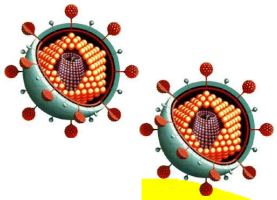
Chapter 6: Branching Processes: The Theory of Reproduction






Royalty

Viruses

Aphids

DNA

Although the early development of Probability Theory was motivated by problems in gambling, probabilists soon realised that, if they were to continue as a breed, they must also study


Reproduction is a complicated business, but considerable insights into population growth can be gained from simplified models. The **Branching Process** is a simple but elegant model of population growth. It is also called the **Galton-Watson Process,** because some of the early theoretical results about the process derive from a correspondence between Sir Francis Galton and the Reverend Henry William Watson in 1873. Francis Galton was a cousin of Charles Darwin. In later life, he developed some less elegant ideas about reproduction — namely eugenics, or selective breeding of humans. Luckily he is better remembered for branching processes.

6.1 Branching Processes

Consider some sort of ***population*** consisting of reproducing individuals.

Examples: living things (animals, plants, bacteria, royal families);
diseases; computer viruses;
rumours, gossip, lies (one lie always leads to another!)

Start conditions: start at time $n=0$ with a single individual.

Each individual: lives for 1 unit of time. At time $n=1$, it produces a family of offspring, and immediately dies.

How many offspring? Could be 0, 1, 2, ... This is the family size, Y. "Y" stands for "number of Young" for a single family.

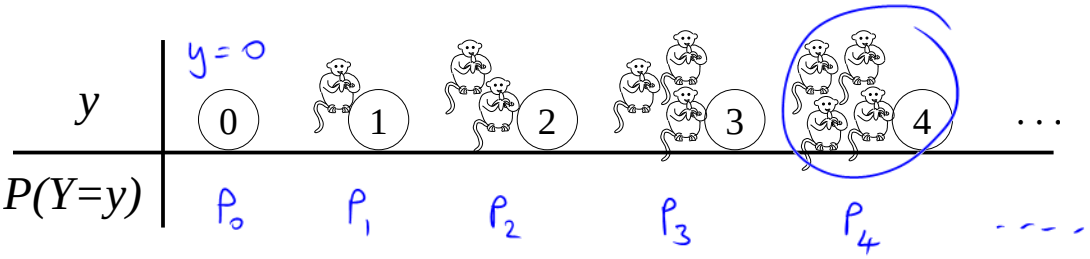
Each offspring: lives for 1 unit of time. At time $n=2$ it produces its own family of offspring, and immediately dies.

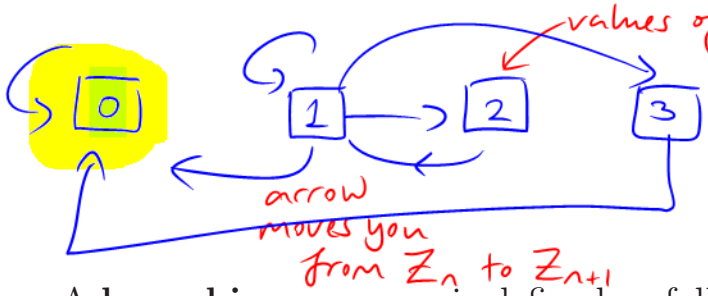
and so on...

Assumptions

1. All individuals reproduce independently of each other.
2. The family sizes of different individuals are independent, identically distributed r.v.s, all with the same distribution Y (number of Young).

Family size distribution, Y





Definition: A **branching process** is defined as follows.

- Single individual at time $n = 0$.
- Every individual lives exactly one unit of time, then produces Y offspring, and dies.
- The number of offspring, Y, takes values 0, 1, 2, ..., and the probability of producing k offspring is $\mathbb{P}(Y = k) = p_k$.
- All individuals reproduce independently. Individuals $1, 2, \ldots, n$ have family sizes $Y_1, Y_2, \ldots Y_n$, where $Y_1 \sim Y_2 \sim \ldots \sim Y_n \sim Y$.
- Let Z_n be the number of individuals born at time n, for $n = 0, 1, 2, \ldots$
  Interpret Z_n as the size of generation n = # indivs alive at time n.
- Then the branching process is $\{Z_0, Z_1, Z_2, Z_3, \ldots\} = \{Z_n : n \in \mathbb{N}\}$.

