2 Wildebeest in the Serengeti: limits to exponential growth

In the previous chapter we saw the power of exponential population growth. Even small rates of increase will eventually lead to very large populations if *r* stays constant. At the beginning of the 19th century Thomas Malthus wrote extensively about the power of exponential growth, pointing out that no population can continue to grow forever. Eventually the numbers of individuals will get so large that they must run out of resources. While Malthus was particularly interested in human populations, the same must be true for all kinds of species. No population can grow exponentially for long. Charles Darwin used those ideas as one of the cornerstones of his theory of natural selection.

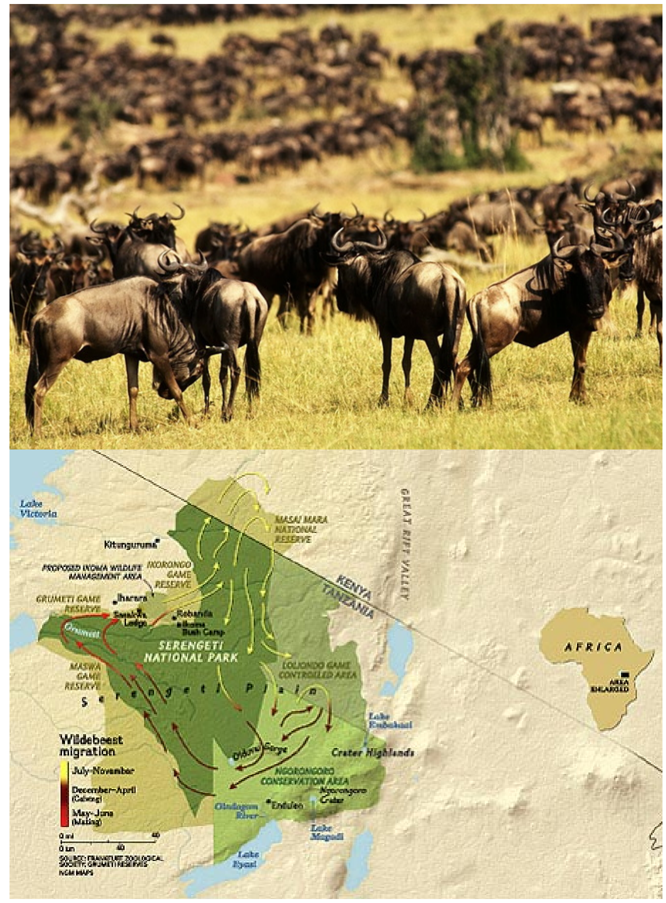


Figure 2.1. top: Herd of Wildebeest. Bottom: Map of the Serengeti-Mara ecosystem showing the annual migration route.

Because of the speed at which exponentially growing populations can increase in size, very few populations in nature will show exponential growth. Once a population has reached sufficient size to balance the available resource supply, there should be only minor fluctuations in numbers. Only when there is a large perturbation of the environment, such as the introduction of a species to a new area or severe reduction in population size due to hunting or disease will you find populations increasing in an exponential manner.

One very well studied system for looking at population dynamics is the wildebeest (*Connochaetes taurinus*) on the Serengeti plains of East Africa. Anthony Sinclair and Simon Mduma from the University of British Columbia have been studying them for 3 decades and have generated a long time series of records of population abundance.

The Serengeti is a land dominated by rainfall patterns, with a gradient in annual rainfall from south to north. In general the southeastern short grass plains are the driest, receiving about 500 mm of rain per year. The northern Mara hills in Kenya are the wettest part and receive about 1200 mm of rain a year. However the rainfall is highly seasonal. During the wet season from November to May the plains are marked by abundant grass and even occasional standing water. Large herds of grazing herbivores (wildebeest, gazelles, zebras) take advantage of the flush of productivity to feed on the new growth. But after the monsoon rains stop in June, the grass withers and browns and the animals struggle to find sufficient food.

Further, the rain is highly variable among years and locations. Some years are marked by abundant rainfall, which produces more new growth, and food is plentiful for the grazers and browsers. In other years the rains end early and thousands of animals starve.

In response to the changing and unpredictable food supply, the wildebeest migrate across the landscape, producing one of the most spectacular phenomena in nature. As the fertile short grass plains dry up at the end of the monsoon rains, herds of a million or more wildebeest migrate west toward Lake Victoria. When that, too, starts to dry up they move north to the relatively wetter hills in the Mara region. Then, with the coming of the next rains, they move back south to the plains, completing an enormous circuit of the Serengeti each year. Early travelers were awed by the "endless" plains of the Serengeti and the herds of migrating wildebeest that stretched as far as the eye could see.

