1 Population growth: The return of the Whooping Crane

By the end of this chapter you should be able to:
- *understand the process of exponential growth*
- *calculate population growth rate from abundance data*
- *differentiate between discrete and continuous time models*
- *forecast population size at some time in the future*
- *understand the effects of environmental variation on population growth and the probability of extinction*

Standing about 1.5 m tall, the whooping crane (*Grus americana,* Fig 1.1) is the largest bird in North America. They are also among the rarest birds on the continent. During the middle part of the 20th century the species came perilously close to extinction. At one point the species was reduced to a single population with only 21 individuals in the world. Since that time, with the aid of various conservation measures, the numbers have been increasing towards the goal of a sustainable population of at least 1000 birds.   The growth of the crane population gives us an opportunity to examine the process of population growth and understand some of the factors that affect the recovery of this great bird.

Figure 1.1

Like all cranes, whooping cranes form long-term monogamous pair bonds that may last for life. Males and females share the job of incubating the eggs and feeding the chicks but usually raise just a single chick each year.
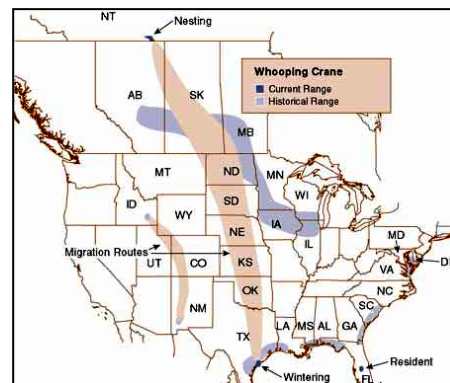
Twice a year Whooping cranes migrate about 4000 km between their wintering ground in south Texas and their breeding territory in northern Alberta.

There were approximately 1500 Whooping cranes in the US in the mid 1800s and the population may have been as high as 10,000 prior to European settlement. Historically they probably bred throughout much of the upper Midwest and wintered in several areas along the Southeastern Gulf coast. Conversion of prairie to farmland, hunting, and other

factors resulted in a steady decline in the numbers of whooping cranes. Whooping Cranes were federally protected in 1916 but the population continued to decline over the next few decades. In 1944 the worldwide total of Whooping Cranes reached the all-time low of only 21 individuals. Eventually, after the creation of the Aransas National Wildlife Refuge in 1937 to protect their winter habitat, the population started to recover. By the winter of 2008/9 there were 270 birds.

Whooping Cranes are long-lived and usually rear only a single offspring per year. Twice a year the entire population must complete the hazardous journey between the wintering ground in south Texas to the breeding territory in Alberta. That puts a real limit on the rate at which a population can increase. Nevertheless we'll see that even small rates of increase will compound over time and can eventually produce large populations.