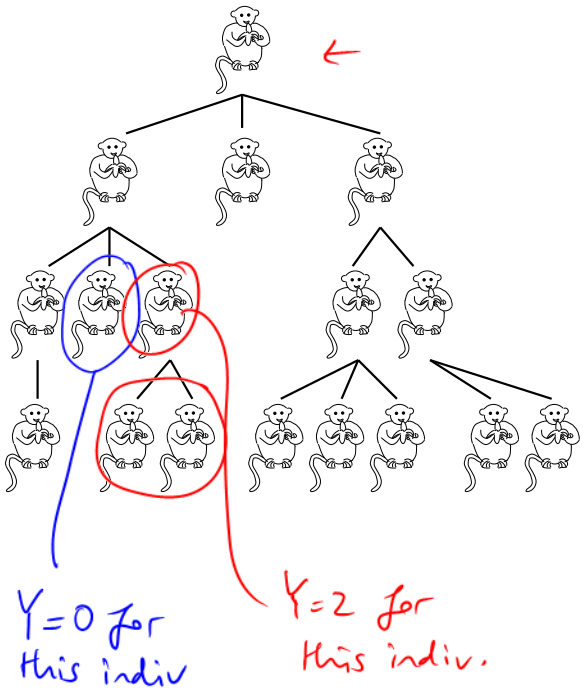
Definition: The **state** of the branching process at time n is
↳ (what goes in the boxes on the transition diagram)

State $= Z_n$, where each Z_n can take values $0, 1, 2, 3, \ldots$.
Note $Z_0 = 1$ always (start with 1 indiv at time 0).

Note: When we want to say that two random variables X and Y have the same distribution, we write: $X \sim Y$.
For example: $Y_i \sim Y$ for all family sizes Y_i.

Note: The definition of the branching process is easily generalized to start with more than one individual at time $n = 0$.

Branching Process



Generation	Popn size
0	$Z_0 = 1$
1	$Z_1 = 3$
2	$Z_2 = 5$
3	$Z_3 = 8$
⋮	⋮

6.2 Questions about the Branching Process

When we have a situation that can be modelled by a branching process, there are several questions we might want to answer.

If the branching process is just beginning, what will happen in the future?

1. What can we find out about the distribution of Z_n (the population siZe at generation n)?
   - can we find the mean and variance of Z_n?
     — *yes, using the probability generating function of family size, Y;*
   - can we find the whole distribution of Z_n?
     — *for special cases of the family size distribution Y, we can find the PGF of Z_n explicitly;* $Y \sim$ Geometric is the only non-trivial case.
   - can we find the probability that the population has become **extinct** by generation n, $\mathbb{P}(Z_n = 0)$?
     — *for special cases where we can find the PGF of Z_n (as above).* $Y \sim$ Geometric.

     specific generation for extinction.
2. What can we find out about eventual extinction?
   - can we find the probability of eventual extinction, $\mathbb{P}\left(\lim_{n\to\infty} Z_n = 0\right)$?
     — *yes, always: using the PGF of Y.* ← can always solve this: it's an easier Q than asking about a specific n.
   - can we find general conditions for eventual extinction?
     — *yes: we can find conditions that guarantee that extinction will occur with probability 1.*
   - if eventual extinction is definite, can we find the distribution of the time to extinction?
     — *for special cases where we can find the PGF of Z_n (as above).*

Example: Modelling cancerous growths. Will a colony of cancerous cells become extinct before it is sufficiently large to overgrow the surrounding tissue?

If the branching process is already in progress, what happened in the past?

1. How long has the process been running?
   - *how many generations do we have to go back to get to the single common ancestor?*

2. What has been the distribution of family size over the generations?

3. What is the total number of individuals (over all generations) up to the present day?

Example: It is believed that all humans are descended from a single female ancestor, who lived in Africa. How long ago?

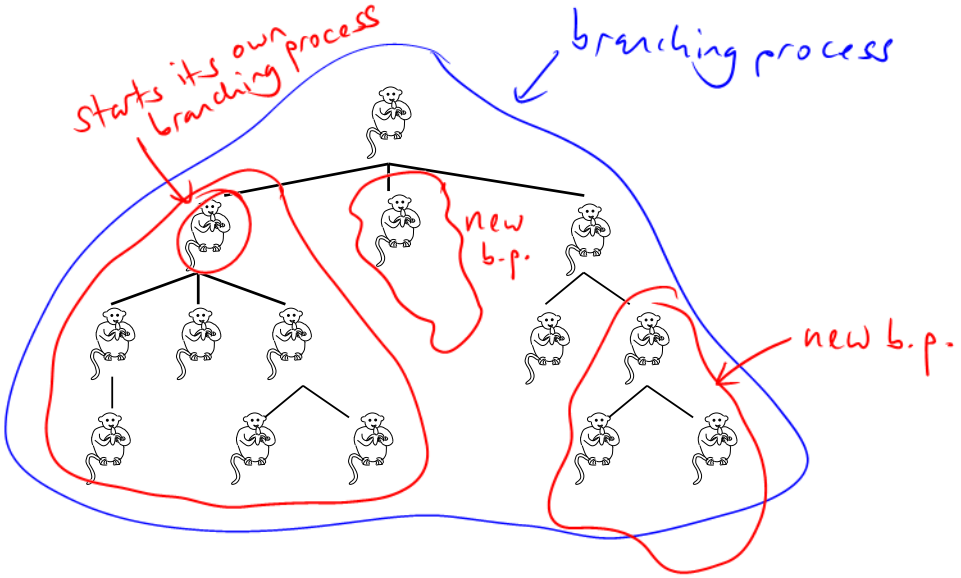
estimated at ~ 200,000 years.