2.1 **Rinderpest: a natural experiment**

Ideally, ecologists try to conduct experiments to understand the processes that control a particular system. But many populations are too simply big to manipulate. In such cases we can sometimes make use of fortuitous "natural experiments" and look at the changes that result from natural perturbations of the system. One example is the massive population crash of East African ungulates caused by the rinderpest disease, and the subsequent recovery of those populations.

In 1889 the rinderpest virus was accidentally introduced into Ethiopia in a shipment of 5 cattle. That accidental introduction started a wildlife disease pandemic. Rinderpest is an RNA virus of cattle that is closely related to the human measles virus. The virus quickly spread throughout the continent of Africa. Within a mere 8 years it killed an estimated 90% of the wild wildebeest and buffalo in east Africa. Travelers described the scene of millions of carcasses dotting the savanna. (Cattle herds, too, were decimated which caused enormous hardship for the traditional herding communities that depended on cattle). In the Serengeti, the population of wildebeest was reduced from over a million to only about 200,000 individuals by 1900. Throughout the 20th century periodic outbreaks of the rinderpest virus continued to occur and the disease kept the population of wildebeest at a low level.

That all changed in the late 1950s when a vaccine against the virus became available. The Kenyan government began a systematic vaccination campaign of all domestic cattle and by 1963 the disease was effectively eliminated. The wild populations of ungulates that had been infected by the cattle-borne disease began to recover.[1] The recovery of the wildebeest population from the rinderpest virus has produced an enormous natural experiment that allows us to examine the growth and regulation of the population on a grand scale.

[1] The worldwide rinderpest vaccination campaign has been enormously successful. In July 2011 the United Nations declared the rinderpest virus officially extinct. It is only the second disease (after smallpox) to be completely eradicated through vaccination.

2.2 **Wildebeest Population Dynamics**

The population of wildebeest in the Serengeti has been censused almost every year since the late 1950s when a father and son team from the Frankfurt Zoological Society started using a small plane to follow and monitor the vast herds on the Serengeti. The same basic technique is still in use today. It is not possible to count every individual wildebeest since the population size is well over a million. Instead, they must use a sampling scheme. Generally they will fly predetermined transects over the plains and take photographs at regular intervals. Later the number of wildebeest in each photograph is counted. By precisely maintaining a constant altitude above the ground, they can determine the area covered in each photograph and hence the density of wildebeest. This method is not foolproof: there will be slight biases caused by different observing conditions and different habitat types, but biologists have learned to make the necessary corrections to account for those variations.

Population estimates for the Serengeti wildebeest in December of each year are shown in Figure 2.2. In the decade following the introduction of the vaccine, the population of wildebeest in the Serengeti increased from 200,000 to over a million animals. Then, starting about 1975, the population growth ceased and stabilized at a population of around 1,200,000.

- Looking only at the first 15 years of data (1960 to 1975) is the pattern of growth consistent with exponential increase? How could you tell?

- What factors do you think cause the population to stabilize?

2.3 **Logistic population growth**

The pattern of rapid initial growth that later stabilizes at a constant number of individuals is common in biological systems, whether you are describing the growth of bacteria in culture, duckweed in a pond, or wildebeest in the Serengeti. That pattern is known as **logistic** population growth.

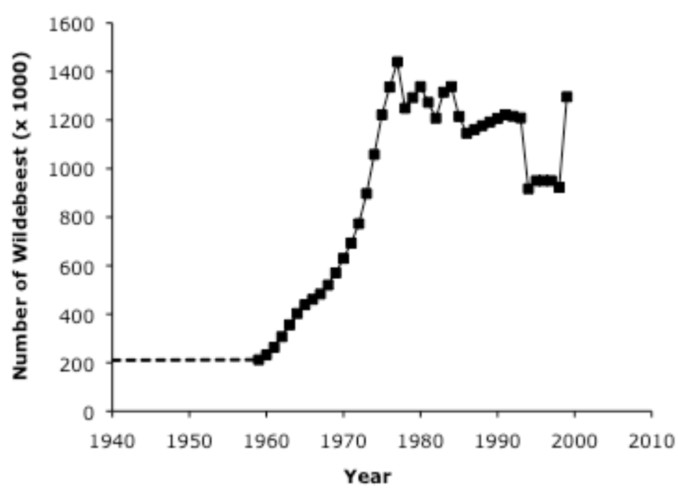


Figure 2.2. Wildebeest population size, 1959 to 2001

In chapter 1 we saw that under pure exponential growth only two results were possible. When $r>0$ then pops will grow exponentially without bounds. When $r<0$ then the population will decline to extinction. However we know that wildebeest are neither extinct nor infinite. These populations have existed for a long time without going extinct, so r must be positive when N is reasonably small. We also know that the population is not infinite, so r must be negative when N is very large. At some point those forces balance and the population is just large enough to use all of the available resources. We call that population size the **carrying capacity, K,** of the environment.

