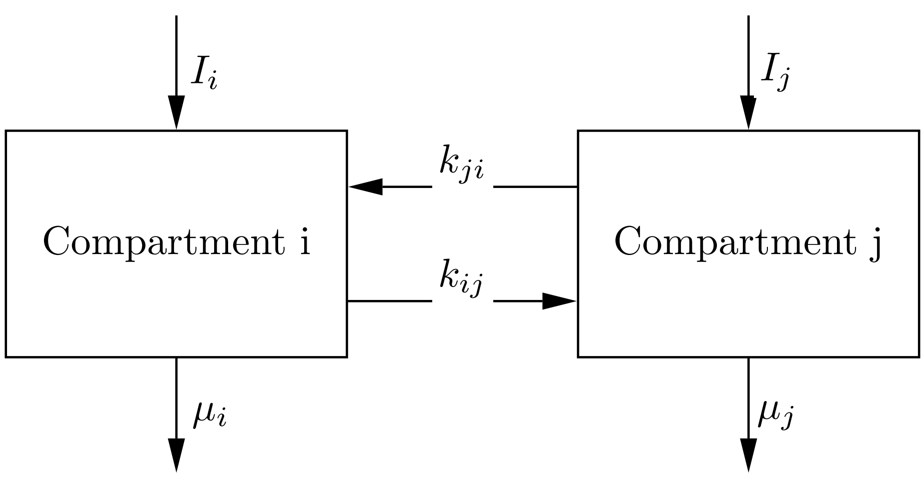


Figure 1: A General Compartmental Model

6.1.1 The Deterministic Compartment Model

We will assume for now that all the flow rates are constants. Then the deterministic model follows the system of differential equations

$$\begin{aligned}
\dot{X}_1(t) &= -(\mu_1 + k_{21} + \cdots + k_{n1})X_1 + k_{12}X_2 + \cdots + k_{1n}X_n + I_1 \\
&\vdots \\
\dot{X}_n(t) &= k_{n1}X_1 + \cdots + k_{n,n-1}X_{n-1} \\
&\quad - (\mu_n + k_{1n} + \cdots + k_{n-1,n})X_n + I_n
\end{aligned}$$

Define the following matrices:

$$\dot{\boldsymbol{X}}(t) = \begin{pmatrix} \dot{X}_1(t) \\ \vdots \\ \dot{X}_n(t) \end{pmatrix}, \; \boldsymbol{X}(t) = \begin{pmatrix} X_1(t) \\ \vdots \\ X_n(t) \end{pmatrix}$$

$$\boldsymbol{K} = \begin{pmatrix} k_{11} & \cdots & k_{1n} \\ \vdots & & \vdots \\ k_{n1} & \cdots & k_{nn} \end{pmatrix}, \; \boldsymbol{I} = \begin{pmatrix} I_1 \\ \vdots \\ I_n \end{pmatrix}$$

The deterministic model can be written as

$$\dot{\boldsymbol{X}}(t) = \boldsymbol{K}\boldsymbol{X}(t) + I$$

The formal solution is

$$\boldsymbol{X}(t) = \exp(\boldsymbol{K}t)\boldsymbol{X}(0) + \int \exp[\boldsymbol{K}(t-s)]\boldsymbol{I}ds$$

6.1.2 Stochastic Compartmental Models

Let

1. $P_{ij}(t), i, j = 1, \ldots, n$; denote the probability that a random animal starting in i at some arbitrary time, say $t = 0$, will be in j after elapsed time t,
2. $X_{ij}(t)$ be the random number of animals starting in i at $t = 0$ that are in j at time t,
3. $\boldsymbol{P}(t) = [P_{ij}(t)]$ and $\boldsymbol{X}(t) = [X_{ij}(t)]$ be matrices of probabilities and counts, respectively,
4. $\boldsymbol{E}[\boldsymbol{X}(t)]$ be the matrix of expected values of $\boldsymbol{X}$.
5. k_{ij}, for $i = 1, \ldots, n$, $j = 0, \ldots, n$, $i \neq j$, be a probability intensity coefficient defined by

   Prob$\{$a given animal in i transfers to j in $(t, t+\Delta t)|\boldsymbol{X}(t)\} = k_{ij}\Delta t + o(\Delta t)$

where 0 represents the system exterior,

6. $k_{ii} = -\sum_{j \neq i} k_{ij}$ be the total outflow coefficient,
7. $\boldsymbol{K} = (k_{ij})$ be the $n \times n$ coefficient matrix, and
8. $\lambda_1, \ldots, \lambda_n$ be the eigenvalues of $\boldsymbol{K}$.