What has been the mean family size over that period?

Estimate 1·002 female offspring per female adult.

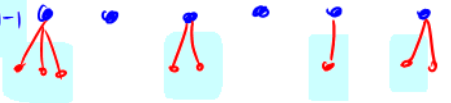
6.3 Analysing the Branching Process

Key Observation: every individual in every generation starts a new, independent branching process, as if the whole process were starting at the beginning again.



pop size in Gen n = #children in Gen n

Z_n as a randomly stopped sum

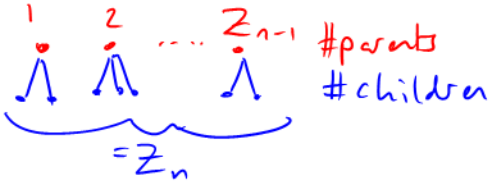


Most of the interesting properties of the branching process centre on the distribution of Z_n (the population size at time n). Using the Key Observation from overleaf, we can find an expression for the probability generating function of Z_n.

Consider the following.

- The population size at time $n-1$ is given by Z_{n-1}.
- Label the individuals (parents) at time $n-1$ as $1, 2, 3, \ldots, Z_{n-1}$.
- Each individual (parent) $1, 2, \ldots, Z_{n-1}$ starts a new branching process. Let $Y_1, Y_2, \ldots, Y_{Z_{n-1}}$ be the random family sizes of the individuals (parents) $1, 2, \ldots, Z_{n-1}$.
- The number of individuals (children) at time n, Z_n, is equal to the total # offspring of the parents $1, 2, \ldots, Z_{n-1}$.

That is,



$$Z_n = \sum_{i=1}^{Z_{n-1}} Y_i$$

Thus Z_n is a randomly stopped sum: a sum of $Y_1, Y_2, \ldots,$ randomly stopped by the unknown #parents (r.v.), Z_{n-1}.

Note: 1. Each $Y_i \sim Y$ (all indivs have the same family size distribution)

2. $Y_1, Y_2, \ldots, Y_{Z_{n-1}}$ are independent.

Thm 4.6: if $T = X_1 + \dots + X_N$ where N is random, $X_1 \sim X_2 \sim \dots$ indept of each other & N
then $G_T(s) = G_N(G_X(s))$.

Here: $Z_n = Y_1 + Y_2 + \dots + Y_{Z_{n-1}}$
$\Rightarrow G_{Z_n}(s) = G_{Z_{n-1}}(G_Y(s))$

$Z_1, Z_2, Z_3, \dots$

Probability Generating Function of Z_n

Let $G_Y(s) = \mathbb{E}(s^Y)$ be the probability generating function of Y.
(Recall that Y is the number of young of one individual, ie. the family size.)

Now Z_n is a randomly stopped sum: it is the sum of $Y_1, Y_2, \dots$, stopped by the random variable Z_{n-1}. So we can use Theorem 4.6 (Chapter 4) to express the PGF of Z_n directly in terms of the PGFs of Y and Z_{n-1}.

By Theorem 4.6, if $Z_n = Y_1 + Y_2 + \dots + Y_{Z_{n-1}}$, and Z_{n-1} is itself random, then the PGF of Z_n is given by:

$$G_{Z_n}(s) = G_{Z_{n-1}}(G_Y(s)) \quad (*)$$

where $G_{Z_{n-1}}(s) = \mathbb{E}(s^{Z_{n-1}})$, $G_{Z_n}(s) = \mathbb{E}(s^{Z_n})$

For ease of notation, we can write:

$$G_{Z_n}(s) = G_n(s), \quad G_{Z_{n-1}}(s) = G_{n-1}(s), \text{ etc.}$$

Note that $Z_1 \sim Y$ (they are both # children of a single parent)
so we can also write:

$$G_Y(s) = G_1(s) =: G(s) \text{ for simplicity.}$$

Thus,

from $(*)$,

$$G_n(s) = G_{n-1}(G(s))$$

Branching Process Recursion Formula

Critical Result for Branching Processes.