Recall that under exponential growth (eq 1.?) $\frac{dN}{dt} = rN$. We can add an additional term to that model that reflects the degree to which the population approaches its carrying capacity. That produces the **logistic equation** of population growth:

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) \qquad \text{eq. 2.1}$$

The new term in parentheses is sometimes called a "braking" factor because it slows the rate of population growth as N increases.

There are lots of mathematical models of density dependence that we might come up with besides this simple linear dependence on N. But this simple description is a good place to start. As you will see, it can describe some populations very well and it can give us insights into some general features of population growth.

Notice that eq. 2.1 is an equation for the growth *rate* of the population, *dN/dt.* However we usually observe population size, *N.* As we saw in chapter 1 we can integrate eq. 2.1 to find N. The equation to predict population size for the logistic model is somewhat more complicated than the corresponding equation for exponential growth, but the principles involved are the same. Integrating equation 2.1 yields

$$N_t = \frac{N_0 K}{N_0 + (K - N_0)e^{-rt}} \qquad \text{eq 2.2}$$

where N_t is the population size at time t, N_0 is the starting population size, and r and K are the intrinsic rate of increase and the carrying capacity.:

The growth of a population in the logistic model is shown in Figure 2.3.

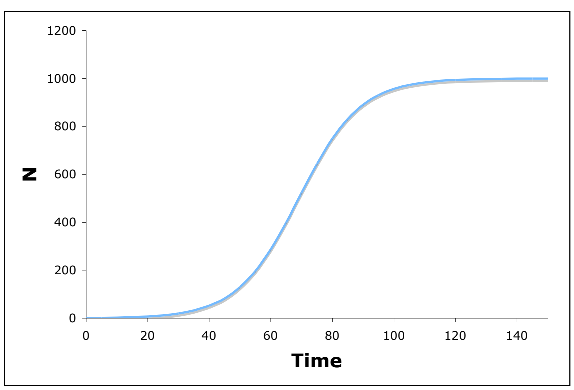


Figure 2.3 Logistic population growth model for the values r=0.1, K=1000, and N_0=1.

How would the graph in Figure 2.3 change if *r* were half as big? Sketch the approximate trajectory for *r*=0.05 on the figure.

Initially the population increases approximately exponentially. But after several generations the rate of growth decreases and finally ceases altogether as the population stabilizes at a constant population size. In terms of equation 2.1, when N is near zero the quantity in parentheses is close to 1 so we have the familiar equation for exponential growth. When N=K the term in parentheses is zero so dN/dt=0 and the population size stays constant.

How will the population change if N>K? ________________________

2.4 **Assumptions of the logistic growth model:**

- All individuals are identical. We can ignore differences between adults and juveniles or between males and females and simply keep track of the total population size, N.
- The population is closed, so there is no immigration or emigration.
- r and K are constant.
- Density dependence is linear: each additional individual reduces the population growth rate by a constant amount.

These assumptions are almost the same as for exponential growth, except the population growth rate is no longer constant. It now declines as the density of the population increases.

The logistic population growth model forms the basis of most of ecological theory. Those assumptions are rarely, if ever, completely correct. But the model captures the essential dynamics of populations and is a very useful starting point. That general pattern that populations increase when densities are low and resources are abundant, and then reach a relatively steady plateau of abundance when resources become limiting is a characteristic feature of most organisms. In later chapters we will use extensions of this basic model to understand competition between species.