Results I.

1. $\boldsymbol{P}(t) = \exp(\boldsymbol{K}t)$
2. If the λ's are distinct and real, the $P_{ij}(t)$ elements have form

$$P_{ij}(t) = \sum_{\ell} A_{ij\ell} \exp(\lambda_\ell t) \quad \text{for } i, j = 1, \ldots, n$$

   where the $A_{ij\ell}$ are constants.

3. $\boldsymbol{E}[\boldsymbol{X}(t)] = \boldsymbol{X}(0)\boldsymbol{P}(t)$

   where $\boldsymbol{X}(0)$ is a diagonal matrix of initial counts.

Result II.

If the λ's are distinct and complex, the $P_{ij}(t)$ have damped oscillations and may be written as

$$P_{ij}(t) = \sum_{\ell} A_{ij\ell} \exp(\lambda_\ell t) + \sum_{\ell} [B_{ij\ell} \sin(\theta_{ij\ell} t) + D_{ij\ell} \cos(\theta_{ij\ell} t)] \exp(\lambda_\ell t)$$

6.2 Basic Methods for Two-Population Models

Let $X_i(t),\ i = 1, 2$ be the random size of population i at time t. Our goal is to make certain simple assumptions about the population and then find the joint distribution of

$$\boldsymbol{X}(t) = [X_1(t), X_2(t)]'$$

We want to obtain the joint pmf of $\boldsymbol{X}$ as

$$p_{x_1,x_2} = P[X_1(t) = x_1, X_2(t) = x_2].$$

6.2.1 A Birth-Immigration-Death-Migration Model

We will assume the populations can change according to the following probabilities:

1. $P[X_i$ will increase by 1 due to immigration$] = I_i \Delta t$,
2. $P[X_i$ will increase by 1 due to birth$] = \lambda_i X_i \Delta t$,
3. $P[X_i$ will decrease by 1 due to death$] = \mu_i X_i \Delta t$,
4. $P[X_i$ will increase by 1 and X_j will decrease by 1 due to migration$] = k_{ij} X_j \Delta t$ for $i \neq j$,

How do we solve for the distribution of $(X_1(t), X_2(t))$?

That is, we wish to find the pmf of $(X_1(t), X_2(t))$:

$$p_{x_1,x_2}(t) = P[X_1(t) = x_1, X_2(t) = x_2]$$

Our approach will be similar to that for single-population models.

- Form the Kolmogorov equations for $p_{x_1,x_2}(t)$.

- Obtain the PDEs for the bivariate pgf:

$$P(s_1, s_2, t) = \sum_{x_1,x_2} s_1^{x_1} s_2^{x_2} p_{x_1,x_2}(t).$$

- Obtain differential equations for the joint cumulant functions.

- Obtain exact or numerical solutions for the cumulant functions.

6.3 Simulation of Predator-Prey Model

We earlier studied a deterministic predator-prey model where

- $X_1(t) =$ the number of prey at time t
- $X_2(t) =$ the number of predators at time t

Their relationship is driven by the system of differential equations:

$$\begin{aligned} \dot{X}_1 &= X_1(r_1 - b_1 X_2) \\ \dot{X}_2 &= X_2(-r_2 + b_2 X_1) \end{aligned}$$

We make the following assumptions to obtain the analogous stochastic model:

$$\begin{aligned} P[X_1(t+\Delta t) = x_1 + 1 | X_1(t) = x_1, X_2(t) = x_2] &= r_1 x_1 \Delta t \\ P[X_1(t+\Delta t) = x_1 - 1 | X_1(t) = x_1, X_2(t) = x_2] &= b_1 x_1 x_2 \Delta t \\ P[X_2(t+\Delta t) = x_1 + 1 | X_1(t) = x_1, X_2(t) = x_2] &= b_2 x_1 x_2 \Delta t \\ P[X_2(t+\Delta t) = x_1 - 1 | X_1(t) = x_1, X_2(t) = x_2] &= r_2 x_2 \Delta t \end{aligned}$$

This results in a Markov process with birth and death rates for the two populations given by the terms that are multiplied by Δt.