Figure 1.2. Increase in numbers of Whooping Cranes from 1938 to 2008.
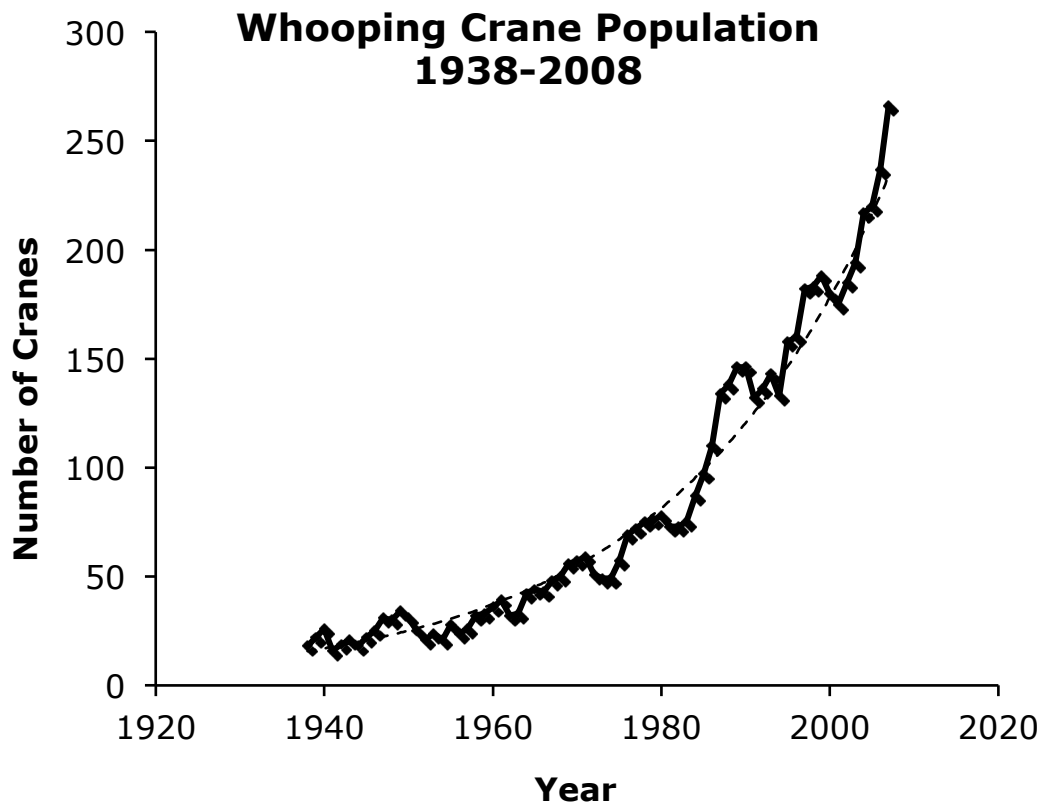
The whooping crane was one of the first species on the US endangered species list and it is also one of the first success stories. The number of birds has been steadily increasing for the past 6 decades (Fig 1.2). Is the species now safe? The recovery plan for the Whooping Crane defines recovery as a period of steady or increasing numbers, and the ability of the population to persist in the face of normal environmental variation and the occasional bad years. There would need to be approximately1000 individuals in the

Aransas/Wood Buffalo population of cranes. Under current conditions, how long it will take that population to reach a total population size of 1000 individuals?   In this chapter we'll examine the process of population growth in order to forecast the expected future growth of the population and the expected time to reach the target size.

1.1   Modeling population growth:

We want to capture the dynamics of this population in a simple model of population growth, and use the model to predict the population size at some time in the future. We'll start with a very simple model of a population with synchronous reproduction and non-overlapping generations, such as you might find in an annual plant or insect that reproduces once a year in the summer.   The population then increases (or decreases) in discrete steps with each new generation of offspring.

In general, the number of individuals in a population can change by only four processes. The population size can increase through births and immigration, or it can decrease through deaths and emigration.

Figure 1.3.
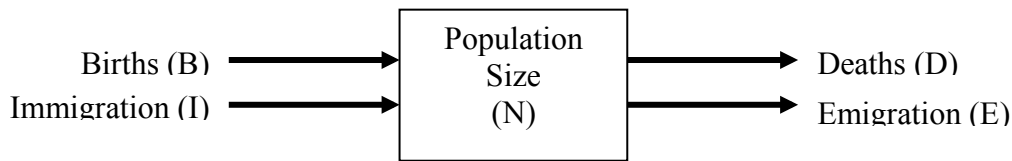
Immigration and emigration are not very important for the whooping cranes because there is only a single wild population. Therefore, we can write down a simple formula that will show how population size will change from one year to the next:

$$N_{t+1} = N_t + B - D \qquad\qquad \text{eq. 1.1}$$

Where N_t is the population size at time t
N_{t+1} is the number of individuals after one time period (e.g. after 1 year)
B is the total number of births during that interval.
D is the total number of deaths.

The total number of births and deaths is something that will change with population size. Large populations are likely to have more total births than small populations, simply because they start with more parents. But the probability of an individual giving birth or dying in a particular time interval is likely to be fairly constant. We call those the *per capita* birth and death rates.
$b = \frac{B}{N}$ and $d = \frac{D}{N}$. Equation 1.1 can then be re-written
$$N_{t+1} = N_t + bN_t + dN_t$$

$$N_{t+1} = (1 + b - d)N_t \qquad\qquad \text{eq. 1.2}$$

Finally, if we assume that *b* and *d* are constant, then the quantity in parentheses is just a constant multiplier of the population size. Ecologists traditionally use the Greek letter λ ("lambda") to specify the annual population growth.