A non-rigorous derivation of the logistic equation, via a thought experiment.
Assume that the habitat is divided into some number (“K”) locations that are each able to support exactly one individual. Starting with a single individual the population can grow at a rate “r”. Because the locations are all empty, 100% of the sites are available. As N increases and the fraction of sites begins to fill, there are fewer locations left in the environment. The proportion of the original locations that are still available is 1-(N/K). The population can then grow only at the rate r (1-N/K). Substituting that adjusted growth rate into the basic equation for population growth and rearranging, you end up with the logistic growth model:

$$\frac{dN}{dt} = rN(1-\frac{N}{K}).$$

2.5 **Exploring the logistic model**

It is interesting to explore the logistic model by graphing the function in different ways. For example, how does the population growth rate, dN/dt, change with population size? For logistic growth the graph of dN/dt vs. N is a humped curve as shown in Figure 2.4.
(To see that it is a quadratic function of N, expand equation 2.1 and notice that there is an N^2 term).

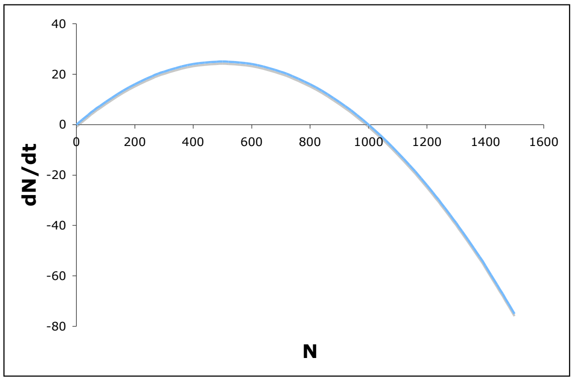


Figure 2.4 Logistic population growth rate as a function of population size. The parameter values used for this example are r=0.1, K=1000.

When the population is small the growth rate of the population is also small. The growth rate increases to a maximum at intermediate population size and then decreases at larger population sizes. If the population is too big, the growth rate of the population will become negative.

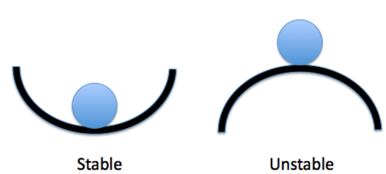
In terms of equation 2.1, when population is small the dN/dt will be small because N is near zero. As N approaches K, the growth rate again declines because the quantity is parentheses is near zero. Then when N>K, growth rate becomes negative because the quantity in parentheses is negative.

What would the graph of dN/dt vs. N look like for pure exponential growth (as in eq. 1.6)?

The population is at equilibrium when dN/dt=0.

In contrast to the exponential growth model of chapter 1 where populations will increase forever, the logistic growth model eventually reaches an equilibrium where the population size does not change. In other words, at equilibrium dN/dt=0. Figure 2.4 shows that dN/dt is zero at two population sizes, so there are two equilibria. One equilibrium is at N=0. If the population starts with zero individuals there can be no births or deaths so the population will not change. The second equilibrium occurs when the population reaches the carrying capacity, K.

It is also interesting to ask whether an equilibrium is **stable**. A stable equilibrium is one where the population will return to the equilibrium value following a small perturbation. For example think of a ball on a hill vs. a ball in a valley. The ball will come to rest at the bottom of the valley where we can say it is at equilibrium. If we move the ball a short distance left or right it will return to the bottom of the valley. We can say that the valley equilibrium is stable. It is also possible to balance the ball on top of the hill, but that is an unstable equilibrium: any small perturbation will cause the ball to roll down one side or the other.



Now let's apply that reasoning to population size. Assume a population has reached its carrying capacity (K) so it is no longer growing. Now, imagine that a severe storm comes through and kills some individuals so N is slightly less than K. Figure 2.4 shows that when N<K, the growth rate is positive so the population will grow and eventually return to the carrying capacity. Similarly, if you imagine that by some perturbation the population size became slightly larger than K, Figure 2.4 shows that when N>K the growth rate will be negative and the population will decrease in size until it is again at the carrying capacity. Therefore, we can conclude that the equilibrium at N=K is stable because the population will always return to the carrying capacity after a small perturbation.

Now do the same thing for the equilibrium at N=0.
Is that equilibrium stable? __________

(Again imagine a small perturbation away from equilibrium where you add a few individuals to a population that starts at zero. Will the population size return to zero?)

Maximum growth rate of the population

Looking at Figure 2.4, at approximately what population size is the growth rate maximized?_____________

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In general, how can we determine at what population size the growth rate is maximized? The same way we find the maximum of any function: find the second derivative of the function, set it equal to zero and solve for N. For the logistic equation, $\frac{d^2N}{dt} = r - 2r\frac{N}{K}$. If we set that equal to zero, then $r = 2r\frac{N}{K}$ so $N = \frac{1}{2}K$

For the logistic model, the growth rate of the population is always highest when the population is at half the carrying capacity.