Note:

1. $G_n(s) = \mathbb{E}(s^{Z_n})$, the PGF of popn size at Generation n, Z_n.
2. $G_{n-1}(s) = \mathbb{E}(s^{Z_{n-1}})$, " " " " " " " $n-1$, Z_{n-1}
3. $G(s) = \mathbb{E}(s^Y) = \mathbb{E}(s^{Z_1})$, the PGF of family size, Y.

We are trying to find the PGF of Z_n, the population size at time n.

So far, we have: $G_n(s) = G_{n-1}\big(G(s)\big)$. $\quad (\star)$

But by the same argument,

$G_{n-1}(r) = G_{n-2}\big(G(r)\big)$ (b) using r instead of s to avoid confusion below.

Substituting (b) in $(\star)$,

$$\begin{aligned} G_n(s) &= G_{n-1}\big(G(s)\big) \\ &= G_{n-1}(r) \quad \text{where } r = G(s) \\ &= G_{n-2}\big(G(r)\big) \quad \text{using (b) above} \\ &= G_{n-2}\big(G(G(s))\big) \quad \text{replacing } r = G(s). \end{aligned}$$

By the same reasoning, we will obtain:

$$G_n(s) = G_{n-3}\Big(\underbrace{G(G(G(s)))}_{3 \text{ times}}\Big)$$

and so on, until we finally get:

$$\begin{aligned} G_n(s) &= \underbrace{G_{n-(n-1)}}_{n-(n-1)=1}\Big(\underbrace{G(G(G(\cdots G(s)\cdots)))}_{n-1 \text{ times}}\Big) \\ &= \underbrace{G_1}_{=G}\Big(\underbrace{G(G(G(\cdots G(s)\cdots)))}_{n-1 \text{ times}}\Big) \end{aligned}$$

$$\Rightarrow G_n(s) = \underbrace{G\big(G(G(G(\cdots G(s)\cdots)))\big)}_{n \text{ times}}$$

We have therefore proved the following Theorem.

Theorem 6.3: Let $G(s) = \mathbb{E}(s^Y) = \sum_{y=0}^{\infty} p_y s^y$ be the PGF of the family size distribution, Y. Let $Z_0 = 1$ (start from a single individual at time 0), and let Z_n be the population size at time n ($n = 0, 1, 2, \ldots$). Let $G_n(s)$ be the PGF of the random variable Z_n. Then

$$G_n(s) = \underbrace{G\Big(G\Big(G\Big(\ldots G(s)\ldots\Big)\Big)\Big)}_{n \text{ times}}. \qquad \square$$

Note: $G_n(s) = \underbrace{G\Big(G\Big(G\Big(\ldots G(s)\ldots\Big)\Big)\Big)}_{n \text{ times}}$ is called the n-fold iterate of G.

We have therefore found an expression for the PGF of the population size at generation n, although there is no guarantee that it is possible to write it down or manipulate it very easily for large n. For example, if Y has a Poisson(λ) distribution, then $G(s) = e^{\lambda(s-1)}$, and already by generation $n = 3$ we have the following fearsome expression for $G_3(s)$:

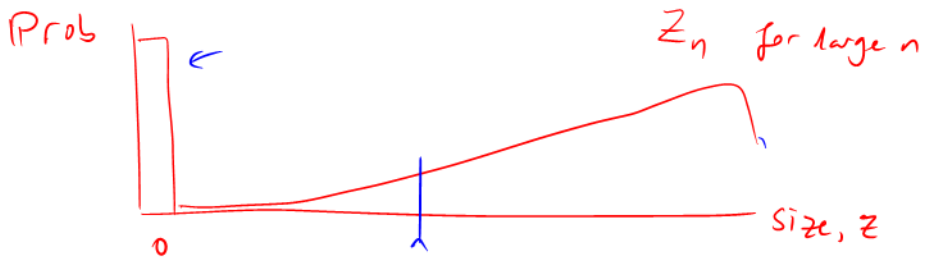
$$G_3(s) = e^{\lambda\left(e^{\lambda\left(e^{\lambda(s-1)}-1\right)}-1\right)}. \qquad \text{(Or something like that!)}$$

However, in some circumstances we can find quite reasonable closed-form expressions for $G_n(s)$, notably when Y has a Geometric distribution. In addition, for any distribution of Y we can use the expression $G_n(s) = G_{n-1}\Big(G(s)\Big)$ to derive properties such as the mean and variance of Z_n, and the probability of eventual extinction ($\mathbb{P}(Z_n = 0)$ for some n).