$$N_{t+1} = \lambda N_t \qquad\qquad \text{eq 1.3}$$

Lambda is called the *finite population growth rate* that gives the proportional change in population size from one time period to the next:

$$\lambda = \frac{N_{t+1}}{N_t} \qquad\qquad \text{eq 1.4}$$

From this equation, you can see that if $\lambda > 1.0$, then $N_{t+1} > N_t$ and the population is growing. If $\lambda < 1.0$,, then $N_{t+1} < N_t$ and the population is declining.t

In our simple model we are assuming that birth and death rates are constant, so lambda is also constant. That makes it possible to project the population size at various times in the future. For example, what will be the population size after a second year of growth (N_{t+2})? Assuming that the growth rate remains constant, we can use equation 1.3, but now the starting population size is N_{t+1}.

$$N_{t+2} = \lambda N_{t+1}$$

We have already found an expression for N_{t+1}, so

$$N_{t+2} = \lambda(\lambda N_t) = \lambda^2 N_t$$

Using the preceding expressions as a model, write down an expression for the population size in the third year:
$$N_{t+3}= \underline{\hspace{3cm}}$$

In general, after t time steps, the population size will be
$$N_t = \lambda^t N_0 \qquad\qquad \text{eq 1.5}$$

If that process is allowed to continue populations can quickly become quite large. For example, imagine that there is a population that is growing at a rate of 20% per year (so $\lambda = 1.20$). If we start with $N_0=10$ individuals, there will be 12 individuals after 1 year of growth. How big will the population be after 10 years? How big will it be after 100 years?

$$N_1=12$$

$$N_{10}=\underline{\hspace{3cm}}$$

$$N_{100}=\underline{\hspace{3cm}}$$

When the population size increases by a constant multiplier each year, we call this pattern of growth *geometric increase*. The change in overall population size is slow at first but

after several years of constant geometric increase the number of individuals in the population can become enormous.
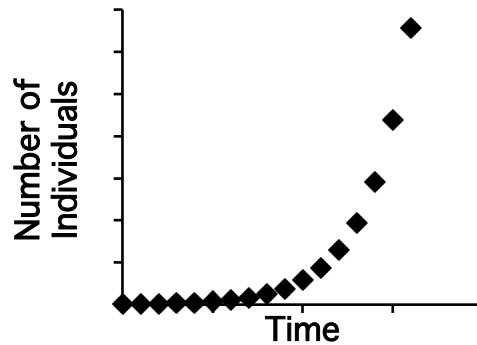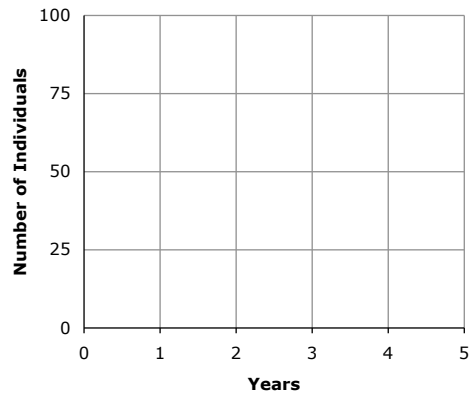

Figure 1.4 If $\lambda > 1.0$ the population will continue to grow, without bounds.

What will happen to the population if lambda is *less than* 1.0? Sketch the population size for $\lambda = 0.5$, starting with N_0=100 individuals.

1.2   Continuous time

The simple model we just developed works for discrete time steps. However in many species generations are overlapping rather than discrete. In such populations births and deaths can occur at any time of the year and the population grows continuously. Examples include humans and bacteria and many other organisms with overlapping generations.

Starting with equation 1.2, the *change* in population size is given by:

$$N_{t+1} - N_t = (b - d)N_t$$
$$\Delta N = (b - d)N$$

With continuous population growth we can let the time step become infinitely small and describe the growth rate using differential equations. The instantaneous population

growth rate is $\frac{dN}{dt} = (b-d)N$. If the instantaneous birth and death rates are constant we can let r=(b-d) and get the equation for continuous exponential growth:

$$\frac{dN}{dt} = rN$$ eq 1.6

where r is known as the *intrinsic rate of increase*.