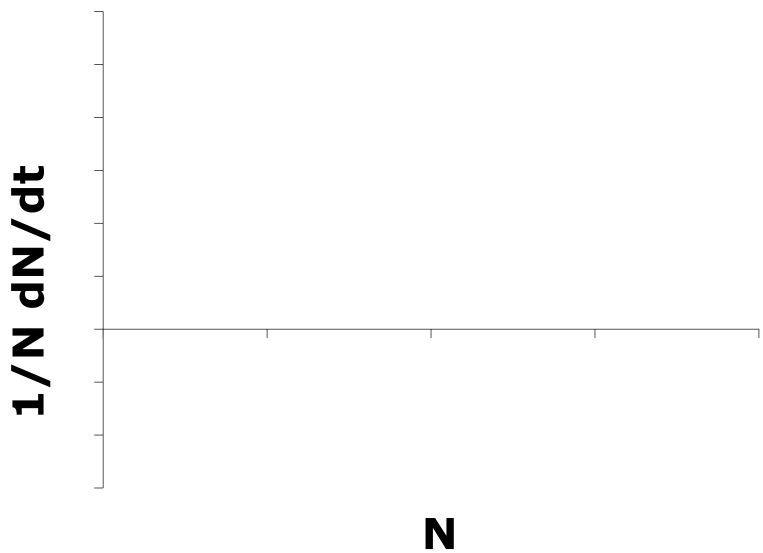
The per capita growth rate declines linearly

Recall from chapter 1 that the overall population growth rate depends on population size, simply because large populations have more parents and therefore have more births. You can correct for the overall population size by looking at the *per capita* growth rate. That is the overall growth rate divided by the number of individuals. If the population grows at a rate dN/dt, then the *per capita growth rate* is $\frac{1}{N}\frac{dN}{dt}$.

Starting with the general logistic growth equation (equation 2.1),
find an expression for the per-capita growth rate.

$\frac{1}{N}\frac{dN}{dt} =$ ____________

Sketch a graph of the per capita growth rate as it relates to population size. As in Figure 2.4,let r=0.1 and K=1000. Label r and K on the graph.
(hint: what is the per-capita growth rate when N is close to 0?
what is the per-capita growth rate when N=K?)



How would that graph look different for exponential growth?

Recall that one of the assumptions of the logistic growth equation was that all individuals are identical. Therefore each additional individual in the population always reduces the average growth rate by a constant amount. That shows up in the linear decrease in the per capita growth rate of the population.

Notice that we have used the term growth rate in related, but slightly different, ways. The parameter *r* is the **intrinsic growth rate** of the population: the rate of growth when the population size is very small. In this model it is assumed to be constant. In contrast, the actual **growth rate of the population** is measured by dN/dt. That realized growth rate shows the actual number of new individuals that are added in a time step and will depend on the number of parents and the distance of the population size from the carrying capacity. Finally, the **per-capita growth rate** (1/N dN/dt) shows the number of new individuals per parent. It, too, depends on the distance of the population size from the carrying capacity. In the logistic model it is assumed to decline linearly as N increases.

2.6 **Density dependent growth of the wildebeest population**

How does all of this apply to the wildebeest? In order to apply the logistic model of population growth to real data we need to have values for the two parameters, r and K. Unfortunately there is no simple transformation like the one we used to fit the model of exponential growth. Modern statistical programs provide various methods for fitting nonlinear models, but that is beyond the scope of this text. One simple approach is to find the approximate value of r by looking at the growth rate when the population size is small and growth is approximately exponential. You can then estimate K separately by the average population size when it is stationary. Alternatively you can find approximate values of r and K by trial and error, overlaying equation 2.2 on the time series and trying various values of r and K until you find a curve that appears to fit the data.

Figure 2.7 shows a best-fit logistic growth curve for the observed population sizes of wildebeest.