6.4 What does the distribution of Z_n look like?

Before deriving the mean and the variance of Z_n, it is helpful to get some intuitive idea of how the branching process behaves. For example, it seems reasonable to calculate the mean, $\mathbb{E}(Z_n)$, to find out what we expect the population size to be in n generations time, but why are we interested in $\mathrm{Var}(Z_n)$?

The answer is that Z_n usually has a "boom-or-bust" distribution: either the population will take off (boom), and the population size grows quickly, or the population will fail altogether (bust). In fact, if the population fails, it is likely to do so very quickly, within the first few generations. This explains why we are



interested in $\text{Var}(Z_n)$. A huge variance will alert us to the fact that the process does not cluster closely around its mean values. In fact, the mean might be almost useless as a measure of what to expect from the process.

Simulation 1: $Y \sim \text{Geometric}(p = 0.3)$

$Y \sim \text{Geo}(p=0.3)$, $\mathbb{E}Y = \frac{q}{p} = \frac{0.7}{0.3} = 2.3$

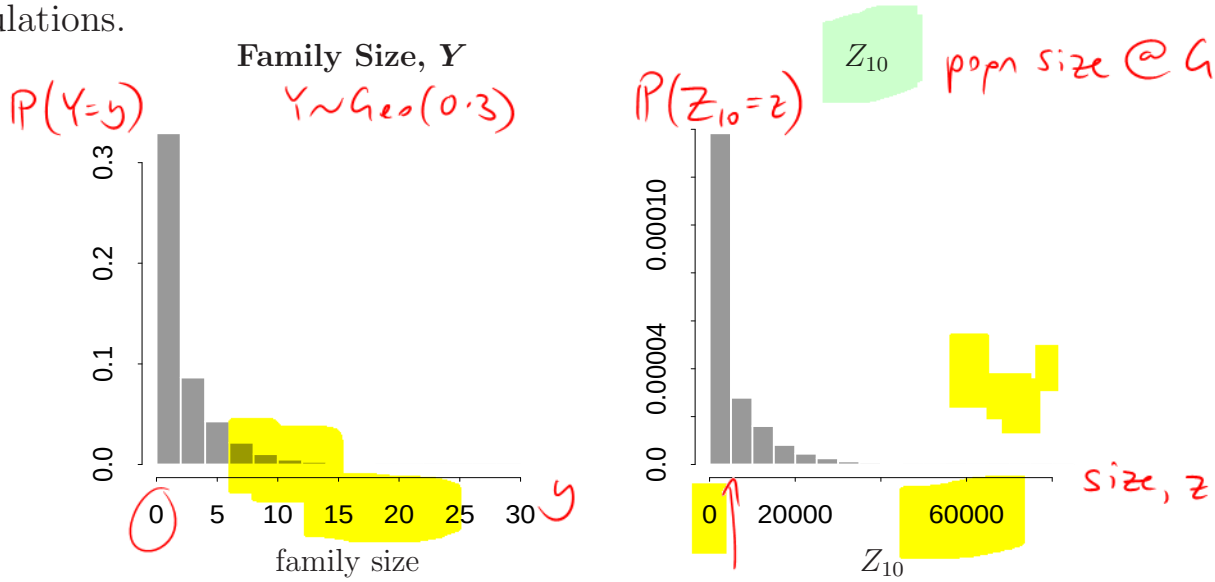
The following table shows the results from 10 simulations of a branching process, where the family size distribution is $Y \sim \text{Geometric}(p = 0.3)$.

Simulation	Z_0	Z_1	Z_2	Z_3	Z_4	Z_5	Z_6	Z_7	Z_8	Z_9	Z_{10}
1	1	0	0	0	0	0	0	0	0	0	0
2	1	1	0	0	0	0	0	0	0	0	0
3	1	4	19	42	81	181	433	964	2276	5383	12428
4	1	3	3	5	3	15	29	86	207	435	952
5	1	0	0	0	0	0	0	0	0	0	0
6	1	1	0	0	0	0	0	0	0	0	0
7	1	2	8	26	68	162	360	845	2039	4746	10941
8	1	1	0	0	0	0	0	0	0	0	0
9	1	1	0	0	0	0	0	0	0	0	0
10	1	1	4	13	18	39	104	294	690	1566	3534

5000 rows

Often, the population is extinct by generation 10. However, when it is not extinct, it can take enormous values (12428, 10941, ...).