Equation 1.6 is an expression for the rate of change of population size. The expression for population size at time t with continuous population growth is a little more complicated. Although we won't derive it here, you can integrate equation 1.6 to get an equation for population size:

$$N_t = N_0 e^{rt}$$ eq 1.7

where *e* is the base of natural logarithms (*e*=2.71828…)

This is an equation for *exponential population growth*. (The only real difference between geometric and exponential increase is that geometric growth is a discrete process whereas exponential growth is a continuous process.)

Unlike λ, which is a dimensionless number, the intrinsic rate of increase (*r*) is expressed in units of new individuals per individual per time ($\frac{ind}{ind \cdot time}$) which reduces to 1/*time*. Because r has explicit units, it is easy to convert a value of *r* into different units of time. Intrinsic growth rates measured per year can be converted to monthly or daily rates simply by dividing by 12 or 365, respectively. For the same reason, it is easy to do simple arithmetic on r, such as calculating the average rate of increase, $\bar{r}$.

Relationship between r and lambda
The discrete and continuous models of population growth represent two extremes, but many organisms have life cycles that are intermediate. For example, breeding may occur in discrete breeding seasons so population growth is not quite continuous, but the adults live and reproduce for many years so generations overlap and growth is not exactly discrete either. Fortunately, the discrete and continuous models of population growth are intimately related and it is easy to convert from one to the other.

$$r = \ln(\lambda)$$ eq. 1.8
$$\lambda = e^r$$ eq. 1.9

(Convince yourself that that is the case by comparing equations 1.5 and 1.7).

One way to think about the relationship between *r* and λ is that λ is the contribution of an individual to the total population size, whereas *r* is the contribution of an individual to the *rate of change* in population size.

In practice, what is often done is to estimate the finite rate of increase (λ) by the observed change in population size over some time step, $\frac{N_{t+1}}{N_t}$. That can then be converted to $r=\ln(\lambda)$ as needed.

Doubling time
One of the questions we might want to ask is how long it will take a population to double in size. At that time the population size will be twice the starting size or $2N_0$. From equation 1.7,

$$2N_0 = N_0 e^{rt}$$
$$2 = e^{rt}$$

Notice that the quantity we want to find (t) is in the exponent. To get rid of the exponent, we'll take the logarithm of both sides and rearrange to get an equation for doubling time:

$$t_{double} = \frac{\ln(2)}{r} \qquad\qquad\qquad \text{eq 1.8}$$

Using the same logic as above, write down an equation for the time it would take the population to *triple* in size _____

1.3   Assumptions for the exponential population growth model:
In building our simple model of population growth we made several simplifying assumptions. The most important assumptions of this model are that:
  - The rate parameters (r or λ) remain constant through time.
  - All individuals are identical. Therefore we can describe the population simply by the total number of individuals, N.
  - There is no immigration or emigration. In other words the population is "closed" so the only changes in population size come from births and deaths.

1.4   The growth of real populations.

Now let's apply this to the whooping cranes. Every year the population size has been monitored while the cranes are densely congregated on the wintering grounds at Aransas National Wildlife refuge. The open habitat allows researchers to make a complete enumeration of the winter population each year. Some of the data are shown in Table 1.1, below.

Is the increase in population consistent with exponential growth? How fast has the population been growing?

Table 1.1 Population size of the Aransas/Wood Buffalo population of whooping cranes from 1938 to 2008.

Year	N	ln(N)	$\lambda = {N_{t+1}}/{N_t}$	$r = \ln(\lambda)$
1938	18	2.89	1.67	0.51
1948	30	3.40	1.07	0.06
1958	32	3.47	1.56	0.45
1968	50	3.91	1.50	0.41
1978	75	4.32	1.84	0.61
1988	138	4.93	1.33	0.28
1998	183	5.21		
2008	270	5.60	xxxxx	xxxxx

$$\bar{r} = 0.39$$

Complete the table for the transition from 1998 to 2008:

What is lambda in 1998? _____

What is the time step for lambda in this table? _____

The average rate of increase for these data is $\bar{r} = 0.39$ *per decade*. What is the rate of increase *per year*? _____

1.5   Estimating population growth rate from time series

Look again at equation 1.7 which predicts population size as a function of time. Notice that the parameter of interest (r) is in the exponent.   You can get rid of the exponent by taking logs of both sides:

$$\ln(N_t) = \ln(N_0 e^{rt})$$
$$\ln(N_t) = \ln(N_0) + rt \qquad\qquad \text{eq. 1.10}$$