We use the following algorithm to generate a realization of the predator-prey process:

- Compute the birth and death rates:

$$\begin{aligned} B_1(x_1, x_2) &= r_1 x_1 \\ D_1(x_1, x_2) &= b_1 x_1 x_2 \\ B_2(x_1, x_2) &= b_2 x_1 x_2 \\ D_2(x_1, x_2) &= r_2 x_2 \end{aligned}$$

- Compute the intensity until the next event:
  $R = B_1 + D_1 + B_2 + D_2$

- Generate the time until the next event:

$$T^* = -ln(U_1)/R$$

- Decide which event occurs by generating U_2
  - If $U_2 < B_1/R$, then $X_1 = x_1 + 1$
  - If $B_1/R < U_2 < (B_1 + D_1)/R$, then $X_1 = x_1 - 1$
  - If $(B_1 + D_1)/R < U_2 < (B_1 + D_1 + B_2)/R$, then $X_2 = x_2 + 1$
  - Otherwise, $X_2 = x_2 + 1$.

6.4 Simulation of a Competition Model

We earlier studied a deterministic competition model where

- $X_1(t) =$ the number of individuals of species 1 at time t
- $X_2(t) =$ the number of individuals of species 2 at time t

Their relationship is driven by the system of differential equations:

$$\begin{aligned} \dot{X}_1 &= X_1(r_1 - s_{11}X_1 - s_{12}X_2) \\ \dot{X}_2 &= X_2(r_2 - s_{21}X_1 - s_{22}X_2) \end{aligned}$$

We make the following assumptions to obtain the analogous stochastic model:

$$P[X_1(t+\Delta t) = x_1 + 1 | X_1(t) = x_1, X_2(t) = x_2] = r_1 x_1 \Delta t$$
$$P[X_1(t+\Delta t) = x_1 - 1 | X_1(t) = x_1, X_2(t) = x_2] = x_1(s_{11}x_1 + s_{12}x_2)\Delta t$$
$$P[X_2(t+\Delta t) = x_1 + 1 | X_1(t) = x_1, X_2(t) = x_2] = r_2 x_2 \Delta t$$
$$P[X_2(t+\Delta t) = x_1 - 1 | X_1(t) = x_1, X_2(t) = x_2] = x_2(s_{21}x_1 + s_{22}x_2)\Delta t$$

This results in a Markov process with birth and death rates for the two populations given by the terms that are multiplied by Δt.

We use the following algorithm to generate a realization of the two-species competition process:

- Compute the birth and death rates:

$$\begin{aligned} B_1(x_1,x_2) &= r_1x_1 \\ D_1(x_1,x_2) &= x_1(s_{11}x_1+s_{12}x_2) \\ B_2(x_1,x_2) &= r_2x_2 \\ D_2(x_1,x_2) &= x_2(s_{21}x_1+s_{22}x_2) \end{aligned}$$

- Compute the intensity until the next event:
  $R = B_1 + D_1 + B_2 + D_2$

- Generate the time until the next event:

$$T^* = -ln(U_1)/R$$

- Decide which event occurs by generating U_2
  - If $U_2 < B_1/R$, then $X_1 = x_1 + 1$
  - If $B_1/R < U_2 < (B_1 + D_1)/R$, then $X_1 = x_1 - 1$
  - If $(B_1 + D_1)/R < U_2 < (B_1 + D_1 + B_2)/R$, then $X_2 = x_2 + 1$
  - Otherwise, $X_2 = x_2 + 1$.