The same simulation was repeated 5000 times to find the empirical distribution of the population size at generation 10 (Z_{10}). The figures below show the distribution of family size, Y, and the distribution of Z_{10} from the 5000 simulations.



In this example, the family size is rather variable, but the variability in Z_{10} is enormous (note the range on the histogram from 0 to 60,000). Some statistics are:

```
Proportion of samples extinct by generation 10:  0.436

Summary of Zn:
     Min   1st Qu   Median     Mean   3rd Qu      Max
       0        0     1003     4617     6656    82486

Mean of Zn:       4617.2
Variance of Zn:   53937785.7
```

— huge variance ⇒ the mean is almost useless as a summary.

So the empirical variance is $\text{Var}(Z_{10}) =$ $5.39 * 10^7$. This perhaps contains more useful information than the mean value of 4617. The distribution of Z_n has 43.6% of zeros, but (when it is non-zero) takes values up to 82,486. Is it really useful to summarize such a distribution by the single mean value 4617? No.

For interest, out of the 5000 simulations, there were only 35 (0.7%) that had a value for Z_{10} greater than 0 but less than 100. This emphasizes the "boom-or-bust" nature of the distribution of Z_n.

Simulation 2: $Y \sim$ Geometric($p = 0.5$)

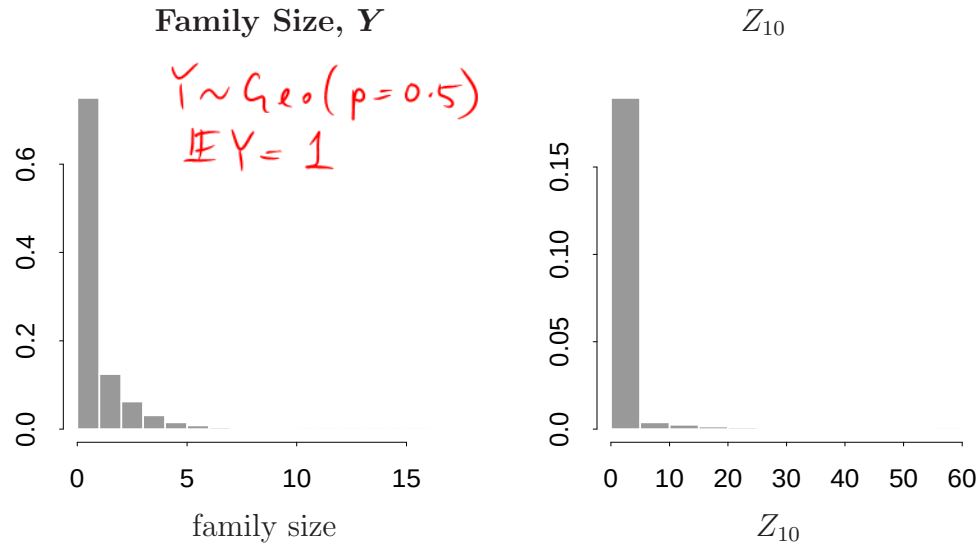
$\mathbb{E}Y = \frac{q}{p} = \frac{0.5}{0.5} = 1$

We repeat the simulation above with a different value for p in the Geometric family size distribution: this time, $p = 0.5$. The family size distribution is therefore $Y \sim \text{Geometric}(0.5)$.

Simulation	Z_0	Z_1	Z_2	Z_3	Z_4	Z_5	Z_6	Z_7	Z_8	Z_9	Z_{10}
1	1	0	0	0	0	0	0	0	0	0	0
2	1	0	0	0	0	0	0	0	0	0	0
3	1	0	0	0	0	0	0	0	0	0	0
4	1	0	0	0	0	0	0	0	0	0	0
5	1	1	0	0	0	0	0	0	0	0	0
6	1	7	9	17	15	20	19	8	7	13	35
7	1	2	5	2	5	8	8	3	3	0	0
8	1	2	0	0	0	0	0	0	0	0	0
9	1	0	0	0	0	0	0	0	0	0	0
10	1	0	0	0	0	0	0	0	0	0	0

This time, almost all the populations become extinct. We will see later that this value of p (just) guarantees eventual extinction with probability 1.