Eq. 1.10 is the equation for a straight line (e.g. it has the form $y = a + bx$). The slope of that line is *r*.   So one way to estimate the intrinsic rate of increase is to fit a straight line to the graph of ln(N) vs time. An example is shown in figure 1.5.
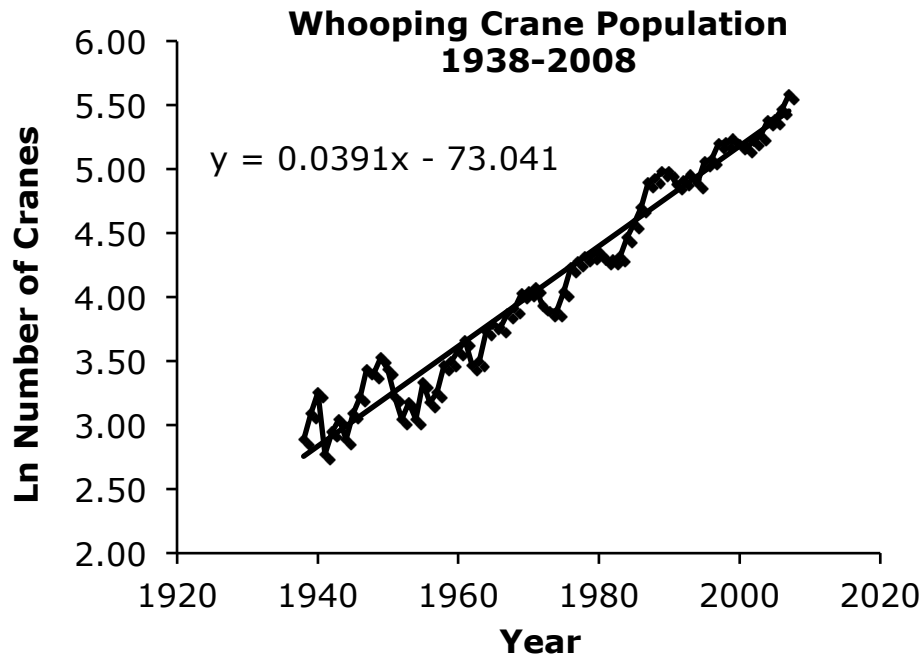
Figure 1.5   When populations grow exponentially the logarithm of population size increases linearly with time.

Compare figure 1.5 with Figure 1.2. Notice that the relationship between ln(N)and time is approximately linear. For this population of cranes, the slope of the line is r=0.0391 per year.

How does that estimate of r compare to your estimate of $\bar{r}$ from Table 1.1? _____

1.6   Forecasting future growth

We've spent a lot of time deriving the exponential population growth model for Whooping Cranes. Why? One purpose of such a model is to forecast the future growth of the population. If the population continues growing along its current trajectory, how long will it take to reach the sustainable size of 1000 cranes? Notice that we said "*if* the population continues along its current trajectory". If we are willing to assume that parameters are constant we can use this model to forecast the population size. But if conditions change then all bets are off!

Starting with the 2008 population of 270 cranes and our estimate of the intrinsic growth rate, r=0.039, what will be the population size after 10 years? _____
What will be the population size after 30 years? _____

Can you derive exact time when this population is expected to reach 1000?

1.7   OPTIONAL: Variation in growth rate among years

Look closely at Figure 1.2 and you'll see that the population has not increased steadily every year. In some years the population increased slightly faster than average. In other years the population actually declined slightly.

Many factors can influence the rate of population growth.   One of the most common sources is random variation in environmental conditions. Some winters are colder than others which lead to higher than average death rates. Some breeding seasons may be particularly productive so there is a higher than average rate of reproduction.