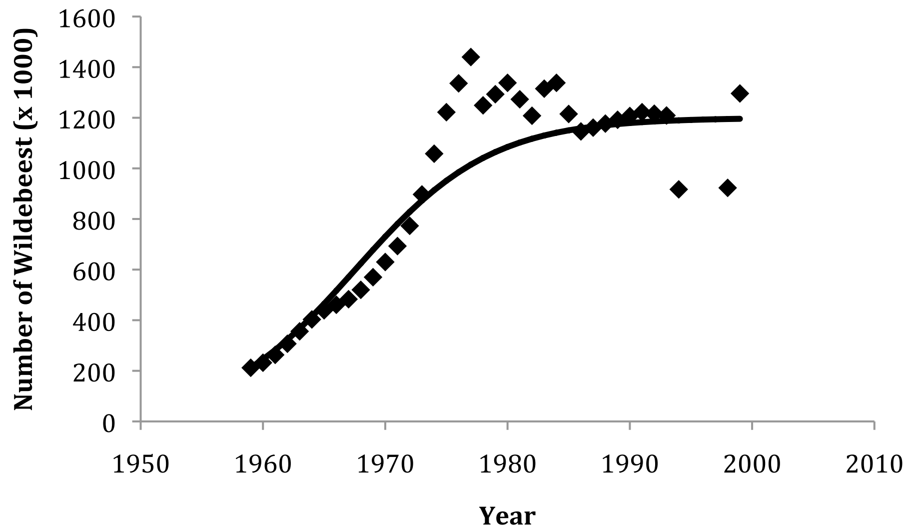


Figure 2.7

What is the approximate carrying capacity for the wildebeest population? ___________

For this real system, the logistic population growth model captures the general pattern of population growth but not all of the details. Initially, the population grows almost exponentially and the logistic equation fits fairly well. When the population stabilizes it is also fairly close to the value predicted by the logistic equation. However, between 1970 and 1977 the population grew much faster than expected. And in 1994 the population suddenly dropped to less than a million.

What kinds of environmental factors might cause the deviations from the expected logistic growth? ___________________________________

2.7 The biological basis of population regulation

The implicit assumption of logistic population growth model is that population growth rate declines because the animals become limited by some resource, often food. The reduction in the amount of food available per individual increases mortality (through starvation) or decreases birth rate, so the net population growth declines. Nevertheless, food does not show up anywhere in the logistic equation. Instead, the model uses population size as a surrogate for the resources that are being used. The assumption is that in a constant environment, if population size increases there will be less food available per individual so births will decrease or deaths will increase. The model works phenomenologically, but it bypasses the actual mechanism of population regulation.

In the case of wildebeest, the food available for an individual can decrease because a) rains don't come or b) too many wildebeest share too little food. The logistic model essentially assumes that only the latter is important. It should be possible to get a better model for the dynamics of wildebeest populations by directly incorporating food supply into our model. For example, the wildebeest population grew faster than predicted by the logistic model during the years 1972 to 1977, a period of higher than average rainfall when the savannas remained lush and green. The drop in population in 1994 followed an extremely severe drought.

Long-term studies of the rate of growth of grass on the Serengeti have shown that the amount of grass biomass production is directly proportional to rainfall. It is reasonable to suspect that the available food will influence the carrying capacity of the environment. Years with high rainfall produce enough grass to support a large population of wildebeest. In drought years there may be too many wildebeest for the available food supply. Therefore, instead of having a constant carrying capacity, what if K varies from year to year, depending on the rainfall? Appendix A shows the observed dry season rainfall in the Serengeti from 1960 to 1994 and a predicted carrying capacity based on that year's rainfall.

Using a model where the carrying capacity is partly determined by rainfall we can get a substantially better fit to the wildebeest data (Figure 2.8).