The family size distribution, $Y \sim \text{Geometric}(p = 0.5)$, and the results for Z_{10} from 5000 simulations, are shown below. Family sizes are often zero, but families of size 2 and 3 are not uncommon. It seems that this is not enough to save the process from extinction. This time, the maximum population size observed for Z_{10} from 5000 simulations was only 56, and the mean and variance of Z_{10} are much smaller than before.




```
Proportion of samples extinct by generation 10: 0.9108

Summary of Zn:
     Min   1st Qu   Median     Mean   3rd Qu      Max
       0        0        0    0.965        0       56

Mean of Zn:       0.965
Variance of Zn:  19.497
```

What happens for larger values of p?

It was mentioned above that $Y \sim \text{Geometric}(p = 0.5)$ just guarantees eventual extinction with probability 1. For $p > 0.5$, extinction is also guaranteed, and tends to happen quickly. For example, when $p = 0.55$, over 97% of simulated populations are already extinct by generation 10.

6.5 Mean and variance of Z_n

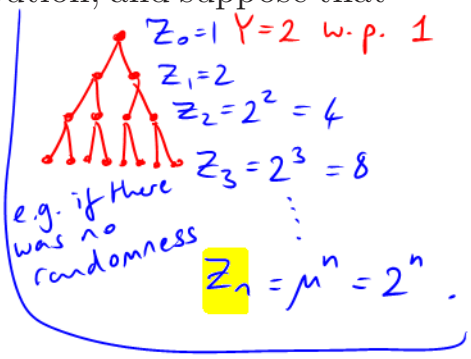
The previous section has given us a good idea of the significance and interpretation of $\mathbb{E}(Z_n)$ and $\mathrm{Var}(Z_n)$. We now proceed to calculate them. Both $\mathbb{E}(Z_n)$ and $\mathrm{Var}(Z_n)$ can be expressed in terms of the mean and variance of the family size distribution, Y.

Thus, let $\mathbb{E}Y = \mu$ and $\mathrm{Var}(Y) = \sigma^2$.

(Mean & variance of #children for a single parent.)

Theorem 6.5: Let $\{Z_0, Z_1, Z_2, \ldots\}$ be a branching process with $Z_0 = 1$ (start with a single individual). Let Y denote the family size distribution, and suppose that $\mathbb{E}(Y) = \mu$. Then

$$\mathbb{E}(Z_n) = \mu^n = \mathbb{E}(Y)^n .$$



Proof:

By p. 121, $Z_n = Y_1 + Y_2 + \cdots + Y_{Z_{n-1}}$ is a randomly stopped sum:

$$Z_n = \sum_{i=1}^{Z_{n-1}} Y_i .$$

So by Section 3.4 (p. 62),

$$\begin{aligned}
\mathbb{E}(Z_n) &= \mathbb{E}(Y) * \mathbb{E}(Z_{n-1}) \\
&= \mu\, \mathbb{E}(Z_{n-1}) \\
&= \mu * \mu\, \mathbb{E}(Z_{n-2}) \text{ by same argument:} \\
&= \mu^2\, \mathbb{E}(Z_{n-2}) \\
&= \vdots \\
&= \mu^{n-1}\, \mathbb{E}(Z_{n-(n-1)}) \\
&= \mu^{n-1}\, \mathbb{E}(Z_1) \qquad \text{note } \mathbb{E}(Z_1) = \mathbb{E}Y = \mu
\end{aligned}$$

$$\Rightarrow \mathbb{E}(Z_n) = \mu^n . \qquad \square$$

Examples: Consider the simulations of Section 6.4.

1. Family size $Y \sim$ Geometric($p = 0.3$). So $\mu = \mathbb{E}Y = \frac{q}{p} = \frac{0.7}{0.3} = 2.33$.

   Expected population size by generation $n = 10$ is:

   $$\mathbb{E}(Z_{10}) = \mu^{10} = (2.33)^{10} = 4784.$$

   The theoretical value, 4784, compares well with the sample mean from 5000 simulations, 4617 (page 126).

2. Family size $Y \sim$ Geometric($p = 0.5$). So $\mu = \mathbb{E}Y = \frac{q}{p} = \frac{0.5}{0.5} = 1$.

   $$\therefore \quad \mathbb{E}(Z_{10}) = \mu^{10} = 1^{10} = 1.$$

   Compares well with the sample mean of 0.965 (page 127).