If you examine the crane population data in Appendix 1A, you will see that the average population growth rate is approximately $r = 0.039$, corresponding to our predicted population growth curve in Figure 1.2. But in some years the estimated value of r is much higher and in others it is negative.
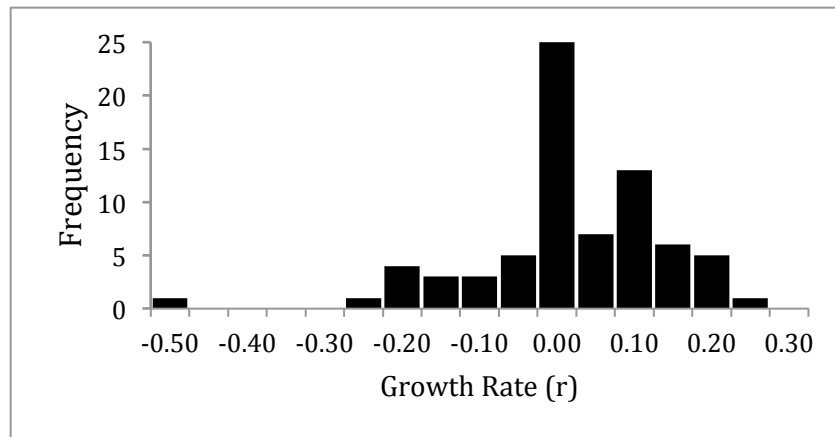

Figure 1.6.   Year to year variation in the growth rate of the Aransas/Wood Buffalo population of whooping cranes (from Appendix 1A).

When there is environmental variation in the population growth rate there can be considerable uncertainty in projecting the future popuation size. As an example, let's consider a simple simulation. We'll start with the same population of 18 cranes in 1938 as in Appendix 1A. Then, each year we'll randomly choose a value of r from the observed distribution and simulate the population to the year 2000. That whole process is repeated several times.

The results are shown in Figure 1.7.   Averaging over all simulations, we still expect the population to grow at a rate of r=0.039. But there is considerable variation in each realization of the process. By chance, some simulations end up with larger numbers and others with smaller numbers of cranes.

Figure 1.7 Ten random simulations of population growth based on the observed variation in growth rate for whooping cranes.
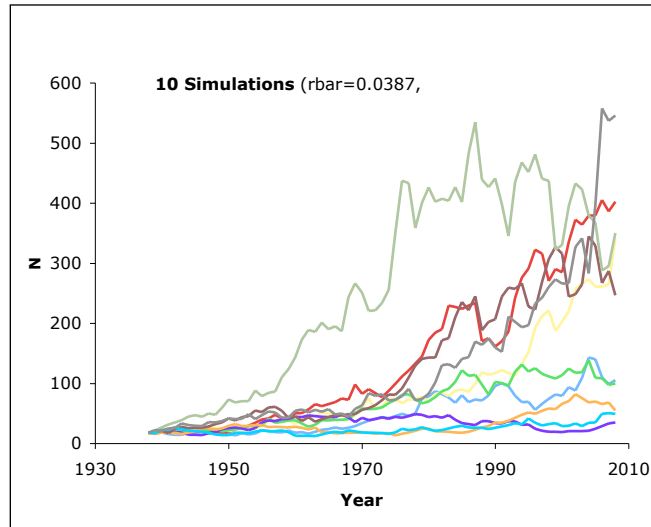
Why is that graph so different from Fig 1.2? Think back on the assumptions of our model. One of our assumptions was that the intrinsic growth rate, r, is a constant. If instead there is variation in r then there will be some uncertainty in the future growth of the population. Our uncertainty about the population size will increase the farther we try to project the population into the future.

Figure 1.8. Prediction error increases as we forecast future growth
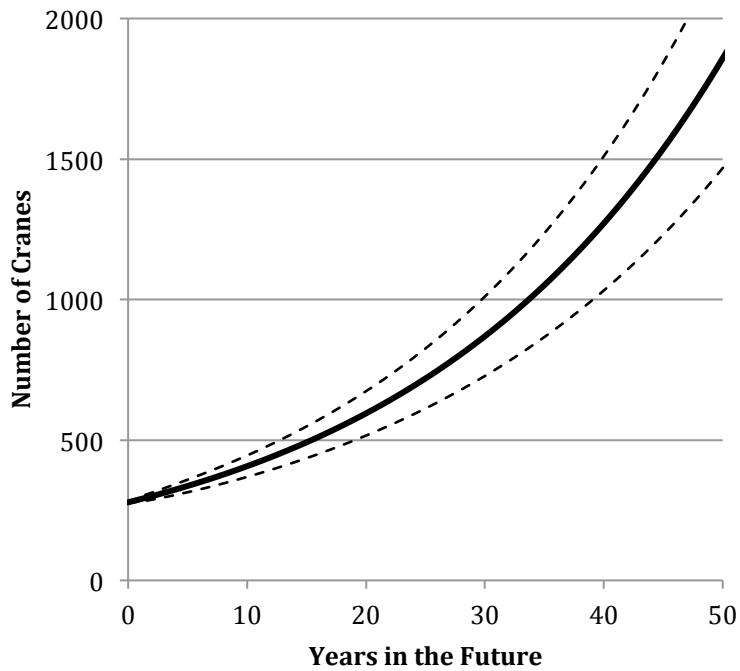
Demographic stochasticity