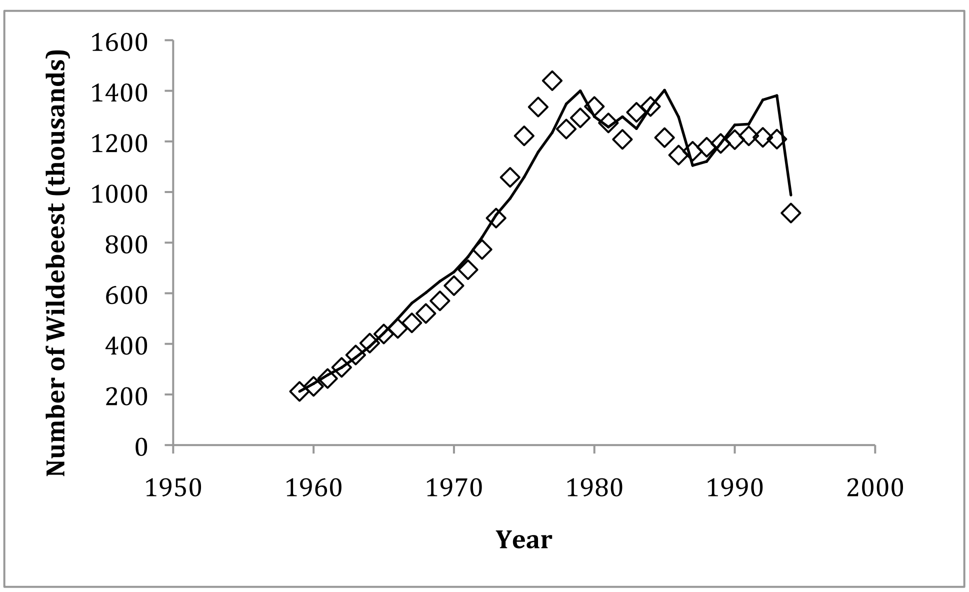


Figure 2.8 Observed and predicted abundance of wildebeest when the carrying capacity depends on rainfall. For this model, r=0.18 and K varies among years as shown in appendix A. The fitted curve was generated by a discrete version of eq. 2.1,

$$N_{t+1} = N_t + rN_t\left(1 - \frac{N_t}{K_t}\right).$$

2.8 **What is the use of this model?**

In general, models are use 1) to make a prediction and/or 2) to understand the system. Understanding the population dynamics of wildebeest allows us to make some predictions about the system. For example, if the population declines due to another drought, how long will it take for the population to return to its carrying capacity? Or, given the link between population growth and rainfall patterns, what is the minimum rainfall necessary to support the wildebeest population? If global climate change alters the rainfall regime on the Serengeti, will the wildebeest population persist?

It is perhaps more useful as a tool for understanding, however. Our analysis showed us that population growth is density dependent and controlled by a combination of intrinsic factors (density) and extrinsic factors (unpredictable rainfall). All else being equal, the logistic model showed us that the population size should remain stable at or near its carrying capacity.

That understanding can come at various points in the analysis. For example, we found that the logistic growth model captured some of the most basic features of the population dynamics, the rapid initial growth followed by stabilization of the population at approximately 1.2 million animals. In particular the fact that the rate of population growth slowed and finally stabilized showed that it was not a simple case of exponential growth.
But there were some systematic departures of the data from our simple prediction. That led us to notice that the population grew faster than expected during a series of years with higher than average rainfall, and pointed to rainfall as a key factor.

2.9 **Density dependent vs. density independent population regulation.**

The standard logistic growth model (eq 2.2) is based only on the population density and shows that it is possible for density dependent processes to maintain populations at a stable carrying capacity. However, the actual wildebeest counts were also related to the rainfall, an extrinsic factor that is unrelated to population size. There has been a longstanding debate among ecologists regarding the importance of density dependent factors vs. density independent factors in regulating populations.

Some ecologists point to large and erratic fluctuations in population size of organisms to say that populations are rarely at equilibrium and are instead kept well below their carrying capacity by extremes of weather or other extrinsic factors. Graphs of per capita growth rate vs. population size rarely show a perfect linear decline. Others argue that even if weather can affect population abundance, real populations fluctuate within fairly narrow bounds that are determined by density dependent factors. The jury is still out, but real populations are probably controlled by a combination of density dependent and extrinsic factors.

2.10 **Further reading:**

Mduma, S. A. R., A.R.E. Sinclair, and R. Hilborn. 1999. Food regulates the Serengeti wildebeest: a 40-year record. J. Animal Ecology 68:1101-1122.

Sinclair, A.R.E. and P. Arcese (eds). 1995. Serengeti II: Dynamics, management and conservation of an ecosystem. University of Chicago Press.

Pearl, R. and L. J. Reed. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proceedings of the National Academy of Science 6: 275-288

2.11 **Your turn**

The ecologist and geneticist Raymond Pearl was largely responsible for the adoption of the logistic model of population growth. One of his early examples used the logistic model to describe the population growth of the United States from 1790 to 1910.

His data are shown below.

Year	Actual US Population (in millions)
1790	3.93
1800	5.31
1810	7.24
1820	9.64
1830	12.87
1840	17.07
1850	23.19
1860	31.44
1870	39.82
1880	50.16
1890	62.95
1900	75.99
1910	91.97

Calculate the predicted population size over this interval using a logistic model and Pearl's estimates of $r=0.0313$ and $K=197$ million. Graph the observed and predicted population sizes to assess the fit of the logistic model to the data.

:

Since Pearl published his analysis in 1920 the US population has grown much faster than Pearl predicted. Here are more recent US census data. How does that compare to Pearl's predictions? What likely changed in the middle of the 20th century to allow the population to continue increasing?