Variance of Z_n

Theorem 6.5: Let $\{Z_0, Z_1, Z_2, \ldots\}$ be a branching process with $Z_0 = 1$ (start with a single individual). Let Y denote the family size distribution, and suppose that $\mathbb{E}(Y) = \mu$ and $\mathrm{Var}(Y) = \sigma^2$. Then

$$\mathrm{Var}(Z_n) = \begin{cases} \sigma^2 n & \text{if } \mu = 1, \\ \sigma^2 \mu^{n-1}\left(\dfrac{1-\mu^n}{1-\mu}\right) & \text{if } \mu \neq 1 \qquad (> 1 \text{ or } < 1). \end{cases}$$

Proof:

Write $V_n = \mathrm{Var}(Z_n)$. The proof works by finding a recursive formula for V_n.

Using the Law of Total Variance for randomly stopped sums from Section 3.4 (page 62),

$$\begin{aligned} Z_n &= \sum_{i=1}^{Z_{n-1}} Y_i \\ \Rightarrow \quad \mathrm{Var}(Z_n) &= \{\mathbb{E}(Y_i)\}^2 \times \mathrm{Var}(Z_{n-1}) + \mathrm{Var}(Y_i) \times \mathbb{E}(Z_{n-1}) \\ \Rightarrow \quad V_n &= \mu^2 V_{n-1} + \sigma^2 \mathbb{E}(Z_{n-1}) \\ \Rightarrow \quad V_n &= \mu^2 V_{n-1} + \sigma^2 \mu^{n-1}, \end{aligned}$$

using $\mathbb{E}(Z_{n-1}) = \mu^{n-1}$ as above.

Also,

$$V_1 = \mathrm{Var}(Z_1) = \mathrm{Var}(Y) = \sigma^2.$$

Find V_n by repeated substitution:

$$V_1 = \sigma^2 \qquad V_1 = \mathrm{Var}(Z_1) = \mathrm{Var}(Y) = \sigma^2$$

$$V_2 = \mu^2 V_1 + \sigma^2 \mu = \mu^2\sigma^2 + \mu\sigma^2 = \mu\sigma^2(1+\mu)$$

$$V_3 = \mu^2 V_2 + \sigma^2 \mu^2 = \mu^2\sigma^2\left(1 + \mu + \mu^2\right)$$

$$V_4 = \mu^2 V_3 + \sigma^2 \mu^3 = \mu^3\sigma^2\left(1 + \mu + \mu^2 + \mu^3\right)$$

$$\vdots \quad \text{etc.}$$

finite sum of a Geometric series.

Completing the pattern,

$$\begin{aligned} V_n &= \mu^{n-1}\sigma^2\left(1 + \mu + \mu^2 + \ldots + \mu^{n-1}\right) \\ &= \mu^{n-1}\sigma^2 \sum_{r=0}^{n-1} \mu^r \\ &= \mu^{n-1}\sigma^2 \left(\frac{1-\mu^n}{1-\mu}\right). \qquad \text{Valid for } \mu \neq 1. \end{aligned}$$

(sum of first n terms of Geometric series)

When $\mu = 1$:

$$V_n = 1^{n-1}\sigma^2 \underbrace{\left(1^0 + 1^1 + \ldots + 1^{n-1}\right)}_{\text{n times}} = \sigma^2 n.$$

Hence the result:

$$\text{Var}(Z_n) = \begin{cases} \sigma^2\, n & \text{if } \mu = 1, \\ \sigma^2 \mu^{n-1} \left(\dfrac{1-\mu^n}{1-\mu}\right) & \text{if } \mu \neq 1. \end{cases} \qquad \square$$

Examples: Again consider the simulations of Section 6.4.

1. Family size $Y \sim \text{Geometric}(p = 0.3)$. So $\mu = \mathbb{E}(Y) = \dfrac{q}{p} = \dfrac{0.7}{0.3} = 2.33$.

$\sigma^2 = \text{Var}(Y) = \dfrac{q}{p^2} = \dfrac{0.7}{(0.3)^2} = 7.78.$

$\Rightarrow \text{Var}(Z_{10}) = \sigma^2 \mu^9 \left(\dfrac{1-\mu^{10}}{1-\mu}\right) = 5.72 * 10^7.$

Compares well with the sample variance from 5000 simulations, 5.39×10^7 (page 126).

2. Family size $Y \sim \text{Geometric}(p = 0.5)$. So $\mu = \mathbb{E}(Y) = \dfrac{q}{p} = \dfrac{0.5}{0.5} = 1$.

$\Rightarrow \sigma^2 = \text{Var}(Y) = \dfrac{q}{p^2} = \dfrac{0.5}{(0.5)^2} = 2.$

Use formula for $\text{Var}(Z_{10})$ when $\mu = 1$ $\Rightarrow \text{Var}(Z_{10}) = \sigma^2 n = 2 * 10 = 20.$

Compares well with the sample variance of 19.5 (page 127).