Another source of variation in population size is known as "demographic stochasticity". Demographic stochasticity results from the fact that population growth can never be truly continuous. Individuals come in discrete units so the population size must always be an integer (i.e. you can't have a population size of 1.3 individuals). And even though the birth and death rates are usually fractional numbers (e.g. the probability of death may be d=0.2), each individual will die completely or not at all. So over time the population size may deviate from the predicted values based on simple exponential growth.

Imagine a very small population of only a single individual. In each time period that individual can either produce one new offspring with probability 0.5 or die, again with probability of 0.5. Because the probability of births and deaths is equal, we expect the population size to remain constant. But the order of those events is important: if by chance the first event is a death, that tiny population will go extinct!

As the population gets larger, the role of this demographic stochasticity is reduced. For a population of 10 individuals there is still a chance that that population will go extinct before reproduction, but only if all 10 die before they reproduce, an unlikely occurrence. Demographic stochasticity need not produce extinction. In that population of 10 individuals with b=d=0.5, we expect 5 births and 5 deaths. But it is not unlikely to have 6 births and only 4 deaths, leading to a new population of 12 individuals after one time step.

In very large populations the actual number of births and deaths will be close to the expected number and demographic stochasticity becomes negligible.

1.8   Further Reading

Canadian Wildlife Service and U.S. Fish and Wildlife Service. 2007. International recovery plan for the whooping crane. Ottawa: Recovery of Nationally Endangered Wildlife (RENEW), and U.S. Fish and Wildlife Service, Albuquerque, New Mexico. 162 pp.

Gotelli, N.J. 2008. A Primer of Ecology, 4th edition. Sinauer

1.9   Your turn:

One common example of exponential growth is in the initial spread of a disease during a new outbreak.   Disease spread can be modeled in much the same way as population growth, where N is the number of infected individuals, "births" are new infections and "deaths" are the loss of infected individuals, by recovery from disease or sometimes by death. Once some individuals develop immunity to the disease the dynamics become more complicated. But the initial spread can be modeled as simple exponential growth. Here are some data from the initial spread of the 2009 outbreak of H1N1 influenza in the UK.

Initial spread of H1N1 Swine flu in the UK, May 26 to July 1, 2009

Week	Date	Confirmed cases	Ln Cases
0	26-May-2009	185	5.22
1	3-Jun-2009	381	5.94
2	10-Jun-2009	750	6.62
3	24-Jun-2009	3254	8.09
4	1-Jul-2009	6929	8.84

Graph the number of cases by week over the first four weeks of the disease.
What was the growth rate of the influenza infections? (per week? per day?)
What is the doubling time (in days) for the number of influenza cases during this phase of the outbreak?

Answers:

page 4

$$N_{t+3}=\lambda^3 N_0$$
$$N_{10}=61.9$$
$$N_{100}=828,179,745$$
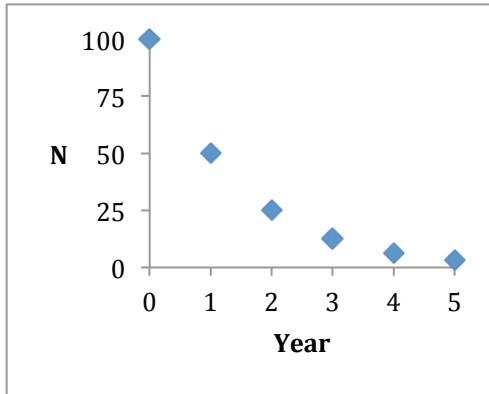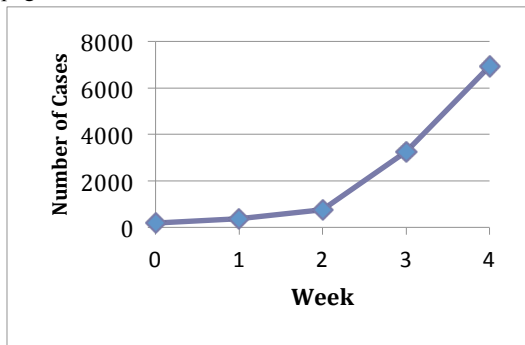