Year	Population (in millions)
1920	105.71
1930	122.78
1940	131.67
1950	151.33
1960	179.32
1970	203.18
1980	226.54
1990	248.71
2000	281.42

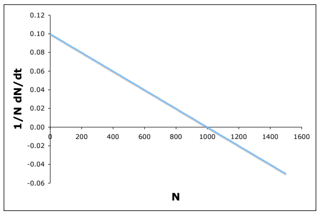
Table 1 Population size and rainfall data (from Mduma et al. 1999). Wildebeest counts are for the number of Wildebeest in December, after the dry season and before new calves are born. Rainfall is for the period July to December. The predicted carrying capacity each year depends on the seasonal rainfall. In this model K=400+7*R.

Year	Number of wildebeest (x 1000)	Dry Season Rainfall (mm)	Predicted carrying capacity based on rainfall
1959	212		
1960	232	100	1100
1961	263	40	680
1962	307	102	1114
1963	356	104	1128
1964	403	168	1576
1965	439	168	1576
1966	461	166	1562
1967	483	78	946
1968	520	91	1037
1969	570	78	946
1970	630	133	1331
1971	693	192	1744
1972	773	235	2045
1973	897	159	1513
1974	1058	211	1877
1975	1222	258	2206
1976	1336	205	1835
1977	1440	303	2521
1978	1249	188	1716
1979	1293	85	995
1980	1338	100	1100
1981	1273	162	1534
1982	1208	97	1079
1983	1315	230	2010
1984	1338	207	1849
1985	1215	84	988
1986	1146	45	715
1987	1161	114	1198
1988	1177	191	1737
1989	1192	201	1807
1990	1207	126	1282
1991	1222	255	2185
1992	1216	152	1464
1993	1209	19	533
1994	917	227	1989

Answers:

p 3. Growth starts out close to exponential (graph lnN vs. time and see if it is linear)
p4. If r is half as big, N will approach K more slowly, but it will still eventually increase to K.
p 6 dN/dt vs N is a straight line with slope=r for pure exponential growth
p. 7 The equilibrium at N=0 is not stable
dN/dt is maximum at 1/2 K (500)

$\frac{1}{N}\frac{dN}{dt} = r\left(1-\frac{N}{K}\right) = r - \frac{r}{K}N$. That is a straight line with intercept=r and slope = -r/K



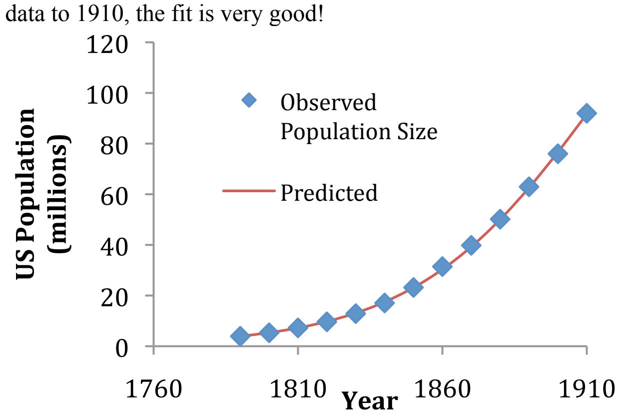
p. 8.
for exponential growth, 1/N dN.dt = r, so the graph would be a horizontal line (i.e. r is constant)
p. 9 K = 1,200,000
The deviations in the growth rate are likely caused by good and bad years (e.g. more or less food).

Your turn:

Here are predicted population sizes for r=0.0313 and K=197 million

Year	Population	Predicted
1790	3.93	3.93
1800	5.31	5.34
1810	7.24	7.22
1820	9.64	9.75
1830	12.87	13.09
1840	17.07	17.48
1850	23.19	23.15
1860	31.44	30.34
1870	39.82	39.27
1880	50.16	50.04
1890	62.95	62.58
1900	75.99	76.64
1910	91.97	91.69
1920	105.71	107.08
1930	122.78	122.05
1940	131.67	135.95
1950	151.33	148.30
1960	179.32	158.85
1970	203.21	167.58
1980	226.5	174.58
1990	249.63	180.09

For Pearl's original data to 1910, the fit is very good!



But when you add more years, we see that the population kept growing much larger than predicted. Presumably that is because technology changed the environment (i.e. better health care and better agriculture increased the carrying capacity of the country).