Page 5

page 7   tripling time $=\ln(3)/r$

page 8

lambda(1998)= 1.48
time step for lambda? 10 yrs
increase *per year*=0.039

page 9:

the two estimates of r are the same.
$N_{10}=399$
$N_{30}=870$
time when this population is expected to reach 1000= 33.5 yrs

page 13 Influenza:

r=0.94/week or 0.13 per day.
doubling time is about 5.3 days

Appendix 1A.
Number of Whooping Cranes in the wild Aransas/Wood Buffalo population, 1938-2007
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Year	N	Ln(N)	λ	$r = \ln(\lambda)$
1938	18	2.89	1.22	0.20
1939	22	3.09	1.18	0.17
1940	26	3.26	0.62	-0.49
1941	16	2.77	1.19	0.17
1942	19	2.94	1.11	0.10
1943	21	3.04	0.86	-0.15
1944	18	2.89	1.22	0.20
1945	22	3.09	1.14	0.13
1946	25	3.22	1.24	0.22
1947	31	3.43	0.97	-0.03
1948	30	3.40	1.13	0.13
1949	34	3.53	0.91	-0.09
1950	31	3.43	0.81	-0.22
1951	25	3.22	0.84	-0.17
1952	21	3.04	1.14	0.13
1953	24	3.18	0.88	-0.13
1954	21	3.04	1.33	0.29
1955	28	3.33	0.86	-0.15
1956	24	3.18	1.08	0.08
1957	26	3.26	1.23	0.21
1958	32	3.47	1.03	0.03
1959	33	3.50	1.09	0.09
1960	36	3.58	1.08	0.08
1961	39	3.66	0.82	-0.20
1962	32	3.47	1.03	0.03
1963	33	3.50	1.27	0.24
1964	42	3.74	1.05	0.05
1965	44	3.78	0.98	-0.02
1966	43	3.76	1.12	0.11
1967	48	3.87	1.04	0.04
1968	50	3.91	1.12	0.11
1969	56	4.03	1.02	0.02
1970	57	4.04	1.04	0.03
1971	59	4.08	0.86	-0.15
1972	51	3.93	0.96	-0.04
1973	49	3.89	1.00	0.00
1974	49	3.89	1.16	0.15
1975	57	4.04	1.21	0.19
1976	69	4.23	1.04	0.04

Year	N	Ln(N)	λ	$r = \ln(\lambda)$
1977	72	4.28	1.04	0.04
1978	75	4.32	1.01	0.01
1979	76	4.33	1.03	0.03
1980	78	4.36	0.94	-0.07
1981	73	4.29	1.00	0.00
1982	73	4.29	1.03	0.03
1983	75	4.32	1.16	0.15
1984	87	4.47	1.11	0.11
1985	97	4.57	1.13	0.13
1986	110	4.70	1.22	0.20
1987	134	4.90	1.03	0.03
1988	138	4.93	1.06	0.06
1989	146	4.98	1.00	0.00
1990	146	4.98	0.90	-0.10
1991	132	4.88	1.03	0.03
1992	136	4.91	1.05	0.05
1993	143	4.96	0.93	-0.07
1994	133	4.89	1.19	0.17
1995	158	5.06	1.01	0.01
1996	160	5.08	1.14	0.13
1997	182	5.20	1.01	0.01
1998	183	5.21	1.03	0.03
1999	188	5.24	0.96	-0.04
2000	180	5.19	0.97	-0.03
2001	175	5.16	1.06	0.06
2002	185	5.22	1.05	0.05
2003	194	5.27	1.12	0.11
2004	217	5.38	1.01	0.01
2005	220	5.39	1.08	0.07
2006	237	5.47	1.12	0.11
2007	266	5.58		